Rats, mice and people:

rodent biology and management

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Australian Centre for International Agricultural Research

Canberra 2003

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This book was published to coincide with the 2nd International Conference on Rodent Biology and Management, Canberra, Australia, February 2003.

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

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Preface

Rats, mice and people: an interwoven relationship

RODENTS are a key mammalian group, and are highly successful in many environments throughout the world. Indeed, they constitute more than 42% of the known mammalian species (see MacDonald 2001). In many instances, rodents provide major benefits to the environment as bio-engineers, but the conservation status of quite a number of species is listed by the International Union for the Conservation of Nature and Natural Resources (IUCN) as ‘at risk’, ‘threatened’ or ‘endangered’. However, some rodent species (less than 5%) are pests and cause significant losses to agricultural crops in many regions of the world. Rodents do not recognise international boundaries, different human cultures, or economic standards—they are major agricultural, urban and social pests across much of the developed and developing world. In Asia alone, the amount of grain eaten by rodents in rice fields each year would provide enough to feed 200 million Asians for a year, with rice providing 50–60% of their daily calorific intake. Many rodent species are also reservoirs of organisms that cause debilitating diseases in humans and livestock.

In Beijing in 1998, scientists and extension specialists met for the first time at an international conference dedicated to the exchange of information on the biology and management of rodents. An important product of that conference was a book published by the Australian Centre for International Agricultural Research (ACIAR) in 1999 that focused on the theme of ecologically based rodent management (Singleton et al. 1999). The authors who contributed to the book were drawn primarily from those who presented papers at the Beijing conference. Four years on, we held the second International Conference on Rodent Biology and Management (2nd ICRBM) in Canberra, Australia. On offer was a broad array of scientific sessions from classical taxonomy and systematics to behaviour, from ecologically based management to applied sciences, as well as state-of-the-art research in fields such as biological control and population modelling. The conference consisted of nine symposia: Disease; Conservation; Behaviour; Management—field; Population ecology and modelling; Sociology and economics of rodent management; Management—urban rodents and rodenticide resistance; Taxonomy; and Rodent biology—contrasting perspectives.

Missing from the first conference were papers from South and Central America, from taxonomy and systematics, the social sciences, and on post-harvest impacts. Taxonomy and systematics, and the social sciences had a strong representation at the 2nd ICRBM, but, alas, we were able to attract only one person from each of Central and South America. Post-harvest impacts were referred to briefly in several papers and as a principal focus in just two papers. Nevertheless, this conference captured a greater representation of the international issues and flavours of rodent biology and management, with representatives from 31 countries, distributed over six continents. The papers presented at the conference demonstrated that the results from basic research in the biological and social sciences now are exerting a major influence in our battle against the ravages and impacts of pest rodent species. Additionally, studies on the conservation biology of rodents have raised the spectre of the ecological services provided by this important group of animals. Ecological studies are essential to enable us to distinguish between the pest and non-pest status of different rodent species in different geographical areas and to target our control technologies appropriately. We have a responsibility to seek to balance the management of pest species with the conservation of beneficial species of rodents.

Of increasing interest is evidence that human disturbance of the ecosystem provides new opportunities for some rodent species to become pests and for current pest species to extend their range. Such disturbances also place some rodent species at risk of local extinction. The diversity of rodent species and an assessment of which species are present in a landscape could be important bio-indicators of the degree of human disturbance and of the resilience of an ecosystem to this disturbance.

Topics of research that have been largely ignored by ecologists are parasites and diseases. There has been too little effort on the role of disease in limiting or regulating rodent populations, and on the impact of rodents on the health of humans and their livestock. We see this as an important area of growth over the next decade.

It is apparent that rodents shall continue to be of major importance as we seek to understand their biology and as we continue to develop new strategies for ecologically based management. In each of our respective research and/or extension fields, advances are being made in concepts and theory, in development and application of new technology and methodology, and in data capture and storage.

An important theme to emerge at this conference is that the lives of rats, mice and people are often interwoven, and scientists and extension staff alike must not ignore this relationship. We are encouraged by the number of papers that considered the influence of human actions on rodent population dynamics, the effect of rodents on human health, the importance of sociological and cultural factors on adoption of rodent management, and the effect of rodent management actions on the sustainability of agricultural production and, most importantly, on the environment.

CSIRO Sustainable Ecosystems and the Central Research Institute for Food Crops (CRIFC) jointly hosted the 2nd ICRBM and the Australian Centre for Agricultural Research (ACIAR) was the main sponsor. The Australian Agency for International Development (AusAID) through their International Seminar Support Scheme and the Technical Centre for Agricultural and Rural Cooperation (CTA-EU) through their seminar support scheme, provided funds to support the attendance of scientists from Asia, Australia and Africa.

All the papers published in this book were presented at the 2nd ICRBM held at Canberra, and their order is based around the nine scientific sessions of the conference. Before being accepted for publication, each paper was reviewed by two referees—we especially thank the many referees we called upon at short notice to assist us. A comprehensive copy editing process followed and we thank Mr Peter Lynch of ACIAR and Dr Mary Webb and Mr Ed Highley of Clarus Design for their excellent efforts in producing such a high-quality product. Finally, we thank Dr John Copland of ACIAR who has been a catalyst in ensuring that both the 1st and 2nd ICRBM progressed beyond ideas; and Ms Alice Kenney, Dr Andi Hasanuddin, Drs Sudarmaji and Ketty for their tireless efforts in ensuring the conference was logistically a success.

Grant Singleton, Lyn Hinds, Charley Krebs and Dave Spratt
February 2003

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SYMPOSIUM 1: DISEASE

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Disease: health effects on humans, population effects on rodents

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Abstract. Infectious diseases in rodent populations are discussed from the twin viewpoints of their threat to human health and their role in rodent population dynamics. This is not, though, a definitive or exhaustive review, but an attempt to identify important and/or interesting themes. As regards human health, most recent attention has been directed at emerging infections, but some rodent-reservoir zoonoses are 'sleeping giants' that may awake at any time. Many human infections are never assigned an aetiological agent, and the 'sources' of many human pathogens remain unknown. Rodent-reservoir zoonoses may be important in both cases. In some cases, the economic damage caused by a pathogen may demand action even though medical effects, by most measures of public health, are trivial. Finally, the 'hottest' topic in human infectious diseases is bioterrorism. Rodent-reservoir zoonoses account for many of the apparently prime candidates. As regards rodent populations, four topics are addressed, focusing on work from our group at Liverpool—the effects of endemic pathogens on host fecundity as evidenced by experimental studies; their effects on host survival as evidenced by the analysis of field data; analyses of the transmission dynamics of infection and the light these throw on common theoretical assumptions; and the possible role of pathogens in microtine rodent cycles. Finally, at the interface between rodent populations and human health, the importance of distinguishing between reservoir, liaison and incidental hosts is emphasised; the contrasts between controlling zoonotic infections and other human infections are discussed; and a connection between contrasting types of rodent zoonosis and the nature of pathogen virulence is suggested.

Introduction

Infectious disease has a long history of neglect in the field of ecology—it was the poor relation to competition and predation throughout the whole of the last century. Recently, however, the role of pathogens in population and community ecology has received increased attention. Needless to say, medicine has not neglected infectious disease in this way. Nonetheless, there was a period of optimism around the 1980s, when medical opinion, at least in the rich world, seemed to feel that the problems of infectious disease were readily soluble and far less pressing than 'lifestyle' and degenerative diseases. But this optimism was short-lived, in large part because of the number of infectious diseases that emerged, re-emerged or resurged. Many of these were zoonotic—the most high-profile being human immunodeficiency virus (HIV)—and for many, the wildlife reservoirs are partly or wholly rodents. Here, then, infectious diseases in rodent populations are discussed from the twin viewpoints of their threat to human health and their role in rodent population and community dynamics. A crucial point here is that zoonotic pathogens that are virulent in humans are typically avirulent in their natural reservoirs: the same pathogens are therefore often medically important but archetypically 'endemic' in a rodent population.

In overview, rodent-reservoir zoonoses are many and various: they range from the relatively trivial (e.g. cowpox—discrete skin lesions at the site of infection, at least in immunocompetent hosts) to the commonly fatal (e.g. bubonic plague), and they may be transmitted directly from rodents to humans (e.g. hantaviruses) or may be carried by arthropods (e.g. fleas in the case of plague, ticks in the case of Lyme disease, flies in the case of leishmaniasis). This is not, though, a definitive or exhaustive review, but rather an attempt to identify some important and/or interesting themes: first in human health, then in rodent populations, and finally at the interface between the two.

Human health

Emerging infections and 'sleeping giants'

Insofar as rodent reservoirs have been studied at all, most recent attention has understandably been directed at emerging infections, though it is likely to be recognition rather than the diseases themselves that has emerged. Notable examples are Argentine haemorrhagic fever (caused by Junin virus) and hantavirus infections (hantavirus pulmonary syndrome, HPS, and haemorrhagic fever with renal syndrome, HFRS) (Mills and Childs 1998). Some rodent-reservoir zoonoses, however, are not so much emerging as sleeping, in the sense that they appear to not be as great a threat now as they have been at times in the past. Plague (*Yersinia pestis*) infection is probably the best example. Allegedly responsible for many millions of deaths during its first (6th and 7th century), second (14th to 17th century) and third (late 19th and early 20th century) pandemics, it is clearly much less of a problem today, though there are an estimated 1000–3000 cases each year (Keeling and Gilligan 2000). From an ecological, as opposed to a purely medical, perspective, however, it is clear that plague is endemic, and has almost certainly been endemic for millennia, in a variety of wild rodent reservoirs, but gives rise to pandemics on those rare occasions when it becomes temporarily established in populations of peri-domestic rodent species. There is no reason to doubt that plague is as prevalent in its natural reservoirs as it has ever been; and in the shanty towns of 21st century, populations of humans and their associated rodents have probably never been larger or denser.

Diseases of unknown origin

Many human infections are never assigned an aetiological agent, and the 'sources' of many human pathogens remain unknown. Rodent-reservoir zoonoses may be important in both cases. Thus, the cyclic incidence of Guillain-Barré syndrome (GBS) in Sweden was found to be highly significantly associated with cycles in the abundance of bank voles (*Clethrionomys glareolus*), though no candidate infectious agent was identified (Niklasson et al. 1998). GBS has been reported as an outcome of infection with a number of agents, but amongst these is lymphocytic choriomeningitis virus (LCMV), a zoonosis borne by rodents usually assumed to be pets (Barton and Hyndman 2000). We have recently found seroprevalences of LCMV of around 40% in bank voles (and other species) in the United Kingdom (UK).

Also, putative cases of tuberculosis (TB) often remain unconfirmed through a failure to isolate a causal agent microbiologically over the culture period normally allowed. It is therefore intriguing that vole TB (*Mycobacterium microti*) is being increasingly reported as a human pathogen, has been recorded by us at high prevalences in field vole (*Microtus agrestis*) populations (and has subsequently been observed in the Czech Republic and Italy), but takes longer than the period normally allowed before it appears on culture plates (Cavanagh et al. 2002).

Medically trivial: economically crippling

It would seem natural to direct most attention and research at those pathogens with the most serious medical consequences. In some cases, however, the economic damage caused by a pathogen may demand action even though medical effects, by most measures of public health, are trivial. Tick-borne encephalitis is a case in point. It circulates naturally in rodent (especially *Apodemus flavicollis*) populations throughout much of central and northern Eurasia with particular foci around the Baltic and between southern Germany and Hungary, though mostly the numbers of human cases are not large. Infection is acquired through a tick bite, often in areas of long grass at forest margins. Forestry workers are therefore at risk, as are picnickers. Initial symptoms of fever and headache usually resolve naturally, though sometimes, after a delay, a higher fever and meningitis may follow, and a residual neuropathy (depression, lethargy etc.) sometimes occurs. An effective vaccine is available and is commonly used by high-risk groups and/or in high-risk areas. Recently, however, human cases have been reported beyond the previous region of endemism, in areas where the local economy is based heavily on tourism. The actual threat to tourists is slight, but the fear within the region is so great that bad publicity regarding even a trivial threat may be sufficient to divert tourists from this to otherwise similar regions. Were this to happen, the local economy could collapse. Already within the region, sites where infection is believed to have been acquired have been abandoned by local picnickers, and local retail outlets have consequently closed.

Bioterrorism

The 'hottest' topic in human infectious diseases, though not necessarily the greatest threat, is bioterrorism. Rodent-reservoir zoonoses account for many of the apparently prime candidates. Recent articles in the June 2002 issue of the *American Journal of the Medical Sciences*, for example, list the following human infections with known or presumed rodent reservoirs as likely weapons in biological warfare: Argentine haemorrhagic fever, hantavirus infections, Lassa fever, Rift-valley fever, Q-fever, tularaemia, brucellosis and bubonic plague. This may herald an upsurge in interest in studies of rodent-reservoir zoonoses. However, it is likely that medical scientists will not yet have realised the full implications of being able to attack a human population indirectly through another host, the chronic and insidious nature of the ensuing threat, and the consequent need to understand not just the zoonosis but its reservoir as well.

Rodent populations

Studies of infectious disease in rodent populations have two major motivations: the fundamental one of seeking to understand the importance of pathogens in the ecological web within which the rodents are embedded; and the applied one of needing to understand the dynamics of pathogens in rodent reservoirs so that those dynamics may be predicted and perhaps even controlled for the benefit of human health. Either way, though, the demands are the same: that we understand the dynamics of pathogens in populations of rodents and the effects of pathogens on the dynamics of rodents.

Following a long period of neglect, the potential role of parasites and pathogens in the population dynamics of their hosts is now well recognised. Theoretical studies have been highly influential in bringing about this change of perception. However, empirical confirmation of theoretical possibilities has remained rare, and the importance of such infections for the dynamics of their hosts remains profoundly uncertain. In the following sections, four topics are addressed, focusing on work from our group at Liverpool.

(i) and (ii) At least two types of data may be of particular value—direct demonstration of an effect of the pathogen on a process of clear demographic importance in the laboratory, and documentation of a demographic effect of a pathogen from the analysis of field data.

(iii) Transmission dynamics are the driving force underlying any interaction between host and pathogen populations—but arguably the least well understood aspect of that interaction.

(iv) Populations of animals exhibiting multi-annual cycles have been the subject of intense study by ecologists for more than 75 years: microtine rodents (voles and lemmings) have been a particular focus of attention.

Pathogens and host fecundity

Feore et al. (1997) describe the effects on fecundity (and the lack of an effect on survival), under experimental conditions, of cowpox virus infection in bank voles and wood mice (*Apodemus sylvaticus*). Cowpox virus is a member of the genus *Orthopoxvirus*, and is endemic in Europe and some western states of the former Union of Soviet Socialist Republics (USSR). Although natural infection and disease occurs in cattle, man, domestic cats and various captive mammals in zoological collections, such cases are relatively uncommon, and the reservoir hosts are generally accepted to be wild rodents. Antibody and, at a much lower prevalence, virus have been detected in wild susliks (*Citellus fulvus*) and gerbils (*Rhombomys opimus*, *Meriones libicus* and *Meriones meridianus*) in Turkmenistan and Georgia, from root voles (*Microtus oeconomus*) on the Kolskiy Peninsula in northern Russia, and evidence of infection has been obtained by polymerase chain reaction (PCR) from various rodents in Norway. In Great Britain, antibody has been found occasionally in house mice (*Mus musculus*) but the highest seroprevalence is in bank voles, wood mice and field voles, and these species are believed to be the reservoir hosts (Chantrey et al. 1999).

Bank voles and wood mice were weaned at approximately 18 days old, and distantly-related, mixed-sex pairs were established in separate cages and inoculated oronasally with either cell culture medium alone or medium containing cowpox virus. Animals were kept until their first litter was weaned or a maximum of 120 days. Amongst animals inoculated with virus, no overt clinical signs were seen in any animals at any time. Thus, as in previous work, there was no demonstrable effect of the pathogen on either the mortality or morbidity of the hosts. Nor were there significant differences between any experimental groups in the proportion of pairs producing a litter, nor in the size of the litters produced. Differences were observed, however, in time to production of first litter. In pairs of virus-infected bank vole, litters were first produced, on average, 61 days after pairing. Among mock-infected pairs, the mean time was 43 days ($t = 2.06$, df = 26, $p < 0.05$). For virus-infected wood mice, the mean was 75 days after pairing, whereas mock-infected mice produced litters at a mean time of 56 days ($t = 2.15$, df = 25, $p < 0.05$).

These studies demonstrate clearly that infection with cowpox virus can reduce the reproductive potential of bank voles and wood mice without causing any overt disease or mortality. This illustrates the possibility, at least, that an endemic virus infection might significantly influence the dynamics of a wild mammal population without causing any other obvious signs of disease. Reduction in fecundity in the manner described here is at once a subtle and profound outcome of infection: subtle because it would be difficult to recognise in a field population, but profound since the absence of a litter has essentially the same effect at the population level as loss of that litter through mortality after birth. The delay observed here was around 20–30 days. Wild bank voles, if they survive, can, during a 6–8 month breeding season, produce up to 5 litters of 3–5 young, and wood mice up to 4 litters of 2–9 young. Even for those that survive the whole breeding season, a delay of up to 30 days in just one litter might represent an approximate 25% reduction in fecundity. For others, the reduction may be far greater—for those that succumb to some other source of mortality in the first months of life, for example, such a delay may reduce fecundity to zero.

Pathogens and host survival

Although the clearest way of estimating parasite-induced mortality is through field-scale experiments, the number and range of populations in which biological and practical difficulties can be overcome, and field experiments carried out, is likely to remain small for the foreseeable future. It is important, therefore, that evidence is accumulated also by other means, including the direct monitoring of infected and uninfected individuals in natural populations. Thus, we investigated the effect of cowpox virus on survival in bank voles and wood mice, using nearly four years of longitudinal data from two sites (Telfer et al. 2002). Recent advances in methodology and the development of appropriate software have enabled survival analyses of capture–mark–recapture data to account for variation in recapture rates. To our knowledge, this is the first such analysis to look at the effects of a pathogen on survival.

Although it does not cause obvious clinical signs or increase mortalities in voles or mice in the laboratory, there are many reasons why infection may have a greater impact on survival in field conditions. Individuals may be nutritionally stressed, subjected to attempted predation or made more susceptible by infection with other pathogens.

Analysis showed that in bank voles, but not wood mice, individuals with high probabilities of infection survived better than uninfected animals. At the level of the population, in both species, the effect of infection on survival varied through the year. Survival rates in late summer increased with cowpox prevalence, whilst survival rates in winter decreased with cowpox prevalence.

Why does cowpox appear to increase host survival? One possibility is not that infected individuals survive better, but that individuals that enjoy higher survival are more likely to become infected. We tested this by examining whether individuals that were infected with cowpox also survived better in the time period immediately after recovering from the infection. There was no evidence of this.

There are (at least) three alternative explanations that could produce a positive effect, all involving an effect of infection on life history strategy or behaviour. First, as the analysis looks at the effect of cowpox on apparent survival, a positive effect could result from infection reducing an individuals' probability of emigrating. Cowpox infection appeared to increase survival predominantly in late summer. If cowpox infection did decrease the probability of dispersing one might expect the effect to be most pronounced in April and May, when most dispersal occurs. However, at least in bank voles, dispersal can also occur in autumn and this explanation deserves more detailed investigation. A second explanation is that cowpox infection changes host behaviour such that exposure to other sources of mortality (e.g. predation) is reduced. Such a change in behaviour may have manifested itself in changes in recapture rates. We found no effect of cowpox prevalence on recapture rates.

Lastly, infection may trigger a change in reproductive strategy that increases survival. Adaptive changes in reproductive effort appear particularly feasible in small mammals, as such species tend to have flexible reproductive strategies and reproduction is known to be costly. Several lines of evidence lend some support to this hypothesis. First, the results of Feore et al. (1997), described above. Second, at the population level, cowpox only has a positive effect on survival in summer when reproduction is occurring. Lastly, excluding individuals first caught as seropositive adults, the average minimum age of individuals at the time of seroconversion is 18 weeks for bank voles and 19 weeks for wood mice, and therefore most individuals will be reproductively active when infected.

If increases in the survival of infected individuals during the summer occur because infected individuals stop reproducing, then the effect of cowpox on winter survival rates may be negative simply because neither infected nor uninfected animals are reproducing. Thus, the patterns observed may be the result of cowpox reducing survival in its own right (the only effect in winter), but also suppressing reproductive effort, and hence increasing survival to an extent that outweighs the negative effect of infection during the reproductive season. On this interpretation, cowpox virus infection has a negative effect on fitness (reproductive output, combining survival and reproduction) throughout the year.

Alternatively, the effect of a parasite may be contingent on extrinsic factors such as food availability or competition. Nutritional deficiencies are known to alter immunocompetence and increase the risk of infection. Individuals infected with cowpox during the summer may be able to compensate for any energetic costs. In winter, mortality of woodland rodents depends on food availability and nutritional stress may make a compensatory response to infection impossible. Consequently, survival may decrease in winters with high cowpox prevalence.

On either interpretation, we appear to have demonstrated for the first time an effect of an endemic microparasite infection on survival rates in natural populations of vertebrates. We have also demonstrated that the pattern of the effect is not simple, and is likely to be the result of subtle and changing interactions with other processes—a conclusion that is almost certain to apply more generally.

Transmission dynamics

Through analyses of time series of numbers of infected and susceptible hosts, we examined the transmission dynamics of cowpox virus in two natural, mixed populations of bank voles and the wood mice (Begon et al. 1998, 1999). We asked first, within both species, whether the density-dependent mode of transmission conventionally assumed, especially in modelling studies, was in fact appropriate. We also compared transmission rates within and between species. This is important, first, for the light it throws on whether coexisting wildlife hosts should be considered joint or independent reservoirs of zoonotic infections, and second, because it allows an assessment of the strength of 'apparent competition' in a host–host–pathogen system to be made from field data, whereas previously this has largely been the subject of theoretical analysis.

In fact, the results call into serious question the assumption that susceptible and infectious hosts mix at random and hence that transmission of cowpox virus is 'density-dependent'. Our analysis, for each species in isolation, indicates that frequency-dependent transmission (conventionally assumed to apply to sexually-transmitted diseases) is a clearly superior descriptor (though this does not, of course, indicate that transmission *is*, simply, frequency-dependent). These results therefore suggest that, generally, random mixing may have been too readily assumed, and that many diseases that are not sexually transmitted may nonetheless be socially transmitted, with essentially the same transmission dynamics.

Moreover, the analysis of the species together indicates that between-species transmission is rare, in spite of the species occupying not only the same general habitat but often, for example, sharing burrows. Thus, for cowpox virus at least, bank voles and wood mice do not ‘combine’ to any significant extent: the between-species coefficients are too low. Each species acts as an effectively independent reservoir: whether or not bank voles act as a reservoir for cowpox virus is independent of wood mouse numbers, and similarly the other way round. Host–host–pathogen models have also helped raise the profile of ‘apparent competition’—an interaction between two ‘prey’ (in this case, host) species, in which both suffer as a result of their shared interaction with a common predator or pathogen. Here, though, while the potential for apparent competition between bank voles and wood mice mediated by cowpox virus undoubtedly exists, since the virus depresses the birth rate and possibly the survival of both host species (above), it is likely to be insignificant in practice because the pathogen is so rarely transmitted from one species to the other.

Pathogens and rodent cycles

The role of microparasites in the dynamics of natural populations (including cyclic rodent populations) remains essentially unknown, despite pathogens being proposed as important in rodent cycles both recently and when the phenomenon was first described. In the 1920s and 30s, Elton (1942) investigated field vole cycles by monitoring wild populations and bringing voles into captivity. When 50% of voles died of toxoplasmosis within a week of arrival, this favoured Elton’s ‘epidemic hypothesis’—that the crashes in cycles were due to recurrent epidemics of infectious disease. However, when there was no evidence of toxoplasmosis during a decline in 1938–39, this was interpreted as seriously undermining the hypothesis; and when attention turned to vole tuberculosis (TB), this was found sometimes to be associated with a decline in numbers, but also found at high prevalence in some populations that did not decline, and at low prevalence in others that did. Chitty (1954) generalised that disease was irrelevant to host dynamics: a statement largely accepted by most in the field (Stenseth and Ims 1993).

As a first step in re-examining the role of infection in rodent population dynamics, we have studied microparasite prevalences (vole TB symptoms and cowpox virus antibody) in relation to host density and cycle phase in cyclic field vole populations in Kielder, North East England (Cavanagh et al. 2002). Because cycles are asynchronous in the site as a whole (resembling a travelling wave), populations from different phases of the cycle could be sampled simultaneously. Specifically, we asked whether patterns of prevalence were density-dependent and, if so, whether this was direct or delayed; whether such patterns themselves varied with season or host functional group; and where possible, whether any such association is with density *per se*, or with another factor that itself varies with density. The results of a very similar study have been reported by Singleton et al. (2000), on the dynamics of antibody to mouse cytomegalovirus (MCMV), minute virus of mice (MVM) and mouse parvovirus (MPV) in house mouse populations in Australia that undergo repeated eruptions in abundance.

Cowpox virus infection tends to rise in prevalence as a population approaches a peak and may either remain at high prevalence following a crash or disappear from such populations. There was clear evidence of delayed density-dependence in the prevalence of cowpox virus antibody, with a lag of around 6 months. Furthermore, seroprevalence (at any given ‘6-month-ago density’) tended to increase between spring and autumn; and this effect of past density on seroprevalence was marked: broadly, an increase in density was associated with a more-than-proportionate increase in seroprevalence.

Tuberculosis in wild rodents was first reported by Wells in 1937. The causal agent, *Mycobacterium microti*, is a member of the *M. tuberculosis* complex. Unlike cowpox virus, it causes clinical signs in rodents, internally and in some cases externally. Like cowpox virus, it is zoonotic, and can cause pulmonary tuberculosis in humans and other species including badgers and cattle (Cavanagh et al. 2002). However, little attention has been paid to *M. microti* since Wells’ studies. In our study, the prevalence of characteristic lesions or obvious lymph-node swellings rose from 0.63% in pre-peak populations (n = 1919) to 2.66% at peak densities (n = 2482), and this increase continued into crash populations (n = 410), reaching 8%. Again, there was strong evidence of delayed density-dependence with a lag of around 6 months. In addition, prevalence increased, bite-wounded animals had a higher predicted prevalence of clinical signs of TB than unwounded animals, and amongst the wounded animals, wounded females had a higher predicted prevalence than wounded males.

Both cowpox virus antibody seroprevalence and the prevalence of clinical signs of TB reflect infection at some ‘undefined time’ in the past. Hence, the seroprevalences observed in the various samples signify the proportion of a population that ‘have had’ rather than ‘have’ cowpox virus infection. At least one aspect of the data is an inevitable consequence of this: seroprevalences were lowest in the youngest animals (juveniles) that had been exposed to infection for the shortest time. More generally, the delayed density-dependence, of the order of 6 months, in cowpox virus seroprevalence may itself reflect in part this cumulative effect: if infection (rather than antibody) prevalence tended to be higher at higher host densities, then seroprevalence would inevitably tend be high more when density *had been* high rather than when it *was* high. The data, however, clearly suggest the nature of the measurement is not solely responsible for the observed delay. Cowpox virus infection rose in prevalence in peak and crashing populations and either remained at high prevalence following a crash or disappeared from such populations. Thus, lags inherent to the transmission process must have contributed to the observed delay between increases in host density and increases in disease prevalence.

Data on TB are more difficult to interpret due to a scanty knowledge of the way TB progresses in rodents. External TB lesions are late-stage signs of what was initially an internal pathology, and this will explain, at least in part, the delayed density-dependence effect observed; but the time elapsed between initial infection and appearance of clinical signs is not known. Furthermore, the true prevalence of infection was certainly much higher than the prevalence of external clinical signs. Only animals that had developed macroscopic lesions or severe lymph node swellings were diagnosed in this study, but dissection of 180 voles of which 13 had clinical signs of TB on capture revealed that a further 25 had internal tuberculous lesions (Cavanagh et al. 2002).

This study demonstrates that microparasites fluctuate with a time delay (of around 6 months) on host density in a cyclic rodent population. It was made possible by the occurrence of adjacent, out-of-phase populations together with the availability of modern techniques for testing for the prevalence of diseases. One interpretation of these patterns is that cohorts of individuals pass through the population with prevalences (of past cowpox virus infection and advancing TB infection) that increase with the density previously experienced by that cohort. Even if infection was direct and not delayed density-dependent, a progressive disease such as TB has the potential to have the strongest demographic impact some time after peak density, when the proportion infected is highest but the disease has progressed to the extent that survival of the voles is affected. The known impact of cowpox on demography includes, as already noted, delayed reproduction and possibly reduced survival in winter. It is striking that a related trait, time to production of first litter in the spring, also varies profoundly between populations at different phases in cyclic field voles populations in Kielder Forest, with populations that over-wintered at high density initiating reproduction later than those that over-wintered at low density.

Thus, while falling well short of demonstrating that micropathogens are responsible for population cycles in Kielder Forest, the pattern of delayed density-dependence is consistent with such a role and warrants more detailed investigation. The difference between cycles observed there and in Fennoscandia (the geographic area covering Finland, Sweden and Norway) (higher density in the low phase and asynchrony), as well as the refutation of the specialist predator hypothesis in this area, makes a role for pathogens plausible. On the other hand, the data are also consistent with the alternative that individual animals in decline phases of the cycle could be disproportionately affected by one or more pathogens. Whether a single pathogen is dominant at one site over time or whether members of community of pathogens interact and consistently influence vole demography in a manner causing cycles is another key question presently being investigated.

The interface

Reservoir, liaison and incidental hosts

It is important that a distinction is made between reservoir, liaison and incidental hosts. A reservoir host is one that, either alone or in concert with other species, plays a significant role in sustaining a pathogen (in epidemiological terms: hosts that typically exceed the threshold population size for the pathogen). A liaison host is one that is capable of acquiring an infection, and by virtue of its natural history, has a significant role in transmitting that infection to humans, but is not capable of sustaining the pathogen long-term (and indeed ‘relies’ on the reservoir host or hosts to do so). An incidental host is one that may acquire an infection but plays no significant role in either sustaining the pathogen or transmitting it to humans.

From a medical point of view, both reservoir and liaison hosts (but not incidental hosts) may be important objects both of scientific study and ultimately of control. From an ecological point of view, the role of a pathogen in the dynamics of a reservoir host (where it is likely to be endemic and relatively avirulent) is likely to be very different from its role in the dynamics of liaison or incidental hosts (where its occurrence may be sporadic but it may be capable of epidemic spread and intermittent high levels of mortality).

Control

The control of zoonotic infections throws up some interesting contrasts with the control of other human infections. Immunisation generally serves a dual role: protection of the immunised individual, and suppression (and perhaps even elimination) of the infection through ‘herd immunity’. But in the case of zoonotic infections, because humans themselves are not the reservoir, the herd immunity concept does not apply and pathogen elimination through immunisation cannot even be an aspiration. Control through culling (or even immunisation) of the wildlife reservoir is possible in principle, but while it is imaginable for, say, the control of rabies in a relatively large and slow-breeding species like the red fox, this seems likely to prove impossible for rodent zoonoses. In some cases, especially where there are identifiable high-risk groups, containment through human immunisation is likely to be the most effective option. Tick-borne encephalitis, as described above, is a case in point, which also, however, emphasises that this strategy does nothing to diminish the underlying threat, nor the risks of range expansion or infection in susceptible people only rarely at risk. In many other cases, the most effective strategy is to limit contact between humans and the reservoir host. Where humans and the reservoir are distributed sympatrically, however, and risk of contact is effectively unavoidable, it is necessary to monitor the prevalence of infection in the reservoir, and then target control of the reservoir host itself or, perhaps, an arthropod vector at those times and places where the risk is greatest. This had been the strategy for the control of bubonic plague in the USSR (targeting fleas), and it was effective: deaths from plague in Kazakhstan, for example, fell from hundreds per year in the mid 20th century to low single figures by the end (V. Ageyev, pers. comm.). Disturbingly, though, a crumbling infrastructure in the ex-Soviet states now threatens to reverse this trend.

Virulence and contrasting types of zoonosis

We are naturally anthropocentric in all things, and with zoonoses, tend to contrast their effects on humans with those on 'wildlife'. But to a pathogen, humans are just another species. The chances, therefore, are diminishingly small that a pathogen will be virulent in humans but avirulent in all other species. Thus, we may expect rodent zoonoses that are virulent in humans to be virulent in at least some other species. Plague is an excellent example: at least 200 species of rodent are susceptible, in some of which, prairie dogs in the United States of America for instance, it is known to have devastating effects. The likelihood is, then, that other rodent zoonoses that are virulent in humans also have devastating effects on wildlife species that are not their reservoir host, even if such species have not yet been identified. Junin virus in the Argentine pampas may be an example. At the other extreme are pathogens that are, at most, of only moderate virulence in humans. These are much better candidates for infections that, through their mode of action, are never highly virulent in any species.

One of the great challenges in the study of rodent infections, of rodent-reservoir zoonoses, and of infectious disease generally, is to understand the evolutionary and the pathogenic basis of variations in virulence from species to species.

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Interaction between rodent species in agro-forestry habitats in the western Usambara Mountains, north-eastern Tanzania, and its potential for plague transmission to humans

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Abstract. This study was carried out to determine rodent species composition and abundance, the interaction between them, and the possible implication in plague dissemination to humans. Over 2000 rodents were captured, identified and the relative species abundance determined. These animals belonged to six species, namely *Mastomys natalensis*, *Arvicanthis nairobe*, *Lophuromys flavopunctatus*, *Grammomys dolichurus*, *Mus* sp. and *Praomys* sp. They were distributed in two principal habitats, namely fallow land and forest. The distribution of the species overlapped, indicating interaction between them, but their abundance varied considerably between the habitats. Three species of fleas were collected from rodents. Of these, *Dinopsylus lypusus* was most abundant, followed by *Leptopsylla aethiopica* and *Nosopsyllus fasciatus*.

Rodent population densities declined rapidly in August and September and were followed by outbreaks of human plague in October. The observations made in the current study suggest that declining rodent population abundance leads to more ‘free’ fleas which probably seek alternative hosts, including humans. This consequently facilitates an increase in the transfer of plague from rodents to humans. The study further indicated that *M. natalensis* and *A. nairobe* form a continuum between forest-inhabiting rodent species and peri-domestic premises which therefore creates an avenue for transferring the disease from a potential forest reservoir to the human population.

The presence of specific anti-plague immunoglobulin (IgG and IgM) antibodies in blood sera of rodents was tested by enzyme-linked immunosorbent assay (ELISA). The presence of *Yersinia pestis* DNA was tested by polymerase chain reaction (PCR). Both tests revealed that *M. natalensis, A. nairobe, Rattus rattus* (captured in houses) and *L. flavopunctatus* were the potential rodent reservoirs of plague in the western Usambara Mountains. *Grammomys dolichurus* and *Praomys* sp. tested negative for plague, but more specimens will be tested to confirm this finding.

Introduction

The western Usambara Mountains, in north-eastern Tanzania, have experienced dramatic ecological changes brought about by government decisions made 40 years ago to open the mountains for agriculture (J. Bell, unpublished report). As a result of these decisions, human pressure on the remaining fragments of the natural montane rainforest has become a serious problem. The immediate impact of opening up the forest for agricultural activities is the destruction of natural habitats and fragmentation of others, which have, in general, some effects on species composition, diversity and distribution. Equally important is that some species are likely to disappear, while opportunistic species, particularly *Mastomys natalensis* and *Arvicanthis nairobe*, find suitable conditions in the newly cultivated land for immediate colonisation. Factors related to land management practices also affect how rodent species interact with each other and with the human population. Rodent–human interaction in the western Usambara Mountains is more evident in the form of crop damage and the spread of diseases, mainly sylvatic plague. Plague has been known in East Africa for many years (Roberts 1935), but remains persistently epidemic in only a few localities. In Tanzania, persistent plague outbreaks during the last two decades have occurred only in the western Usambara Mountains (Kilonzo et al. 1997). In view of the persistence and epidemic nature of the disease, several studies have been carried out in the past to elucidate the factors involved in maintaining the disease in the area (Kilonzo and Mhina 1982; Kilonzo and Msangi 1991; Kilonzo et al. 1992, 1997). It has been suggested that some species of rodents found in the area are potential reservoirs and carriers of the disease (Kilonzo and Mhina 1983; Njunwa et al. 1989; Kilonzo et al. 1992). Rodent fleas, of which several species have been identified, are suspected to be the principal vectors of the disease (Njunwa et al. 1989; Kilonzo et al. 1992; Makundi and Kilonzo 1994). House-infesting fleas, particularly *Pulex irritans*, occur abundantly, but their role in the transmission of the disease in Lushoto District is not well understood. This species has been reported to be important in inter-human transmission in other countries (Karimi and Farhang-Azal 1974; Twigg 1978). Ecological factors responsible for the outbreaks and persistence of plague in Lushoto District have not been adequately studied. Previous studies investigated the breeding patterns of some of the rodent species (Makundi 1995). Ecological studies on a wider area were initiated in the western Usambara Mountains in May 1998. The long-term objective of these studies is to develop ideas for ecological approaches to management of both rodents and fleas in the plague outbreak foci.

We aimed to show that species interaction does occur in suitable habitats due to habitat fragmentation and overlap, and that both savanna and forest species are most likely to be reservoirs of plague in the areas, by examining the following hypotheses:

(i) the existence of suitable reservoirs of plague with a stable population in the natural forest reserve is responsible for maintenance of the disease;

(ii) the interaction of savanna and forest-inhabiting rodent species enables the transfer of plague from forest animals to peri-domestic rodent species; and

(iii) both forest and savanna species in the area are equally exposed to plague bacteria, *Yersinia pestis*, and are responsible for its dissemination to people.

Materials and methods

The study area

The study was carried out in Shume Ward, Lushoto District, in the western Usambara Mountains. Shume Ward is located north of Lushoto town (04°42'16"S, 38°12'16"E) and has experienced persistent outbreaks of human plague. The climate of the area has pronounced temperature and humidity differences during the year. The coldest months are June to September with the lowest temperature usually in July (mean temperature = 19°C). It is usually warmer between December and March when the mean temperature ranges from 25–26°C. The rainfall pattern is characterised by two discernible rainy seasons, with the wet season extending from late February/early March to end of May. Short rains fall mainly in November and December, but usually start towards the end of October and extend to January. July to mid-October is usually a dry period.

Trapping procedures

Removal trapping of rodents was carried out for 12 months between May 1998 and May 1999. Trapping was carried out for 6 days each month using Sherman live-traps baited with peanut butter mixed in maize bran. The traps were placed in four lines, each consisting of 25 traps, and approximately 10 m apart in the fallow land. In the forest, there were 2 lines of 25 traps each, 10 m apart and 10 m between trap stations. The traps were inspected every morning, with captured animals removed and taken to the laboratory for processing. The animals were brushed to remove fleas, which were later identified. Additionally, 10 traps baited with peanut butter were placed in houses (1 trap/house) for three consecutive nights to capture *Rattus rattus*. Sera from captured animals were used to test for anti-plague antibodies.

A correlation analysis was carried out between the flea load on hosts and the incidence of plague between October and March.

Tests for *Yersinia pestis* DNA and anti-plague antibodies

Venous blood was collected from the orbital sinus of rodents and centrifuged to separate serum. *Mus* sp. was excluded because sufficient sera could not be obtained. All specimens of *R. rattus* (n = 12) captured in houses were included in these tests. The sera were preserved at –20°C and selected samples were tested for the presence of anti-plague immunoglobulin (IgG and IgM) antibodies by enzyme-linked immunosorbent assay (ELISA) and for *Yersinia pestis* deoxyribonucleic acid (DNA) by polymerase chain reaction (PCR), as described by Chu (2000). Human plague cases were obtained from the records of the local district hospital.

Results and discussion

The two principal rodent habitats (forest and fallow) were characterised by fragmentation brought about by deforestation and agricultural activities. Cultivated land interspersed the two principal habitats forming a continuum with peri-domestic areas and human settlements. Separation between these three main rodent habitats was minimal, and therefore allowed rodent movements between them (Figures 1 and 2).

Within the fallow land, *M. natalensis* and *A. nairobe* were the dominant species. Other species found in fallow habitats in relatively smaller numbers included *Grammomys dolichurus*, *Mus* sp. and *Lophuromys flavopunctatus* (Figure 2). Temporal and spatial fluctuations of rodent numbers occurred. Species inhabiting the forest, despite the lower trapping effort relative to the effort in fallow habitats, were at lower densities throughout the year. The distribution of *M. natalensis* and *A. nairobe* extended into the forest while *L. flavopunctatus* was also found in the fallow land close to the forest.

Three species of fleas were collected from rodents. These were, in order of abundance, *Dinopsylus lypusus*, *Leptopsylla aethiopica* and *Nosopsyllus fasciatus*. The monthly mean numbers of fleas (flea index) for all rodent hosts collected are shown in Figure 3. There was a marked increase in the abundance of fleas on rodents between August and September, and more fleas on rodents in October than in any other month. Fleas were found mainly on *M. natalensis*, *A. nairobe* and *L. flavopunctatus*. No fleas were found on *Mus* sp., and relatively few were collected on *Praomys* sp. and *G. dolichurus*.

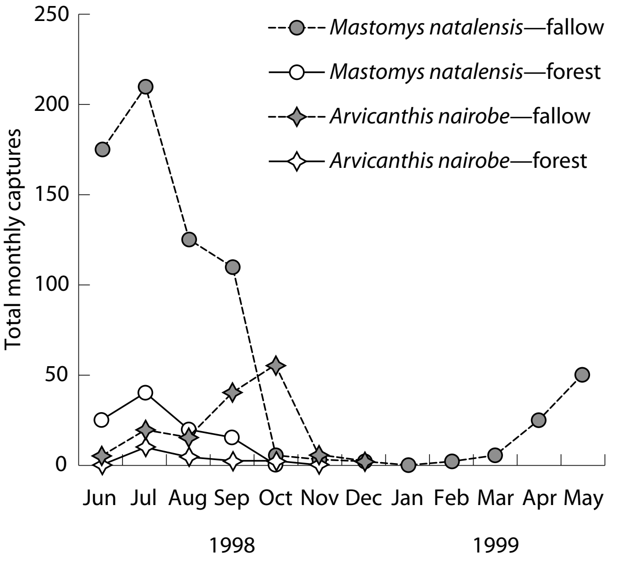

Figure 1. Abundance of *Mastomys natalensis* and *Arvicanthis nairobe* in fallow and forest habitats in Shume Ward, Lushoto District, Tanzania in 1998–1999.

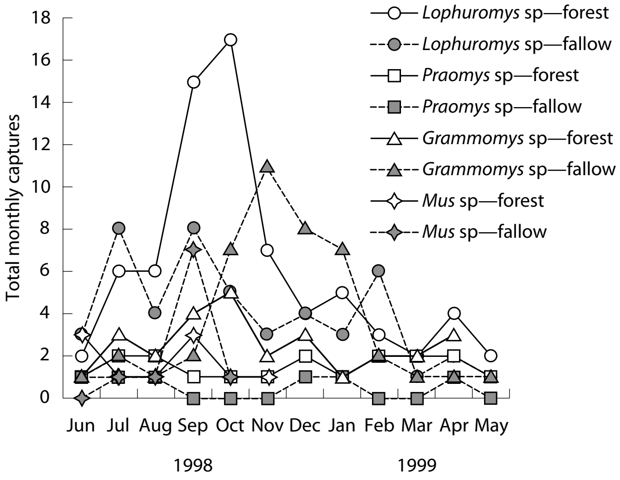

Figure 2. Abundance of non-savanna species of rodents in fallow and forest habitats in Shume Ward, Lushoto District, Tanzania, in 1998–1999.

The data show considerable variation in abundance of rodents from one season to another, and within and between habitats. Seasonal variations in the abundance of the population of *M. natalensis* were well pronounced, with the highest densities occurring after the rainy season and during the onset of the dry season in July. It is noteworthy that fluctuations of rodent populations in the forest, particularly *L. flavopuncatus*, were just as dramatic relative to the lower populations present. Although these species occupy a more stable habitat, it is uncertain how fragmentation and agricultural encroachment have affected their population dynamics. More is known about the ecology of *M. natalensis* and the factors causing population fluctuations in other areas of Tanzania (Leirs 1992; Christensen 1996; Leirs et al. 1996, 1997; Mwanjabe and Leirs 1997) than for the rodent species found in the western Usambara Mountains.

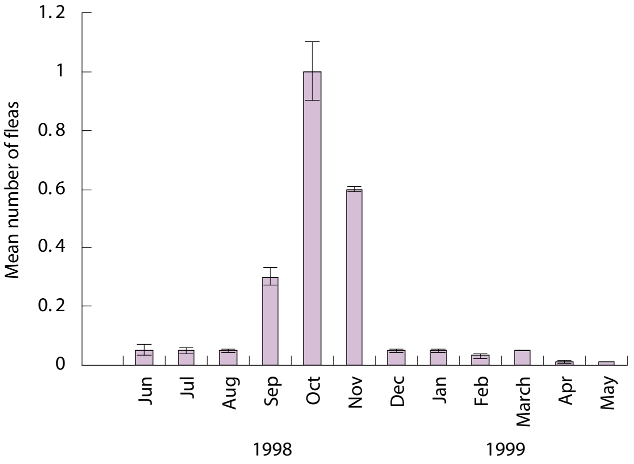

Figure 3. Changes in abundance of fleas on rodent hosts in Shume Ward, Lushoto District, Tanzania.

There has been a great human impact on the ecology of the western Usambara Mountains caused by agricultural encroachment into the natural forest. This has led to modifications of habitats, making them less suitable for forest-inhabiting species, but more favourable for colonisation by savanna species, specifically *M. natalensis* and *A. nairobe*. The distribution of these species overlaps with that of species found in the remaining forested area. This overlap of habitats leads to unrestricted interaction and potentially makes it possible for exchange of fleas and the disease pathogen between them. The presence of specific anti-plague IgG and IgM antibodies and *Y. pestis* DNA in rodent sera is shown in Table 1. Rodent species that tested positive for *Y. pestis* DNA and anti-plague antibodies probably are the natural reservoirs of the disease. It could also be inferred that the species inhabiting the forest are most likely to maintain the disease throughout the year since a residual population is present when the savanna species populations are extremely low. Before the disease outbreak, the most important link between forest and peri-domestic species appears to be *M. natalensis* and *A. nairobe* because they occurred in relatively large numbers and due to their close proximity to both peri-domestic and forest-inhabiting rodent species. Both species were positive for *Y. pestis* DNA, and anti-plague IgM and IgG antibodies, indicating previous and current infection/ exposure.

It is likely that the decline in rodent populations, particularly *M. natalensis* and *A. nairobe* from October–March, led to more fleas seeking alternative hosts. The increasing number of fleas on rodent hosts between September and October was associated with increasing human plague cases in October and November. However, the number of fleas on rodents declined throughout December to May. Plague prevalence was also low in December, but increased again in January and declined in subsequent months. The declining numbers of rodent hosts, particularly *M. natalensis* and *A. nairobe*, did not lead to a marked increase in the flea load on remaining hosts, but there was an increase in human plague cases, particularly in November and January (Figure 4).

Table 1. Presence of anti-plague immunoglobulin (IgG and IgM) antibodies and *Yersinia pestis* DNA in rodent sera in the western Usambara Mountains, north-eastern Tanzania (NT = not tested).

Species	No. of sera (samples) tested	Percentage with *Y. pestis* DNA	Percentage positive	
			IgG	IgM
Mastomys natalensis	86	10.5	9.4	15.3
Arvicanthis nairobe	25	28.0	23.1	26.9
Lophuromys flavopunctatus	14	7.1	7.7	15.4
Rattus rattus	12	16.7	8.3	16.7
Grammomys dolichurus	14	0	NT	NT
Praomys sp.	6	0	NT	NT

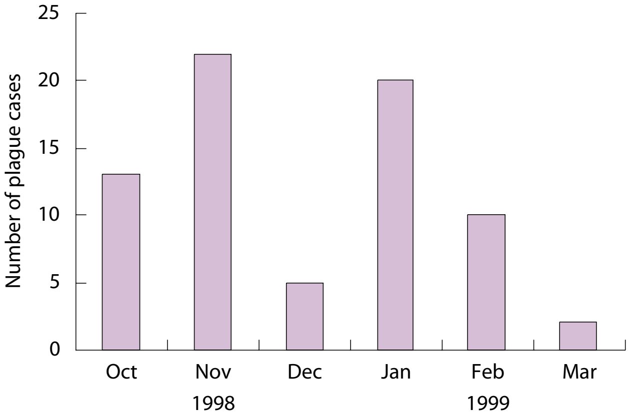

Figure 4. Human plague cases during the 1998–99 outbreak in Shume Ward, Lushoto District, Tanzania.

The correlation between flea loads on rodents and plague cases in humans ($r = 0.397$, $p = 0.43$) was weak and not significant, indicating that once the disease outbreak occurs, transmission to humans may not be mediated by fleas but possibly by inter-human transmission. This suggests that inter-human transmission of the disease, probably mediated by the human flea (*Pulex irritans*) in houses, was responsible for the plague cases recorded in January after the initial rodent to man transmission between October and November. Therefore, it appears that during plague outbreaks in the Usambara Mountains, there are two distinct phases in transmission of the disease. In the first phase, fleas from rodents play a central role in disseminating the disease to man, while in the second phase, the disease is disseminated between people by *P. irritans*. This follows a trend similar to that reported by Karim and Farhang-Azad (1974) and Twigg (1978), and probably occurs when there are few natural hosts of the disease in the fallow and cultivated areas, particularly in November to March. However, inter-human transmission by droplet infection cannot be ruled out as contributing to the disease outbreaks, especially when the disease advances to pneumonic status among some patients (Kilonzo et al. 1997).

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Rodent diseases in Southeast Asia and Australia: inventory of recent surveys

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Abstract. We provide an inventory of rodent diseases that we have screened over the past decade in Southeast Asia and Australia. Our main interest is to provide baseline information for future epidemiological studies, particularly for potential rodent-borne zoonoses. We have identified a range of diseases circulating in rodent populations in both Australia and in Southeast Asia. The zoonotic diseases detected in Australia were *Streptobacillus moniliformis, Angiostrongylus cantonensis*, lymphocytic choriomeningitis virus, leptospirosis, rickettsia and cryptosporidia. The zoonotic diseases detected in Southeast Asia were hantaan virus and leptospirosis. The latter is drawn from less-intensive sampling of a subset of rodent diseases. We need to determine the occurrence of important rodent zoonoses such as leptospirosis, plague, hanta- and arena-viruses, and lungworm in agrarian communities and rat populations in selected regions of Asia. Once we have this information, then we will need to identify the main species of rodent that are reservoirs for each of the diseases in each region and examine the influence of population dynamics of and patterns of habitat use by these rodents on disease transmission.

Introduction

> In poorer communities, if a rodent zoonotic causes disability for a poor farmer for a month at a key time then it may lead to no crop, a late crop, or reduced crop yield. Each can lead to a debt treadmill!
>
> (Singleton 2001)

Rats are becoming a most serious pest of rice in Asia, causing annual pre-harvest losses of about 5–10%. In addition, to these losses, reports of 20% losses to grain post-harvest from rats are not unusual (Singleton 2001). Rats are also transmitters of important human diseases, such as the plague, arena- and hanta-viruses, rat typhus, lungworms and leptospirosis (Gratz 1994; Mills 1999). Since 1995, more than 25 new hanataviruses and arenaviruses have been identified in rodents (Mills 1999). The impact of these diseases on human livelihoods, in both urban and agricultural communities, is poorly documented. The epidemiology of most of these diseases in Asia is poorly understood. For instance, little is known about which species of rodents are the major reservoirs, how long infective life stages of bacteria, viruses, spirochaetes and helminths persist in domestic and rural environments, how theses diseases are transmitted under 'natural' conditions, how prevalent these diseases are in both the rodent and human populations, and the basic human epidemiology of these diseases (incidence of infection, morbidity rates, transmission rates, age and sex-related effects, effects of socioeconomic status).

There is rising concern that rodents are a major health risk in rice agro-ecosystems because of increased movements of people between rural and urban areas and between countries, an increased population density of people which amplifies the ability of a disease to spread through populations, and increased clearance of natural habitats which promotes rodent–human contact. However, little research is being done on the epidemiology of rodent diseases in Southeast Asia or in Australia. This situation is similar in Europe (Begon, this volume) and Africa. A promising recent development is a new European Union-funded project in Africa (RATZOOMAN) focusing on the rodent epidemiology of the plague, *Yersinia pestis*, and on species of *Leptospira* and *Toxoplasma gondii* (S.R. Belmain and H. Leirs, pers. comm.).

Leptospirosis alone is having a major impact on rural communities in developing countries in Asia. From 1995 to 2000, the cases of leptospirosis have markedly increased in north-eastern Thailand and in the year 2000, 6000 cases and 320 deaths associated with this disease were reported among rice farmers (W. Tangkanakul, pers. comm.). Information on leptospirosis in other regions in Asia is extremely limited. The symptoms are flu-like and can easily be mistaken and neglected in the rural areas until serious clinical damage has occurred. If left untreated, patients can develop kidney damage, meningitis, liver failure and respiratory distress. Because of lack of information, appropriate precautions are rarely taken when either handling rats, consuming (contaminated) food or working in rice fields. By improving the farmers' knowledge and practices for rat management, the spread of various zoonoses, particularly leptospirosis, could be greatly reduced.

This paper provides an inventory of the rodent diseases that we have screened over the past decade in Southeast Asia and Australia. Our interest in these surveys is twofold: (i) to provide baseline information for future epidemiological studies of rodent-borne diseases that affect humans and their livestock; and (ii) to raise awareness of the diseases which may be circulating in field populations of rodents for researchers who are interested in the impact of disease on rodent populations (see Begon, this volume).

Materials and methods

All rodents were trapped live and identified to species. Information was recorded on the sex, breeding condition, head–body length, weight, and season and habitat of capture. For *Mus* species, blood samples were obtained from the sub-orbital venous plexus using micro-capillary tubes. For larger rodents, blood samples were obtained from cardiac puncture immediately after the animal had been euthanased (CO_2 where available, otherwise CO). In some cases, organs (liver and lung) were collected and transferred immediately into liquid nitrogen, sections of kidney were collected and transferred to Ellinghausen McCullough Johnson Harris (EMJH) medium solidified with 1.5% agarose culture medium (Faine et al. 1999) and faecal samples were collected and stored in 70% ethanol.

Antiviral antibodies were detected by immunofluorescence assay (IFA) except antibodies to murine cytomegalovirus, which were detected by enzyme-linked immunosorbent assay (ELISA) (see Smith et al. 1993 for details) for mice and for rats. The viruses screened for mice were mouse hepatitis virus (MHV), rotavirus (epizootic diarrhoea of infant mice (EDIM) virus), lymphocytic choriomeningitis virus (LCMV), ectromelia virus, mouse adenovirus (two strains: MAdV-FL, MAdV-K87), minute virus of mice (MVM), murine cytomegalovirus (MCMV), reovirus serotype 3 (reo 3), Sendai virus, Theiler's mouse encephalomyelitis virus (TMEV), pneumonia virus of mice (PVM), polyoma virus, and hantaan virus. The viruses screened for rats were MAdV-FL, MAdV-K87, MVM, ectromelia virus, TMEV, Reo 3, PVM, LCMV, rat parvovirus (RPV), Sendai virus, hantaan virus, Seoul virus, rat coronavirus (RCV), rat parvovirus-virus (ROPV), encephalomyocarditis virus, and rat cytomegalovirus (RCMV). Both mouse and rat sera were tested for *Mycoplasma pulmonis* antibodies by IFA.

To isolate LCMV from *Mus domesticus* trapped in northern New South Wales (NSW), spleen and kidney homogenates were inoculated onto BHK21 cell monolayers. After 4 days, cell scrapings were transferred to microscope slides, air-dried, fixed in acetone and stained by indirect immunofluorescence with a pooled reference antibody specific for LCMV and fluorescein isothyocyanate-conjugated goat anti-mouse immunoglobulin (IgG).

Leptospiral antibodies were screened using a microscopic agglutination test (MAT) against a panel of 21 serovars. All sera were tested beginning at a serum dilution of 1:50. A low level MAT titre does not exclude an active infection or carrier status (Faine et al. 1999). Cryptosporidia was screened as described in Morgan et al. (1999). Rickettsial antibodies were assessed using the indirect fluorescent antibody test. Titres > 1:32 were considered positive. Antibodies to three antigenic rickettsial groups were examined: spotted fever group (*Rickettsia australis*—Queensland tick typhus); typhus group (*R. typhi*—murine typhus); and scrub typhus (*Orientia tsutsugamushi*—scrub typhus). *Streptobacillus moniliformis* was noted through the appearance of obvious lesions and swelling around the foot or tail and the subsequent bacterial culture of three animals as described in Taylor et al. 1994.

Results and discussion

Metropolitan Melbourne

Cryptosporidiosis is a major health concern in metropolitan areas in Australia, especially if the organism gets into drinking water or swimming locations. Two black rats were detected with *Cryptosporidium* sp. (Table 1). Not all species of *Cryptosporidium* are a threat to human health, however the results suggest caution. Further interpretation of the health implications would require genetic typing of the species of *Cryptosporidium* that was isolated.

Internationally and historically, rat typhus caused by *Rickettsia* spp. has had a greater effect on human health than the plague. The high prevalence of antibodies to rickettsial agents in each of the introduced rodent species is cause for concern (Table 1). Tick typhus or spotted fever caused by *R. australis* is common in subtropical and tropical climates of Queensland. It is now known to extend down the east coast of Australia well south of Sydney to East Gippsland in Victoria (Campbell and Domrow 1974; Graves et al. 1993). A genetically distinct organism, *Rickettsia honei*, responsible for what has been termed Flinders Island spotted fever is now recognised there and probably occurs also on the island of Tasmania (Dwyer et al. 1991; Graves et al. 1991; Stewart 1991; Baird et al. 1996). Natural reservoirs of this organism appear to be marsupial antechinuses, bandicoots and possums, and rats and mice (Graves et al. 1993). More recently, there has been a new species of typhus (*Rickettsia felis*) recorded in human patients in Victoria (B. Paspaliaris, Swinburne University of Technology, pers. comm.). In each of these cases, there was prolonged illness (more than 12 months). The IFA test used to differentiate the three groups of rat typhus in the current study would cross-react with the new species *R. felis*. The results of the present study highlight the need for further studies of the role of introduced rodent species as reservoirs of *Rickettsia* species and possible implications for human health.

All of the Australian rodents sampled were sero-negative to plague (*Yersinia pestis*) and hantavirus (Table 1). In the early 1900s, plague occurred in Australia in epidemic proportions (Curzon and McCracken 1993) with the black rat being the main rodent reservoir, but only a few cases have been reported since. There have been no reports of hantavirus in Australia.

Melbourne and Brisbane, Australia

The rat lungworm (Nematoda), *Angiostrongylus cantonensis*, causes neurological disease in humans and several fatalities have occurred in Australia (see review in Prociv et al. 2000). It is of increasing concern due to the continuing expansion of its geographical range which now encompasses much of Southeast Asia, Melanesia, Polynesia, eastern Australia, parts of Africa, India, the Caribbean and the south-eastern United States of America (USA). A wide spectrum of snails and semi-slugs (Gastropoda), including the African giant land snail, *Achatina fulica*, serve as intermediate hosts of the lungworm and it may occur also in a range of paratenic hosts. As a consequence, the route of infection in human cases varies geographically. In Asia and Australia, most cases are probably acquired by ingesting raw intermediate hosts—snails, slugs or planarians—either directly (e.g. by children) or on fresh vegetables that have not been thoroughly washed. This contrasts with the situation in Tahiti and other Pacific Islands where paratenic

Table 1. Prevalence (%) in Australia of murine viruses (serology), bacteria (culture), mycoplasma (serology) and cryptosporidia (stain) in house mice, *Mus domesticus*, and in *Rattus rattus* and *R. norvegicus* where indicated. Results are given as % positive (number tested). Also 17 *Rattus rattus* from metropolitan Canberra were sero-negative to hantaan virus and the newly described Mossman virus.

Rodent agent	Prevalence				
	North-western Victoria	South-eastern Queensland	Northern New South Wales	Metropolitan Sydney	Metropolitan Melbourne
Murine viruses[a]					
MHV	97 (269)	76 (536)	84 (57)	100 (2)	60 (10)
EDIM	36 (269)	61 (465)	52 (61)	100 (3)	90 (10)
MCMV	93 (311)	80 (348)	61 (41)		100 (8)
MVM	23 (269)	7 (464)	0 (33)	33 (3)	30 (10)
Reo 3	25 (269)	13 (463)	8 (62)	33 (3)	0 (10)
MAdV-K87	36 (269)	5 (469)	22 (63)	0 (3)	10 (10)
LCMV	0 (269)	0 (208)	42 (182)	0 (3)	0 (15)
Ectromelia	0 (269)	0 (208)	0 (43)	0 (3)	0 (10)
Hantaan	0 (269)	0 (208)	0 (43)	0 (3)	0 (15)
TMEV	0 (269)		0 (43)	0 (3)	0 (10)
Polyoma	0 (269)		0 (43)	0 (3)	0 (10)
PVM	0 (269)		0 (43)	0 (3)	0 (10)
Bacteria					
Streptobacillus moniliformis (lesions)	0 (311)	6 (1469)			
Yersinia pestis					0 (5) 0 (6 *R. rattus*) 0 (2 *R. norvegicus*)
Mycoplasma pulmonis	0 (269)	1 (81)	0 (63)	0 (3)	
Cryptosporidia					
Cryptosporidium spp.					
C. parvum	Positive				
Rickettsia					
Rickettsia australis					20 (5) 100 (6 *R. rattus*) 50 (2 *R. norvegicus*)
Rickettsia typhi					40 (5) 17 (6 *R. rattus*) 0 (2 *R. norvegicus*)
Leptospira serovars				0 (26 *R. norvegicus)*	

[a] MHV = mouse hepatitis virus; EDIM = epizootic diarrhoea of infant mice virus (rotavirus); MCMV = murine cytomegalovirus; MVM = minute virus of mice; Reo 3 = reovirus serotype 3; MAdV-K87 = a strain of mouse adenovirus; LCMV = lymphocytic choriomeningitis virus; TMEV = Theiler's mouse encephalomyelitis virus; PVM = pneumonia virus of mice.

hosts—freshwater prawns and terrestrial crabs—are the major source of infection. Two additional and closely related species, *A. mackerrasae* and *A. malaysiensis*, occur in native rats in south-eastern Australia and the Indo-Malayan region, respectively, but to date only *A. cantonensis* has been associated with human neuro-angiostrongyliasis. It is noteworthy, however, that clinical presentations of human infection in Asia, in contrast to the situation in Australia, may be disguised by the abundance of other infectious diseases and diagnosis prevented either by limited resources or cross-reactivity with other helminths in diagnostic tests.

Rural areas of Australia

Potential human zoonoses

Streptobacillus moniliformis is the aetiological agent of rat bite fever and is a cause of the human epizootic Haverhill fever. The symptoms in humans are variable but they include fever and malaise and can lead to arthritis in joints. Not much is known about this disease or its epidemiology. In Australia, there has been one human fatality accredited to *S. moniliformis* (Rountree and Rohan 1941).

Leptospirosis is a notifiable disease in all states and territories of Australia. More than 200 human cases of leptospirosis are reported in Australia each year—more than half of these are from Queensland. An outbreak in 1999 in Queensland resulted in 216 notifications compared to 108 for the previous year. The symptoms are general and may present as severe fever, headache, chills, myalgia, sweats, arthralgia and vomiting. The serovars most commonly reported are hardjo, pomona, zanoni, australis and tarassovi (Queensland Health 2002). Leptospirosis has been reported in at least three native rodent species in North Queensland in the proximity of agricultural land along the coast between Tully and Cairns (L. Smythe and A.L. Smith, unpublished data).

LCMV was isolated from mice trapped at two sites in Moree, NSW. At the first site, isolations were made from 7 of 23 tissues tested, representing 5 of 14 mice tested. At the second site, LCMV was isolated from 15 of 20 tissues

Table 2. Sero-prevalence (%) of *Leptospira* (against panel of 21 serovars) and murine viruses and *Mycoplasma pulmonis* in rodents in Southeast Asia. Sample size in brackets. All rodents from Indonesia and Malaysia were *Rattus argentiventer.*

Rodent/agent[a]	Prevalence						
	Lao PDR Luang Prabang	Vietnam Soc Trang	Vietnam Bac Lieu	Indonesia West Java	Indonesia Central, East Java	Indonesia South Sulawesi	Malaysia Peninsula
Leptopirosis			(79)				
Bandicota indica	0 (3)		0 (14)				
Cannomys badius	0 (1)						
Chiromyscus chiropus	0(1)						
Maxomys surifer	0 (1)						
Mus pahari	0(1)						
Mus cervicolor	0 (2)						
Rattus argentiventer		19.4 (62)	0 (61)				
R. losea		0 (1)	0 (1)				
R. norvegicus		100 (1)	0 (1)				
R. rattus	0 (38)		0 (2)				
Rhizomys proinosus	0 (1)						
Murine viruses							
Hantavirus[b]				7 (41)	2.4 (42)	7 (14)	0 (121)
MAdV-K87				5 (40)	0 (42)	7 (14)	5.7 (122)
MAdV-FL				0 (40)	0 (42)	0 (14)	4.1 (121)
MVM				0 (40)	0 (42)	0 (14)	0.8 (122)
TMEV				0 (40)	0 (42)	0 (14)	1.6 (122)
RCMV				0 (8)	2.4 (42)	7 (14)	0 (122)
PVM				0 (40)	0 (42)	0 (14)	2.5 (122)
Reo 3				0 (40)	0 (42)	0 (14)	0.8 (122)
RCV				5 (41)	0 (42)	7 (14)	13.9 (122)
Sendai				0 (38)	2.4 (42)	7 (14)	0 (122)
ROPV				5 (41)	2.4 (42)	7 (14)	0 (122)
RPV				0 (40)	0 (42)	0 (14)	0 (122)
LCMV				0 (40)	0 (42)	0 (14)	0 (122)
Mycoplasma pulmonis				2 (41)	2.4 (42)	0 (14)	35.2 (122)

[a] MadV-K87 and MadV-FL = mouse adenovirus (two strains); MVM = minute virus of mice; TMEV = Theiler's mouse encephalomyelitis virus; RCMV = rat cytomegalovirus; PVM = pneumonia virus of mice; Reo 3 = reovirus serotype 3; RCV = rat coronavirus; ROPV = rat parvovirusvirus; RPV = rat parvovirus; LCMV = lymphocytic choriomeningitis virus.

[b] Species and sample sizes as for leptospirosis—all were sero-negative

tested, representing 10 of 14 mice tested. These LCMV isolates are the first ever recorded in Australia. There have not been any confirmed human cases of LCMV in Australia. Singleton et al. (1993) discuss the relative impact of the other murine diseases on mouse populations and their status as zoonotic diseases.

Southeast Asia

The presence of hantavirus(es) and leptospirosis (Table 2) confirms results from recent studies in Thailand (Tangkanakul et al. 1998; Nitatapattana et al. 2002).

The presence of rodent zoonoses is of added concern in regions where rats are caught and prepared for consumption. For instance, in the Mekong Delta region of Vietnam, some 3500 t of rat meat reaches the markets each year. This requires the handling of approximately 35 million rats in a production chain that can have up to six handling points before the rat meat is sold at market (Nguyen Tri Khiem et al., this volume). Indeed, the rats we screened in Vietnam were from rat processing 'households' where the sero-prevalence of leptospirosis was >20% in one instance. Yet the people involved in this distribution chain take little precaution in their handling of rats because they have virtually no knowledge of the risks that they face from rodent-borne diseases (Nguyen Tri Khiem et al., this volume).

A detailed epidemiological study of rodent zoonoses has a high chance of reducing the debilitating impacts of disease for the following reasons:

1. A number of rodent zoonoses, such as plague and leptospirosis, are readily treated in humans if detected at an early stage.
2. Increased sanitation can markedly reduce the likelihood of infection—a knowledge of which diseases are high in prevalence, which age classes of humans are at greatest risk of infection, which rodent species are reservoirs of the diseases, and the spatial use of the environment by these rodents can aid in reducing risks of exposure.
3. Few human health programs in Asia include rodent diseases simply because there is minimal knowledge of what is of importance for that region.

Conclusions

Our studies on diseases of rodents that may affect humans in Australia and Southeast Asia have been done as adjuncts to other projects. The data set is therefore sparse, yet it is one of the largest available. What is of concern is that, although the study effort has been low, a number of zoonotic diseases have been found, including LCMV for the first time in Australia. Also, when dealing with pathogens, we by necessity are confined to those for which a test has been developed—we may therefore be dealing with a small subset of rodent-borne diseases. The rapid growth in the number of different hantaviruses and arenaviruses in the Americas as a result of increased research effort (Mills 1999) is testament to this point. This inventory therefore raises many needs for research on rodent disease in both Australia and Southeast Asia. We conclude with some discussion of these needs.

We need to determine the occurrence of important rodent zoonoses such as leptospirosis, plague, hanta- and arena-viruses, and lungworm in agrarian communities and rat populations in selected regions of Asia. Once we have this information then we will need to identify the main species of rodent that are reservoirs for each of the diseases in each region and examine the influence of population dynamics of and patterns of habitat use by these rodents on disease transmission. Indeed, we may find that many species are not reservoir rodents (in which the pathogen is enzootic), but instead liaison hosts (important in transmitting infection to humans, but may not be the reservoir). This is an important distinction because the prevalence of disease in liaison hosts is likely to be highly variable, and often very low.

We lack also information on the epidemiological determinants of rodent-borne diseases in human communities in rural and peri-urban areas (incidence of infection, morbidity rates, transmission rates, age and sex-related effects, effects of socioeconomic status). This knowledge would assist in identifying domestic and occupational factors that influence the risk of infection for specific diseases. A separate, but significant, issue is the regular handling of rats by people in developing countries who consume rats as a regular source of protein.

These studies are needed urgently if we are to be able to provide recommendations on practices for rat management and general public health to reduce the transmission and impact of rodent zoonoses.

Acknowledgments

This research was partially funded by the Grains Research and Development Corporation, Australia, and the Australian Centre for International Agricultural Research (AS1/94/20; AS1/98/36). We thank Professor Charles Krebs for his comments.

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Developments in fertility control for pest animal management

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Abstract. In south-eastern Australia and in Asia, the economic and social impact of pest rodent species is high. Chemical control is widely applied as the primary method for managing these and other mammalian pests, as well as weeds and pest insects in agricultural production or conservation areas. Chemicals often provide effective short-term control, but are neither target specific nor cost-effective in the long term. With widespread and increasing concerns about the use of chemicals in the environment, and pressures to produce environmentally acceptable products for domestic and export markets, alternative approaches to pest management are required. For mammalian pests, fertility control using immunocontraception is being developed.

We are examining whether mouse populations can be managed using fertility control delivered either by a non-infectious infertility agent in a non-toxic bait, or by infectious viruses which are carriers of the agent. To date, laboratory studies have demonstrated that genetically engineered mouse viruses, such as mouse cytomegalovirus (MCMV) and ectromelia virus expressing mouse zona pellucida 3 can induce long-term infertility in laboratory and wild house mice. Field enclosure studies have shown that surgical sterilisation of 60–70% of each cohort significantly reduces recruitment over 32 weeks, and we have demonstrated that wild-type viruses introduced into field enclosures will transmit to uninfected adults and their young.

This is a large, multi-disciplinary research program where biotechnological approaches, studies of the population ecology of mice and the epidemiology of the viral vector, MCMV, are being addressed. The use of this technology requires acceptance by the public of the risks and benefits, and must comply with Australian government (and international) regulatory requirements. There are still many steps to be completed before this fertility control approach can be applied in the field as part of an integrated management strategy.

Introduction: impacts of rodent pests

In Australia, the principal rodent pest in agricultural crops is the house mouse, *Mus domesticus*. Its biology and population dynamics are well understood for the Australian grain-growing regions where it causes devastation to crops (Singleton 1989; Pech et al. 1999). Mouse populations erupt irregularly causing losses in the range of US$50–150 million (Caughley et al. 1994), equivalent to average annual losses of around US$10 million. This cost estimate does not include any of the indirect impacts in rural society or the damage caused by mice to infrastructure in rural communities.

The frequency of house mouse plagues has increased in Australia in the last 15 years (Singleton and Brown 1999) and has emphasised the continuing need for alternative approaches for management. While various strategies for reducing mouse populations have been recommended for the mallee and Wimmera regions of Victoria (Singleton and Brown 1999) and could be broadly effective if undertaken by groups of farmers, a cost-effective and environmentally friendly management strategy for use on the broad scale is still needed. An alternative to mortality-control agents used for crisis management is to develop fertility-control methods whereby viruses or non-toxic baits are used as potential delivery vectors (Tyndale-Biscoe 1994; Seamark 2001).

Non-toxic, bait-delivered fertility control also is highly relevant for the future management of pest rodents in agriculture in Southeast Asia (Singleton and Petch 1994; Singleton et al. 2001). For example, each year in Indonesia, losses in rice production due to rat damage average 17%. If no damage occurred, there would be sufficient rice to provide 52% of the food requirements for 33 million people for each year (Singleton et al. 2001).

The development of fertility control for the house mouse involves a multi-disciplinary approach with essential studies required in both the laboratory and field in order to ensure that several key characteristics are a feature of the immunocontraceptive vaccine. It must evoke a sustained immune response that blocks a critical step in the reproductive process (e.g. fertilisation) and be species-specific so that non-target species are not affected. An effective mechanism for the delivery of the vaccine throughout the target population must be developed. Finally, any immunocontraceptive vaccine used for large-scale population control must be stable, cost-effective to produce and deliver, not pose any environmental hazard, and be acceptable to the public.

Physiological context of fertility control

The antigen and the delivery vector

Initial studies using ectromelia virus expressing the gene for the mouse egg coat protein, zona pellucida 3 (ZP3) (Jackson et al. 1998), provided laboratory evidence that a virally delivered immunocontraceptive vaccine for the mouse caused sustained infertility. Parallel studies using mouse cytomegalovirus (MCMV), a vector already present in the field in Australia (Shellam 1994; Singleton et al. 2000), clearly confirmed the potential of virally vectored immunocontraception. Several strains of laboratory mice, as well as wild mice, were infertile after infection with MCMV expressing mouse ZP3 and remained infertile for more than 250 days (Chambers et al. 1999a; M. Lawson, unpublished results). That anti-ZP3 antibodies caused the infertility was shown by transfer of antibodies from infected, infertile mice to uninfected, fertile female mice; these mice showed inhibited fertility (M. Lloyd and M. Lawson, unpublished results). In addition, infertility is mediated by cytotoxic T-cell destruction of developing ovarian follicles, causing permanent sterility (Lou et al. 1996). The initial studies employed intraperitoneal inoculation as the route of infection, although infection via different routes, including intramuscular, intraperitoneal, intradermal and intranasal, in mice also induces infertility (M. Lawson, unpublished results).

The original studies with recombinant MCMV were undertaken using a laboratory strain of MCMV. However, in order to meet some of the Australian regulatory requirements for the release of an engineered mouse virus, it was essential to isolate and engineer wild Australian strains of MCMV and test their effects in mice. Recently, two Australian isolates of MCMV have been successfully engineered to express the mouse ZP3 antigen and, in breeding experiments in laboratory mice, have shown a similar inhibition of fertility as the prototype recombinant MCMV (M. Lawson et al., unpublished results).

Species specificity

An essential feature of a fertility-control agent delivered via a virus or non-toxic bait is species specificity. The cDNAs encoding several ZP antigens from a variety of species have been cloned and sequenced (Harris et al. 1994): these genes and their expressed proteins show high identity between species (Harris et al. 1994; Zhu and Naz 1999). Therefore, a key challenge is to identify or engineer the reproductive antigen to be species-specific. This may be achievable using specific peptides or epitopes. Indeed, one of the most divergent regions within the ZP3 protein consists of overlapping B-cell and T-cell epitopes and is thought to be involved in fertilisation. This 21 amino acid region was first identified in the mouse, using a monoclonal antibody that blocked fertilisation (Millar et al. 1989). Peptide vaccines based on this epitope produce long-term contraception in female mice (Millar et al. 1989) and wild mice (Hardy et al. 2002a).

Clearly, it could be difficult to mount an immune response to such small peptides which will then have the ability to block fertility. The use of epitopes alone or in combination with immunomodulatory molecules (such as cytokines or T-cell help epitopes) to enhance the species-specific immune responsiveness to these antigens (Dalum et al. 1997; Ramsay and Ramshaw 1997) warrants further investigation.

Several other mouse-specific peptides involved in reproductive processes have been identified and artificial antigens, which combine these peptides with various immune modulators, have been constructed. They are currently being trialled to determine their ability to enhance immune responses and/or affect fertility (Hardy et al. 2002b).

The addition of other reproductive antigens and immune-enhancing elements offers another refinement for contraceptive vaccines because they may also address the need to induce an immune response in all recipients. By presenting several epitopes which will cause infertility, the proportion of non-responders to an individual epitope within a population should be reduced.

Is MCMV itself species-specific? A 2-year field study of house mice co-existing on an island with an Australian native rodent species, *Leggadina lakedownensis*, revealed that even though house mice were infected with MCMV, *Leggadina* were not sero-positive and MCMV deoxyribonucleic acid (DNA) could not be isolated from them. Furthermore, *L. lakedownensis* experimentally infected with MCMV showed no evidence of viral replication in the tissues in which the virus replicates in the mouse (spleen, liver, salivary gland, lung) (Moro et al. 1999). Similarly, in laboratory studies using *Rattus tunneyi* and *Pseudomys australis*, no infectious virus or viral DNA was recovered and animals did not sero-convert after experimental inoculation with live MCMV (G. Singleton, M. Lawson and G. Shellam, unpublished results). In recent experiments, intraperitoneal infection of laboratory *Rattus norvegicus* with recombinant MCMV expressing mouse ZP3 did not lead to either recovery of viral DNA, sero-conversion to the virus, or any effects on fertility (L. Smith, pers. comm.). These are highly encouraging results, but further experiments may need to be undertaken in a range of species to adequately demonstrate species specificity of the virus when it is expressing the additional DNA.

Ecological context of immunocontraception

How many mice must be sterilised in the field?

The impact of sterilising two-thirds of the adult females on the rate of growth and population structure of confined populations of wild mice has been examined in outdoor field enclosure studies (Chambers et al. 1999b). When 67% of adult females were surgically sterilised, either by ovariectomy or tubal ligation, the growth rate of mouse populations in the enclosures was significantly reduced. The results indicated that hormonally competent, sterile females were unable to prevent fertile females from breeding, and that there was also some compensation through increased breeding performance (increased percentage of females breeding, and slightly higher litter size) relative to the control populations over 18 weeks. However, given that the breeding season of mice in south-eastern Australia can extend for up to 32 weeks (Singleton and Redhead 1990), a single application of sterility at 67% may lead to only a transient effect in the field populations.

In a second series of experiments, we applied two treatments—one which simulated two applications of an immunocontraceptive vaccine via bait delivery and the other which simulated continual sterility as for a disseminating viral-vectored immunocontraceptive vaccine. These experiments (L. Chambers, G. Singleton and L. Hinds, unpublished data) indicated that two applications of a sterility vaccine via bait would not be sufficient to prevent the eruption of mouse populations. However, results for the simulation of a virally delivered vaccine indicated that it could keep mouse populations at economically acceptable levels if two-thirds of each cohort were sterilised.

Field studies on transmission of MCMV in mouse populations

The key population and ecological factors that may influence the persistence, transmission and rate of spread of MCMV in field and semi-natural enclosure populations must be understood before a recombinant virus could be released into the field. Several questions have been addressed using studies of field populations and of populations living under semi-natural conditions in nine field enclosures (15 m × 15 m) at Walpeup (central Victorian mallee wheat lands).

Singleton et al. (2000) examined the sero-prevalence of MCMV in mice living in wheat fields at Walpeup over 3 years. During this period, there were initially low mouse numbers (<1 mouse per ha), an increase to high numbers (approximately 250 mice per ha), followed by a decline. When populations of mice had been at a low density for at least 18 months, MCMV was in low prevalence, but once there were more than 40 mice per ha, the virus spread rapidly through the population. Also, after the mouse population had rapidly declined again to low densities, MCMV persisted at high prevalence for a minimum of 6 months (Singleton et al. 2000). These results support the view that MCMV would be an appropriate vector for delivery of an immunocontraceptive vaccine.

In the field enclosures, the impact of one and/or two non-sterilising Australian field strains of MCMV on the mouse population was examined (Farroway et al. 2002). There was no detectable effect of MCMV on adult survival, which was greater than 95% in all enclosures. Although similar numbers of the first cohort of young entered the trappable population in all enclosures, there was lower survival of young mice when there were two strains of MCMV circulating within an enclosure population. Thus, the only impacts of infection with MCMV were in young mice, suggesting that infection with multiple strains of MCMV may only have negative effects on survival when the host immune system is not fully developed or the host is immunocompromised. These results again support the view of the suitability of an Australian field strain of MCMV as a vector for a fertility control vaccine.

This experiment also provided some information about the transmission of two Australian field strains, which are genetically different and can be distinguished from each other using polymerase chain reaction (PCR) analyses. The first strain of MCMV ‘released’ into the enclosures led to sero-conversion to MCMV in about 35% of the adult population within 9 weeks and 75% of the population within 12 weeks (L. Farroway, G. Singleton and M. Lawson, unpublished results). After a mouse is infected with MCMV, it usually takes about 2 weeks for it to sero-convert. Transmission of the second virus, which was ‘released’ 6 weeks into the study, also occurred. The transmission rates obtained from this study will be used to develop a model of the likely spread of a laboratory strain of MCMV through a field population of mice.

For field use, a recombinant MCMV will need to be broadcast over a large area to ensure a high percentage of mice are effectively vaccinated. This is necessary whether the bait contains a transmitting virus or not. Field and laboratory trials were conducted during the spring and summer of 2000/01 in the Victorian mallee to monitor the uptake rate by mice of a non-toxic bait containing a biomarker (rhodamine B). The laboratory results indicated that rhodamine marker dye was retained in whiskers of mice for a minimum of 7 weeks (Jacob et al 2002a). In subsequent field trials, uptake rates of 60 to 90%, based on fluorescence detection of rhodamine B in sera and whiskers were observed (Jacob et al. 2002b).

Socio-political aspects of immunocontraception

The assessment of environmental risks or impacts of genetically modified organisms (GMOs), real or perceived, requires a transparent process which clearly defines the probability of any identified hazards happening. Many of the risks are not related to technical aspects associated with the development of fertility control, but to the issues of public acceptability of GMOs. The public needs to gain an excellent understanding of the technology, its safety, and costs versus benefits. It is imperative that the public can separate the perceived and real risks of GMOs and balance these against the benefits gained in reducing the damage caused by the pests (Chambers et al. 1997). Inevitably, it will be the social and political reaction that determines the outcome for a release of any GMO. Recent surveys conducted by Biotechnology Australia (YCHW 1999) indicate that the level of public understanding of biotechnology is limited but that attitudes over the last 3 years have shown changes in favour of GMO products as understanding of the risks and benefits increases. Similar surveys in New Zealand have found that biological control in a generic sense was more acceptable to the public than conventional control strategies, and the use of a GMO was considered the most acceptable of the biological methods (Fitzgerald et al. 2000). The New Zealand public was most accepting of fertility control for control of possums—it was considered acceptable by 83% of respondents (Fitzgerald et al. 2000).

Often the first question asked by the public about fertility control using recombinant viruses is whether it will affect humans or other species. This response needs to be dealt with incrementally through ongoing discussion with all members of society, including those in the political arena. For fertility control agents, this can only be achieved by ongoing, extensive national and international debate (Tyndale-Biscoe 1994; Oogjes 1997; Stohr and Meslin 1997; Williams 1997, 2002).

Clearly, the major concern with immunocontraceptive vaccines is their species specificity. In Australia, the recently formed Office of the Gene Technology Regulator (OGTR), which monitors and controls GMO research, has stated that at least two specific conditions must be met in a virally vectored vaccine: the delivery system (whether viral or bait) and the agent causing infertility must both be demonstrated to be specific to the host. How this is achieved will depend on the target animal, the ecosystem, the delivery system, local non-target species, and the overall aims of the particular fertility-control program.

Animal welfare concerns and natural selection against the fertility-control agents are also commonly raised by both the public and scientists as important issues. Concerns for animal welfare reflect existing requirements that management of individuals and populations must be humane. Some authors have argued that there is potential for behavioural/hormonal disruptions to cause ill effects in sterilised individuals, that infertile animals may live longer and so suffer the diseases of old age, and that natural selection against a fertility-control agent may select for animals with poor immune systems, which could increase their susceptibility to pathogens (Guynn 1997; Nettles 1997). Other authors contend that fertility control delivered by immunocontraceptive vaccines may be more humane than existing control techniques (Oogjes 1997; Singer 1997). Whether natural selection will diminish the effectiveness of an immunocontraceptive vaccine itself is currently being researched.

While the results to date for immunocontraceptive vaccines are promising (Jackson et al. 1998; Chambers et al. 1999b; Kerr et al. 1999), the technology will not be available for several years to come. Much remains to be completed in terms of demonstrating full species specificity and related issues. Public acceptability will be heavily influenced by the media's interpretation of this technology (Williams 1997, 2002) as well as by international debate and agreement on its safety (Tyndale-Biscoe 1995; Oogjes 1997; Stohr and Meslin 1997; Williams 1997, 2002). Thus, it will be the socio-political decisions that decide the outcome for the use of fertility control agents involving GMOs.

Conclusion

Progress towards developing fertility control of mice using immunocontraceptive vaccines has been very encouraging. Both field and laboratory results show high promise that viral-vectored vaccines could be used for managing eruptions of mouse populations. While the scientific progress is promising, public acceptability of the technology is yet to be confirmed. The issues of species specificity, delivery system stability and other potential risks require open and wide-ranging debate, nationally and internationally, before a field release of a genetically modified virus for controlling field populations of mammals goes ahead.

Acknowledgments

Funding for this project has been provided by Grains Research Development Corporation, Pest Animal Control CRC (Cooperative Research Centre) and Commonwealth Scientific and Industrial Research Organisation (CSIRO) Sustainable Ecosystems. We thank our many technical staff for their excellent support in the laboratory and field.

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Trypanosome parasites in the invading *Rattus rattus* and endemic rodents in Madagascar

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Abstract. The threat of introduced parasites to the native Malagasy rodent species was studied by monitoring the occurrence of trypanosomes in six endemic rodent species and the invading *Rattus rattus* in pristine and disturbed rainforests in the Ranomafana National Park in south-eastern Madagascar. *Trypanosoma lewisi* was found in 40% of the *R. rattus*. Of the endemic species, *Trypanosoma* sp. was detected in one *Nesomys rufus*. The trypomastigotes from the native rodent were morphologically different from those of *T. lewisi*. These results indicate that *T. lewisi* was not a threat to native rodents of the park, at least in the early phase of *R. rattus* invasion of the pristine forests.

Introduction

The importance of parasites is expected to increase in shrinking ecosystems, with the promotion of transmission of new parasites into native animals by invading or introduced host species (Holmes 1996). Commensal rats have inhabited Madagascar for centuries, and today *Rattus rattus* (Linnaeus 1758) is found even in the rapidly shrinking pristine forests (Goodman and Carleton 1996). Besides exploitation and interference competition, *R. rattus* may affect the distribution and abundance of native rodent species in the form of introduced murine pathogens (Goodman 1995).

Of the wide array of parasites infecting *R. rattus* (Roberts 1991), *Trypanosoma lewisi* blood parasites have been indicated as the cause for the extinction of an endemic *Rattus* species in Christmas Island (Pickering and Norris 1996), and it has been found also in other rodents from Australia and Egypt (Mackerras 1959; Sakla and Monib 1984). This widespread trypanosome of rats is transmitted by invertebrate vectors (fleas).

T. lewisi is known to occur in *R. rattus* also in Madagascar (Anonymous 1941), but little is known about its distribution or effect on native rodents. The aim of this paper was to investigate whether *T. lewisi* occurs in rodents of the Ranomafana National Park (RNP) located in south-eastern Madagascar. In contrast to the other areas in Madagascar (Goodman 1995), the distribution of *R. rattus* seems to follow human habitation in RNP (Lehtonen et al. 2001). This provided us with a rare opportunity to investigate the possible exchange of parasites between the invading and native species in the early phase of the *R. rattus* invasion.

Materials and methods

Research was conducted in the RNP (21°16'S, 47°20'E) in relatively pristine (Vatoharanana, Valohoaka) and disturbed rainforests (Talatakely, Miaronony I, Ambatolahy and Ambatovory) from September to December in 1998–2000. Talatakely is heavily logged (in 1986–1990) rainforest at 1000 m in elevation, and it contains two research cabins, campsites, and extensive trail systems. Miaronony I, Ambatolahy and Ambatovory located at the park edge are still exploited by local people. Vatoharanana is selectively logged (in 1986) montane rainforest at 1000 m in altitude, 4 km south of Talatakely. This site has a research bush camp but no permanent buildings. The first *R. rattus* was captured in the pristine forest of Vatoharanana in 1997 (A. Dalecky, pers. comm., Institute for the Conservation of Tropical Environments). By 2000, eight more had been caught in the pristine forest sites. Valohoaka is a pristine rainforest at 1100 m in altitude, 6 km south of Talatakely. This site has a research bush camp that is used a few weeks per year. In Valohoaka, the first *R. rattus* was captured by us in 1999 and a second one in 2000.

Rodents were caught with big, locally made (10 × 10 × 29 cm) and small (2.5 × 7.8 × 6.5 cm, Ugglan special, Grahnab, Marieholm, Sweden) live-traps, mostly in the forest, but a few rats were captured also inside research cabins and in the houses of villagers (for details of the sites and trapping techniques, see Lehtonen et al. 2001). Of the eight rodent species examined (Table 1), *Nesomys* *rufus* (Peters 1870), *Nesomys audeberti* (Jentink 1879), *Eliurus tanala* (Major 1896), *Eliurus minor* (Major 1896), *Eliurus webbi* (Ellerman 1949) and *Gymnuromys roberti* (Major 1896) are endemic to Madagascar. Of the introduced species, *Mus musculus* (Linnaeus 1758) was caught in addition to the *R. rattus*. The number of rodents examined is shown in Table 1.

A few voucher specimens of native rodents (deposited in the Département de Biologie Animale, Université d'Antananarivo and Finnish Museum of Natural History, University of Helsinki) and all captured *R. rattus* were killed humanely. All other animals were released after sampling at the site of capture. Blood samples were obtained by clipping the distal end of the tail and palpating the tail, if necessary, to initiate blood flow to produce thin blood smears which were fixed with methanol and stained with Giemsa. Blood smears were thoroughly scanned with a light microscope (×10 and ×1000). The intensity of infections was recorded as trypomastigotes per 100 red blood cells. Chi-square test (Statistix® Analytical Software) was used to analyse the prevalence in different sexes and broad age groups (immature or adult).

Results and discussion

Trypomastigotes were found in the plasma of *R. rattus* (prevalence 40%, pooled data) and *N. rufus* (prevalence 2%, pooled data; Table 1). In *R. rattus*, the prevalence did not differ significantly between sexes ($P = 0.34$) or age groups ($P = 0.53$). The size and morphological characteristics of the trypomastigotes found in *R. rattus* corresponded to those reported previously for *T. lewisi* (Kreier and Baker 1987). The intensity of the infection varied from 0.33–1.00 trypomastigotes per 100 red blood cells. Only three trypomastigotes were found in the infected *N. rufus*, even after the entire smear was re-examined. The trypomastigotes found in *N. rufus* were smaller (mean 22 µm) than those found in *R. rattus* (mean 24 µm). The means of trypomastigotes from both host species fall within the range of *T. lewisi* (Kreier and Baker 1987). The location of the kinetoplast and the length of the free flagellum of trypomastigotes from *N.rufus* differed from those found in *R. rattus*. The infected *N. rufus* was caught in the pristine forest of Vatoharanana.

Table 1. Trypanosome infections in *Rattus rattus*, *Mus musculus* and endemic rodents in the Ranomafana National Park in south-eastern Madagascar in 1998–2000 (+ = number of infected; N = number examined;% = prevalence).

Host species	Year	Pristine forest		Disturbed forest		Total	
		+ / N	%	+ / N	%	+ / N	%
Rattus rattus (N = 92)	1998	1 / 1	100	5 / 22	23	6 / 23	26
	1999	1 / 6	16	23 / 48	48	24/ 54	44
	2000	0 / 1	0	7 / 14	50	7 / 15	47
Mus musculus (N = 5)	1998	0 / 0	–	0 / 2	0	0 / 2	0
	1999	0 / 0	–	0 / 3	0	0 / 3	0
	2000	0 / 0	–	0 / 0	–	0 / 0	–
Nesomys rufus (N = 44)	1998	0 / 9	0	0 / 9	0	0 / 18	0
	1999	1 / 13	8	0 / 3	0	1 / 16	6
	2000	0 / 10	0	0 / 0	–	0 / 10	0
Nesomys audeberti (N = 29)	1998	0 / 0	–	0 / 6	0	0 / 6	0
	1999	0 / 0	–	0 / 17	0	0 / 17	0
	2000	0 / 2	0	0 / 4	0	0 / 6	0
Eliurus tanala (N = 49)	1998	0 / 3	0	0 / 4	0	0 / 7	0
	1999	0 / 12	0	0 / 21	0	0 / 33	0
	2000	0 / 3	0	0 / 6	0	0 / 9	0
Eliurus webbi (N = 9)	1998	0 / 0	–	0 / 0	–	0 / 0	–
	1999	0 / 1	0	0 / 6	0	0 / 7	0
	2000	0 / 1	0	0 / 1	0	0 / 2	0
Eliurus minor (N = 3)	1998	0 / 0	–	0 / 0	–	0 / 0	–
	1999	0 / 0	–	0 / 2	0	0 / 2	0
	2000	0 / 0	–	0 / 1	0	0 / 1	0
Gymnuromys roberti (N = 2)	1998	0 / 0	–	0 / 0	–	0 / 0	–
	1999	0 / 0	–	0 / 2	0	0 / 2	0
	2000	0 / 0	–	0 / 0	–	0 / 0	–

Although *T. lewisi* was commonly found in *R. rattus*, the parasite was not detected in native rodents either in disturbed or in pristine forests. It should be noted also that native rodents from pristine forests may have been in contact with *R. rattus*. Since hardly anything is known about the microscopic endoparasites of native Malagasy mammals (Laakkonen and Goodman 2002), and only a few parasite organisms were found in the infected *N. rufus*, replicate studies from areas with long-term presence of *R. rattus* in pristine areas are warranted to determine the origin and nature of the trypanosome infection found in *N. rufus* in this study. Besides quantitative morphological and genetic analyses of the trypanosomes from different host species, information on flea species acting as vectors of trypanosomes is needed to further assess the ability of *T. lewisi* to infect native Malagasy rodents.

Whether the lack of *T. lewisi*-like trypomastigotes in native rodents is due to a lethality effect in naïve hosts cannot be determined on the basis of the present study. However, we saw no significant decrease in numbers of native rodents, or clinically ill animals that would indicate mass mortality either in pristine or disturbed sites.

The lack of age effect (see above) indicated that *R. rattus* of all ages were exposed to infection. This was somewhat surprising, considering the strong acquired immunity associated with related trypanosomes (Albright and Albright 1991). We do not know enough about *T. lewisi* infection in wild rats (Kreier and Baker 1987) to assess possible differences in the nature of *T. lewisi* infection between different (island) populations of *R. rattus*.

Conclusion

In contrast to the disappearance of the native rodent within a few years after the invasion of Christmas Island by trypanosome-infected *R. rattus* (Pickering and Norris 1996), the invasion of the pristine forests of RNP by infected rats did not cause the rapid disappearance of native rodents. The effect of *T. lewisi* may be more significant within the genus *Rattus* than in other rodent groups. Comparative studies from other *Rattus* species are warranted to test this hypothesis. We are presently doing replicate studies (of the one reported in this paper) in other Malagasy sites in order to determine the effect of the site on the prevalence and diversity of *Trypanosoma* spp. in *R. rattus* and in the native rodents. Finally, it should be noted that other concurrent infections may affect the susceptibility and the outcome of trypanosome infections in both *R. rattus* and the native rodents.

Acknowledgments

This research was facilitated by the Association Nationale pour la Gestation des Aires Protégées (ANGAP). We are grateful to members of MICET and RNP for assistance with logistics and research permits. We thank J. Rakotoniana, V. Rasataharilala and F. Zakamanana for field assistance, and H. Leirs and D. Spratt for valuable comments during revision of the manuscript. This research was funded by the Academy of Finland (JL, # 43542), Finnish Cultural Foundation and the University of Helsinki (JTL).

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Characterisation of *Leptospira* isolates from captive giant African pouched rats, *Cricetomys gambianus*

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Abstract. In an ongoing study to determine the potential of the giant African pouched rat, *Cricetomys gambianus*, as a biodetector of antipersonnel landmines, *Leptospira interrogans* 'sensu lato' was isolated from 8 of 83 (9.6%) newly captured *C. gambianus* from suburban Morogoro, Tanzania. Two of the *Leptospira* isolates (designated Sh9 and Sh25) were characterised by the microscopic agglutination test (MAT) using rabbit antisera and monoclonal antibodies. The isolates were found to be related to serovar kenya of the Ballum serogroup. Further characterisation by cross-agglutination absorption test (CAAT) and polymerase chain reaction (PCR) fingerprinting is in progress.

This first report on isolation of leptospires from *C. gambianus* in Tanzania serves as caution to researchers on the risk of leptospiral infection when handling newly captured rats for breeding or training purposes. It is recommended that newly captured *Cricetomys* rats be screened for pathogens before they are admitted into breeding or research programs.

Introduction

Leptospirosis is a zoonosis distributed worldwide and is caused by a spirochete, *Leptospira interrogans* sensu lato. *Leptospirosis* is, however, not well studied in Tanzania (Feresu 1990; Machang'u et al. 1997). Rodents are the most commonly affected animals, and are the natural reservoirs of this microorganism (Thierman 1984; Everard 1992).

Humans acquire leptospirosis through direct or indirect contact with the urine or blood of infected rats. Leptospirosis may present as a hyper-acute fatal disease, but in most cases it manifests as a mild febrile condition ('pyrexia of unknown origin') and is therefore difficult to diagnose (Terpstra 1992). In any event, leptospirosis assumes an occupational disease status and persons who handle wild rodents as pests, food, or experimental animals may be at a high risk of infection.

The microscopic agglutination test (MAT) is the standard test for serodiagnosis of leptospirosis and characterisation of *Leptospira* in epidemiological studies (Cole et al. 1973). Other methods used include enzyme-linked immunosorbent assay (ELISA) (Terpstra et al. 1985), indirect fluorescent antibody test (IFAT), cross-agglutination absorption test (CAAT) and polymerase chain reaction (PCR) (Merien et al. 1992; Gravekamp et al. 1993; Zuerner and Bolin 1995; Hartskeerl et al. 2000).

This study reports on the characterisation of *Leptospira* isolates from urine samples of newly captured *Cricetomys gambianus* in Morogoro, Tanzania, as part of an ongoing, pioneer study aimed at exploring the potential of this rat as a biodetector of antipersonnel landmines.

Materials and methods

Isolation of leptospires from urine samples

Urine samples (1 mL) from the bladders of freshly dissected *Cricetomys* rats ($n = 83$) captured from suburban Morogoro, Tanzania, were inoculated into 5 mL of Fletcher semi-solid *Leptospira* medium (Hartskeerl et al. 2000) and incubated for 56 days at ambient temperature (25–30°C). Cultures were examined at 7-day intervals by dark-field microscopy for growth of *Leptospira*. *Leptospira*-positive cultures were subsequently subcultured in Ellinghausen-McCullough Johnson-Harris (EMJH) liquid medium, supplemented with 5-fluorouracil (200 µg/mL medium)(Johnson and Rogers 1964).

Determination of pathogenicity status of isolates

The isolates were initially assessed for pathogenicity by inoculating them in EMJH medium at 13°C and 30°C (Johnson and Rogers 1964). Subsequently, the isolates were grown in EMJH medium with and without 8-azaguanine at 30°C for 56 days. Pathogenic leptospires do not grow well at 13°C or in media containing 8-azaguanine (Johnson and Harris 1967). Growth was determined by dark-field microscopy according to Cole et al. (1973). Following the pathogenicity assessment, two isolates (designated Sh9 and Sh25) were further characterised.

Characterisation at the serogroup level

The microscopic agglutination test (MAT) was performed as described by Cole et al. (1973) using isolates Sh9 and Sh25 as test antigens against a battery of 42 reference rabbit antisera (antibody source), representative of all known serogroups (Hartskeerl et al. 2000).

Cross agglutination (MAT) was determined to establish the relationship between the isolates (Sh9 and Sh25) and serovars of Ballum group by comparing homologous and heterologous agglutination titres, i.e. agglutination of the reference rabbit antisera with homologous reference serovars of the Ballum group, and with the isolates, respectively. In all cases, only agglutination titres ≥ 1:160 were considered positive.

Further characterisation using monoclonal antibodies

Isolates Sh9 and Sh25 were further analysed by MAT using monoclonal antibodies (in brackets) specific for serovars belonging to selected three serogroups namely: Ballum (F74 C1-6, F74 C4-4, F74 C7 -3, F74 C2-2), Javanica (F12 C3-10, F20 C3, F20 C4-1, F70 C20-3, F98 C4-3, F98 C5-1, F98 C8-1, F98 C12-2, F98 C17-2, F98 C19-3, F98 C20-2) and Ranarum (F152 C1-1, F152 C2-1, F152 C5-3, F152 C7-3, F152 C8-3, F152 C10-1, F152 C11-1, F152 C13-1, F152 C14-3, F152 C17-3, F152 C18-3) as described by Terpstra et al. 1985.

Results and discussion

Isolation, pathogenicity and serogrouping

Leptospires were obtained from 8 of 83 (9.6%) urine samples examined. Two of the isolates (Sh9 and Sh25) were subjected to serological typing. Neither isolate grew at 13°C nor in media containing 8-azaguanine, suggesting that they are pathogenic. The MAT titres of the Sh9 and Sh25 isolates against 42 reference rabbit antisera representative for all known serogroups showed that both isolates belong to serogroup Ballum with some cross-reaction to serogroups Javanica and Ranarum (Table 1).

Table 1. Microscopic agglutination test (MAT) assay of isolate Sh25 with rabbit antisera raised against reference antigens (serogroups) of *Leptospira interrogans* ‘sensu lato’ (serogroups with no agglutination titres not shown). MAT titres of isolate Sh9 (not shown) were the same as for the Sh25 isolate.

Serogroup	Serovar	Strain	Sh25 isolate
Ballum	kenya	Njenga	>1:1280
Ballum	ballum	Mus 127	1:1280
Javanica	poi	Poi	1:320
Ranarum	ranarum	ICF	1:320

Agglutination with rabbit antisera for serovars of selected serogroups

In MATs with rabbit antisera against serovars of selected serogroups (Ballum, Javanica and Ranarum), the two isolates gave highest titres with antisera for serovars kenya (1:2560), peru (1:320), ballum (1:320) and arborea (1:160) of the Ballum serogroup; serovars dehong (1:2560), mengma (1:640), sorexjalna (1:640), sofia (1:640), vargonicas (1:640) and yaan (1:640) of the Javanica serogroup; and serovar ranarum (1:320) of the Ranarum serogroup. This suggested that isolates Sh9 and Sh25 are serologically related, and most likely belong to serovar kenya.

Cross-agglutination of Sh9 and Sh25 with serovars of the Ballum group

Cross-agglutination assays of isolates Sh9 and Sh25 with antisera of the Ballum group (serovars: arborea, ballum, kenya and peru) gave comparatively similar titres to those obtained when these Ballum serovars were reacted with their homologous antisera, with the exception of serovar arborea (cross-agglutination less than 10%). These results show that isolates Sh9 and Sh25 are closely related to serovars kenya, peru and ballum but not arborea (Table 2).

Table 2. Microscopic agglutination tests with homologous and heterologous rabbit antisera for serovars of serogroup Ballum and isolate Sh25 (cross-agglutination assay). Results of Sh9 isolate (not shown) were the same as for the Sh25 isolate.

Rabbit antiserum against serovar	Homologous titre with reference serovars	Heterologous titre with the isolates	Cross-agglutination (%)
arborea	1:2560	1:160	6.2
ballum	1:640	1:320	50
kenya	1:5120	1:2560	50
peru	1:1280	1:320	25

Characterisation by monoclonal antibodies

MATs of Sh9 and Sh25 with the panel of monoclonal antibodies specific for different serovars within each of the three closely related groups (Ballum, Javanica and Ranarum) gave no agglutination. This situation is characteristic with serovars kenya and peru, again indicating their close relatedness with Sh9 and Sh25 (R.A. Hartskeerl, pers. comm., 2000).

The MAT is the ‘gold standard’ assay for serological diagnosis and characterisation of leptospires in epidemiological studies (Wolf 1954). In this study, MATs with rabbit antisera and monoclonal antibodies suggest that the two Morogoro *Leptospira* isolates (Sh9 and Sh25) are similar. This is plausible, also because the *C. gambianus* rats were captured from neighbouring suburbs of Morogoro. Our findings further suggest that isolates Sh9 and Sh25 are closely related to serovars kenya and peru, and strains Njenga and MW10, respectively. This is based on the observation that the polyclonal antisera for the former gave the highest MAT titres (1:2560 and 1:320, respectively), and these were comparable to those obtained with their homologous antigens. Strain Njenga was first reported in *Cricetomys* rats in neighbouring Kenya (Kranendonk et al. 1968; Forrestier at al. 1969).

Isolates Sh9 and Sh25 gave no agglutination with panels of monoclonal antibodies for the serovars of Ballum, Javanica and Ranarum groups, which is a common feature for serovars kenya and peru (R.A. Hartskeerl, pers. comm.). This observation further supports the similarity of Sh9 and Sh25 to the serovars kenya and peru. Ongoing studies (CAAT and PCR) will provide the definitive characterisation of Sh9 and Sh25 in terms of serovar(s) and strains.

Our findings support the existence of this serovar (serogroup Ballum) in rats in the East African region. Although the definitive prevalence of the leptospires in *Cricetomys* rats is yet to be established (for our case, 9.6%), it can be presumed that the *Cricetomys* rats are potential carriers of the serovar kenya in Morogoro.

Rats, including *Cricetomys*, are known to be reservoirs of leptospires, but they rarely show clinical disease in their natural environments (Kranendonk et al. 1968). It is yet to be established whether captive *Cricetomys* rats develop clinical disease. Therefore, apparently healthy *Cricetomys* could be carriers and hence readily transmit leptospirosis to unsuspecting humans.

Researchers working with *C. gambianus* therefore should be cautious, especially when dealing with rats recently captured from the wild. It is recommended that all newly captured *Cricetomys* rats initially be kept in isolation and screened for leptospires. Rats that test positive should receive appropriate antibiotic treatment, or eventually be vaccinated, before they are admitted for breeding or for landmine detection studies. If this is done, the health of the handlers would be protected, and it will ensure a healthy colony of rats for breeding and training purposes.

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Potential of *Trypanosoma evansi* as a biocide of rodent pests

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Abstract. *Trypanosoma evansi* is highly pathogenic to all laboratory animals in which an acute phase of infection occurs with regular peaks of parasitaemia. Present studies were carried out to assess the potential of *T. evansi* as a biocide of rodent pests by experimentally infecting the lesser bandicoot rat, *Bandicota bengalensis*, and the house rat, *Rattus rattus*, which are the predominant rodent pests in agricultural and commensal habitats in India. Both species of rats were inoculated by intraperitoneal injection of purified *T. evansi*, originally isolated from a naturally-infected buffalo and maintained in Swiss albino mice by serial syringe passages. Infection proved fatal to all rats. The course of *T. evansi* infection in both *B. bengalensis* and *R. rattus* showed two peaks of parasitaemia with a period of intermission. No rat survived after the second peak of parasitaemia. Before death, rats showed depressed behaviour with posterior paralysis. Impression smears from various organs revealed the presence of a few trypanosomes in the spleen, brain and testes/uterus and moderate to large numbers in the lungs, kidneys, heart and liver. Smears of cauda epididymal fluid of all *T. evansi* infected rats and mice revealed equivalent numbers of *T. evansi* and spermatozoa, indicating the possibility of sexual transmission of trypanosomes. Post-mortem examination of *T. evansi* infected pregnant females of *B. bengalensis* revealed the presence of mummified foetuses in the uterus, indicating a foeticidal effect of *T. evansi*. There is a need for further detailed study to open up this new research area on biocontrol of rodents. Humans are naturally immune to *T. evansi* infection and also its transmission from infected rats to other mammals is less probable because the tabanid fly vectors do not feed on rats. The present studies thus suggest the potential of *T. evansi* as a biocide of rodent pests.

Introduction

Trypanosomiasis or surra, a haemoprotozoan disease recorded in all the principal species of domestic animals (Gill 1991), is caused by *Trypanosoma evansi* (Steel 1985) Balbiani 1988, the first pathogenic trypanosome recognised by Evans in 1880 from the blood of Indian horses and camels suffering from surra. The disease is transmitted mechanically through the bite of flies, most commonly *Tabanus* spp. It has been confirmed that *T. evansi* is highly pathogenic to all laboratory animals (Patel et al. 1982). The parasite undergoes an acute phase in these animals with regular peaks of parasitaemia. Infection follows different courses in different animals depending mainly upon their innate susceptibility or resistance to *T. evansi* (Gill 1991). Present studies were carried out to assess the potential of *T. evansi* as a biocide of rodent pests by experimentally infecting the lesser bandicoot rat, *Bandicota bengalensis*, and the house rat, *Rattus rattus*, which are the predominant rodent pests in agricultural and commensal habitats in India (Parshad 1999).

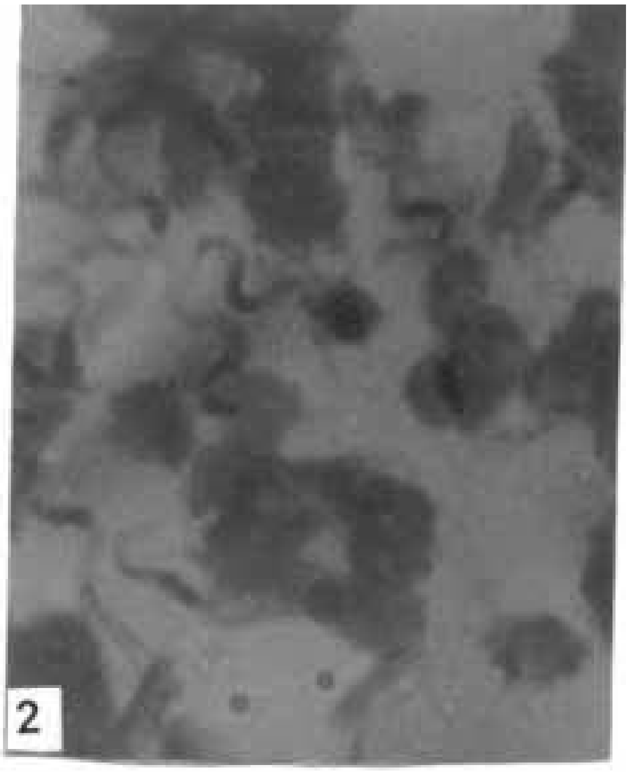
Materials and methods

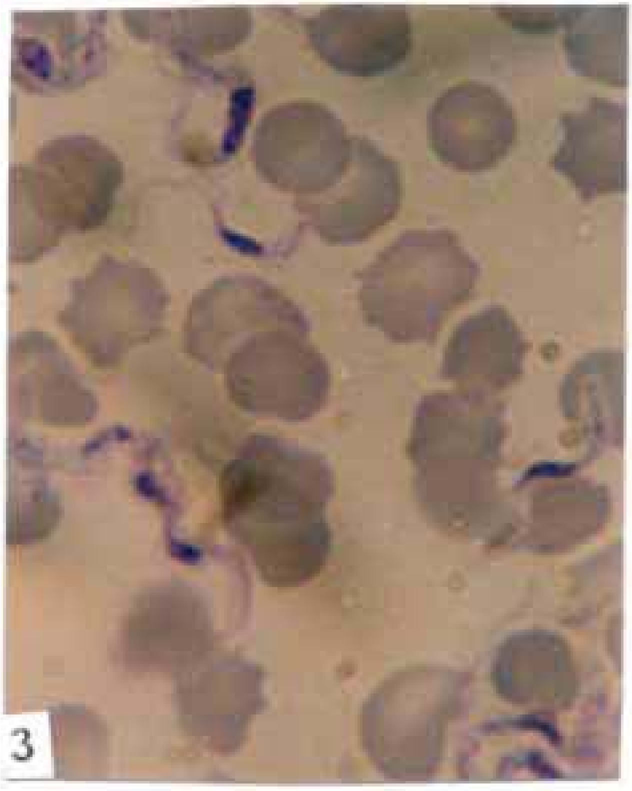
Isolation of *T. evansi*

The strain of *T. evansi* was isolated from a naturally-infected buffalo and maintained in adult Swiss albino mice by regular serial syringe passages at 48–72 h intervals in the laboratory. For the purpose of inoculation, *T. evansi* parasites were purified (Figure 1) from infected blood of mice by diethyl amino ethylene (DEAE) cellulose, diluted with Alsever’s solution and were counted on a Neubeaur’s Chamber, according to the method of Lanham and Godfrey (1970).

Experimental infection

Adult rats of *Bandicota bengalensis* and *Rattus rattus* were live-trapped from crop fields and poultry farms, respectively. All the rats were apparently in good health. Before experimentation, each rat was sexed and examined for the presence of any haemoprotozoan infection by thin Giemsa-stained blood-smear examination from tail blood, three times at weekly intervals.





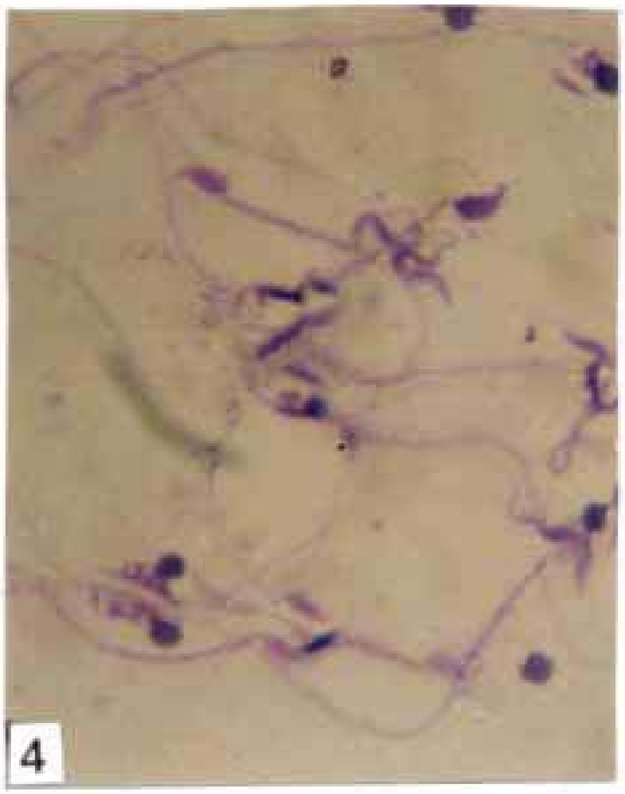


Figure 1. Purified *Trypanosoma evansi* used for inoculation of experimental rats (×200).

Figure 2. Impression smear of liver of *Bandicota bengalensis* infected with *Trypanosoma evansi* (×500).

Figure 3. Impression smear of heart of *Bandicota bengalensis* infected with *Trypanosoma evansi* (×500).

Figure 4. Smear of cauda epididymal fluid of Swiss albino mice infected with *Trypanosoma evansi* (×200).

Clean rats, free from infection (37 *B. bengalensis* and 14 *R. rattus*), were kept individually in cages for acclimatisation to laboratory conditions for 10–15 days with food (cracked wheat, powdered sugar and groundnut oil in a ratio of 96:2:2) and water provided *ad libitum*. After the period of acclimatisation, all the rats were inoculated by intraperitoneal injection of 0.5 mL of Alsever's solution containing 1×10^5 trypanosomes/mL.

Anti-mortem examination

Tail blood of inoculated rats was examined daily by the wet blood film method (Gill 1991) to observe the first appearance of *T. evansi* in peripheral blood and its further course of infection. Rats were also regularly observed for any mortality, changes in their behaviour and other clinical signs.

Post-mortem examination

Post-mortem examination of *B. bengalensis* and *R. rattus* was carried out immediately after the death of rats. Wet blood films from heart were examined for the presence of *T. evansi*. The liver, lungs, kidneys, heart, spleen, brain and testes/uterus were examined for gross morphological changes and impression smears were prepared from these organs, stained with Giemsa and examined for the presence and concentration of trypanosomes. Cauda epididymides of male rats were dissected out, incised and pressed in 0.5 ml of 0.9% saline solution pre-incubated at 37°C for 5 minutes, to obtain the cauda epididymal fluid. Smears of this fluid were prepared, stained with Giemsa and examined for the presence of *T. evansi*. Similar post-mortem examinations were also carried out in Swiss albino mice kept for maintaining the strain of *T. evansi*. Some of the rats and mice were also killed at the height of parasitaemia before death due to infection, to examine the site of multiplication of the parasite during the paroxysmal phase of infection, i.e. when the parasite is present in peripheral blood.

Results and discussion

Anti-mortem examination

Trypanosomes first appeared in the peripheral blood circulation of Swiss albino mice at 96 hours and mice survived for 6 days. In mouse-to-mouse passage, the parasites appeared in peripheral blood within 2–3 days of inoculation. The survival time varied from 4–7 days after inoculation. The parasitaemia was progressively fatal resulting in the death of mice at its first peak (Table 1).

The course of *T. evansi* infection in both *B. bengalensis* and *R. rattus* was found to be a little longer than in Swiss albino mice. The infection proved fatal for all the rats except those killed before death due to infection. In *B. bengalensis*, trypanosomes first appeared in peripheral blood within 4–5 days of inoculation. Thereafter, parasite numbers increased and reached the first peak of parasitaemia within 6–11 days of inoculation. Nearly 40% of the infected bandicoot rats died within 1 or 2 days of the first peak of parasitaemia. In the remaining bandicoot rats, however, the trypanosomes disappeared from the peripheral blood for 2–4 days. Thereafter a relapse in parasitaemia occurred resulting in a second peak of parasitaemia within 13–22 days of inoculation, after which no bandicoot survived (Table 1). Misra (1980) reported the death of all *B. bengalensis* inoculated with *T. evansi* immediately after the first peak of parasitaemia, which was observed on the sixth or seventh day of infection. In *T. evansi* infected *B. indica*, he reported the death of rats after the second peak of parasitaemia which was observed on the 13th or 14th day of infection. Dipeolu et al. (1981, cited in Gill 1991) infected African giant rats, *Cricetomys gambianus*, with *T. evansi* and observed parasites in peripheral blood 6 days after inoculation.

In *R. rattus*, trypanosomes first appeared in the peripheral blood 4–6 days after inoculation and reached the first peak of parasitaemia within 6–12 days of inoculation. About 64% of house rats died within 1 or 2 days of the

Table 1. Course of *Trypanosoma evansi* infection in *Bandicota bengalensis*, *Rattus rattus* and Swiss albino mice (n = number in sample, sd = standard deviation).

Experimental animals	Days after inoculation, mean ± sd (range)			
	First appearance	First peak	Second peak	Death
B. bengalensis ($n = 37$)	4.67 ± 0.47 (4–5)	7.81 ± 1.24 (6–11)	16.64 ± 3.05 (12–22)($n = 22$)	9.0 ± 1.60 (6–11)($n = 15$)[a]
				18.14 ± 3.37 (12–23)($n = 22$)[b]
R. rattus ($n = 14$)	4.93 ± 0.73 (4–6)	7.36 ± 1.60 (5–9)	14.20 ± 2.59 (11–17)($n = 5$)	8.22 ± 1.79 (6–11)($n = 9$)[a]
				15.40 ± 2.88 (12–19)($n = 5$)[b]
Swiss albino mice ($n = 12$)	2.50 ± 0.52 (2–3)	4.83 ± 0.83 (4–6)	–	5.50 ± 1.09 (4–7)($n = 12$)[a]

[a] Rats/mice died after first peak of parasitaemia.

[b] Rats died after second peak of parasitaemia.

first peak of parasitaemia. In the remaining rats, trypanosomes disappeared from the peripheral blood circulation for 2–3 days. A relapse in parasitaemia occurred, resulting in a second peak of parasitaemia within 13–18 days of inoculation, after which no rat survived (Table 1).

After the first peak of parasitaemia, rats of both the above species were found weak and sluggish but became somewhat active after the disappearance of the parasite from peripheral circulation. Rats did not show any nervous signs until shortly before death when depressed behaviour was observed and posterior paralysis led to difficulty in walking.

Post-mortem examination

Post-mortem examination immediately after the death or killing of animals revealed the presence of *T. evansi* in heart blood. No gross morphological changes were observed in organs except the enlargement of spleen and atrophy of testes. Impression smears of the liver (Figure 2), lungs, heart (Figure 3), kidneys, spleen, brain and testes/uterus contained trypanosomes. The concentration of trypanosomes was, however, found to vary from organ to organ. Depending upon the number of trypanosomes/field, the impression smears were graded as having few (<5), moderate (5–10) or large (>10) numbers of trypanosomes. Few trypanosomes were observed in the impression smears of the spleen, brain and testes/uterus and moderate to large numbers were observed in the lungs, kidneys, heart and liver. Raisinghani et al. (1997) also observed very few trypanosomes in the impression smears of the spleen and brain and moderate to large numbers in the liver, lungs, heart and kidneys during the paroxysmal phase of *T. evansi* infection in albino rats. Singla et al. (2001) found trypanosomes in interstitial spaces and blood vessels of Giemsa-stained tissue sections of all the above organs of *T. evansi* infected albino mice.

Examination of Giemsa-stained smears of cauda epididymal fluid of male *B. bengalensis*, *R. rattus* and albino mice prepared after death revealed the presence of large numbers of *T. evansi* equivalent to numbers of spermatozoa (Figure 4) indicating the possibility of sexual transmission of trypanosomes. However, there is a further need to evaluate this process by releasing *T. evansi* infected males with untreated females or by artificially inseminating the females with cauda epididymal fluid containing *T. evansi*. Vrijburg (1900, cited in Gill 1991) was successful in infecting a mare by rubbing urethral secretion of a surra-affected stallion into the vaginal mucosa.

Of the bandicoot rats inoculated with *T. evansi*, eight were field-captured, pregnant females. Post-mortem examination of these pregnant females carried out both after and before death due to infection revealed the presence of mummified foetuses in the uterus, indicating the foeticidal effect of *T. evansi*. Kraneveld and Mansjoer (1954, cited in Gill 1991) examined five surra-affected mares 2–3 weeks after the infection and found mummified foetuses in all of them. They experimentally infected pregnant bitches and guinea pigs with *T. evansi* and established the possibility of transplacental infection of surra in dogs and guinea pigs. However, their similar experiments in rabbits and rats failed. Pathak and Kapoor (1999) reported foetal abortion in a donkey mare naturally infected with *T. evansi*. There is no satisfactory explanation available as to the mechanism by which trypanosomes cross the placenta. Misra (1980), however, reported failure of *T. evansi* to invade the placental barrier of *B. bengalensis*.

Conclusions

The present studies suggest the potential of *T. evansi* as a biocide of rodent pests. The presence of *T. evansi* in large numbers in the cauda epididymal fluid of infected male rats and mice indicates the possibility of sexual transmission of *T. evansi*. Presence of mummified foetuses in the uterus of pregnant females before the death of the mother indicates the foeticidal effect of *T. evansi* infection. However, there is a need to study these aspects in detail to open a new line on biological control of rodent pests.

Regarding safety, it can be said that humans are naturally immune to *T. evansi* infection as the human serum has a trypanocidal property (Gill 1991). Also, in nature, the tabanid fly vectors of *T. evansi* do not feed on rats (Misra 1980) and direct blood contamination between rats and other mammals is not common. So the transmission of this haemoflagellate from infected rats to other mammals is improbable.

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A retrospective analysis of a vole population decline in western Oregon, USA

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Abstract. Gray-tailed voles, *Microtus canicaudus*, in western Oregon followed typical annual demographic patterns for 7 years, then drastically declined in numbers in the spring through autumn 1999. The decline occurred throughout the Willamette Valley of western Oregon in naturally occurring populations and in enclosed experimental populations. We use data from field surveys, an open-field study, and results from 8 years of experimental research in our enclosures to address alternative hypotheses that could explain the decline. Our conclusions do not support food, predator, or self-regulation hypotheses. The wide-scale and rapid population decline is consistent with a disease epizootic and its characteristics were similar to those associated with a tularemia outbreak during a vole decline in 1958.

Introduction

The most credible hypotheses to explain rapid declines in rodent populations are food limitation, predation, self-regulation, and disease (Batzli 1992; Krebs 1996). Theoretical arguments have been presented for all of these hypotheses, however empirical evidence is lacking or equivocal for most of them. Since 1991, we have studied the population and behavioural ecology of the gray-tailed vole, *Microtus canicaudus*, in the Willamette Valley, Oregon. Most of our work has been with experimental populations enclosed in 0.2 ha fenced enclosures (e.g. Edge et al. 1996), though we also studied voles on open trapping grids (e.g. Wolff et al. 1996). During the first 7 years of our studies, we saw no indication that gray-tailed voles 'cycled' or exhibited dramatic fluctuations in numbers. However, vole numbers were unusually high in 1998 and declined precipitously to low numbers in spring 1999 and remained low throughout summer and autumn. Populations in our semi-protected enclosures and in predator-proof pens also declined and remained low, as did wild populations. Herein, we test four hypotheses to explain this population decline (other hypotheses were also rejected but are not presented here).

Evidence for a peak population in 1998

Complaints of crop damage in 1998 provide evidence that vole numbers greatly exceeded levels of previous years. More than 80% of the mid-Willamette Valley has been converted to agriculture production, with grass grown for seed being the largest crop in terms of annual sales and area under production. During most years, crop damage by voles is minimal. However, during summer 1998, large numbers of producers reported vole damage in grass-seed fields with estimated losses often exceeding 25%. In 1998, grass-seed production was reduced by as much as 35% in research plots at sites not previously receiving vole damage.

Evidence for a population decline

Field sites

From 1991 to 1998 we typically captured several hundred voles from a 10 ha area of a large (>100 ha) grass-seed field 5 km south of Corvallis. Runways and burrow systems dominated the area with 3–15 entrance holes clustered in an area of about 1–2 m^2 and separated from the next cluster by about 7–10 m. We estimated about 5000 active burrow entrances/ha. We surveyed this same area in August 1999 and found only three active burrows per hectare of the same habitat. In 1998, 53 voles were captured in 450 trap-nights at a grassland site on a wildlife refuge—none were captured in 1999 following a similar trapping effort. In spring 1995, we collected about 300 voles from 0.5 ha, fenced, predator-proof pheasant pens and surrounding habitat at the E.E. Wilson Wildlife Area, 15 km north of Corvallis. In May 1999, we caught no voles in 600 trap-nights in these same pens. Numerous runways and burrow entrances were present, but a survey of this area in August 1999 revealed no active use of runway systems.

Enclosure site

Our research facility consists of 24 0.2-ha enclosures in a 4 × 6 array. In spring each year from 1992–1999, we trapped all voles in our enclosures and removed or added animals to start populations with about six males and six females/enclosure (slight variations occurred in some years). Voles were live-trapped in 81 to 100 Sherman live-traps at 2-week intervals until mid-September each year—details are described in Edge et al. (1996) and Wolff et al. (1997). Juvenile recruitment occurs about 5–6 weeks after animals are placed in the enclosures and peak population sizes are typically 60–100 animals/enclosure, except in 1999 when populations remained low throughout the summer (Table 1). Population growth rates for the first 6 weeks of recruitment were positive in all years except 1999. Similarly, vole survival and female reproductive rates were lower in 1999 than in previous years (Table 1). After initial introductions of 10 voles in late May, all voles disappeared from two enclosures by 30 July, something that had never happened in previous years. Vole populations remained low from May through the entire summer and into November in all enclosures. Thus, vole demography was similar from 1992–1998 with a drastic decline in most parameters in 1999.

Evaluation of hypotheses for population decline

Food limitation

The food-limitation hypothesis asserts that vegetation quantity or quality in the form of nutrients and/or plant secondary compounds are degraded at high densities causing populations to decline. There was no indication that food was limited in quantity or quality. The major crop in the Willamette Valley of western Oregon is grass seed of several species and varieties, which is optimal habitat for gray-tailed voles. New planting occurs on about a 3-year rotational basis depending on the species, so newly planted grass is always available. During the first 4 years of research, our enclosures were planted with alfalfa, and for the last 4 years with a mix of pasture grasses with some residual alfalfa. Vegetation is green throughout winter and rapid growth occurs from mid-April through late July. Green vegetation declines in late August and September, but some green material is available throughout the year. Also, vole numbers seem to have declined over much of the Willamette Valley and it is unlikely that a reduction in food could explain this wide-scale decline in vole numbers.

Predation

The predation hypothesis asserts that predators are directly responsible for high mortality causing populations to ‘crash’ from peak to low numbers. Terrestrial predators are uncommon at our Oregon site. During our 8-year study, we removed six short-tailed weasels, *Mustela erminea*, from our enclosures, and no more than two in any 1 year. Red foxes, *Vulpes vulpes*, and feral cats, *Felis catus*, are observed occasionally and a coyote, *Canis latrans*, was observed once. In 1999, we set three medium-size National live-traps around our enclosures and caught one striped skunk, *Mephitis mephitis*, one raccoon, *Procyon lotor*, and two feral cats (which were removed). No weasels were captured in 1999. We have no evidence that predation by terrestrial carnivores was any higher in 1999 than in any previous year.

The major avian predators in our area are American kestrels, *Falco sparverius*, northern harriers, *Circus*

Table 1. Demographic parameters (means[a]) for gray-tailed voles in four control enclosures at the Hyslop research facility from 1992–1999. Data other than maximum population size are from May through early July and represent the spring and early summer periods of most rapid population growth.

Parameter	1992	1993[b]	1994	1995	1996	1997	1998	1999
Maximum population size[c] (voles/enclosure)	86	64	100	34	91	67	122	15
Maximum population growth rate[d]	0.25	0.17	Not avail.	0.60	0.80	0.34	0.23	–0.13
Proportion of reproductively active females	0.80[e]	0.77	0.95	0.80	0.95	0.90	0.75	0.28
Recruits/female[f]	2.0	0.59	0.66	1.16	2.1	1.8	2.5	1.66
Male survival rate[g]	0.89	0.84	0.96	0.71	0.89	0.89	0.64	0.47
Female survival rate	0.91	0.84	0.96	0.71	0.90	0.93	0.87	0.48

[a] Annual data sources: Edge et al. (1996); Wolff et al. (1997); Wang et al. (2001).

[b] Population size was controlled at 30 voles/enclosure through early July 1993.

[c] Maximum population size is the highest population estimate (based on CAPTURE) in a given year which usually occurs in mid August.

[d] Population growth rate was calculated by log (MNA_{i+1}) – log (MNA_i), where: MNA = minimum number alive; i = initial population size.

[e] Reproductive rate from Edge et al. (1996) adjusted for methods used in 1993–1999.

[f] Recruits/female is the number of juveniles caught/number of reproductive females 4 weeks earlier.

[g] Survival rates were calculated as 2-week survival rates (Φ_i) by use of derivations of the Cormack-Jolly-Seber mark–recapture methodology.

cyaneus, and red-tailed hawks, *Buteo jamaicensis*, however they are present primarily during the winter and not spring or summer. In an experiment in which we erected perch sites in our enclosures from December 1997 through early March 1998, we recorded an 11-fold increase in kestrel visitation to the enclosures (Wolff et al. 1999). During 69 hours of observations, kestrels and harriers were at the enclosures 55% and 25% of the time, respectively. We detected no significant treatment effect on population size, growth rate, or survival of voles during this period. Vole populations increased from about 50 to 70 voles/enclosure during the study even with enhanced predation pressure. The vegetation height in our enclosures was about 30 cm throughout the winter and 60 cm during summer, making it difficult for avian predators to catch voles. Also, the total absence of voles inside the pheasant pens at the E.E. Wilson site in spring and summer 1999 suggests that predation was not causing the population decline. The pheasant pens exclude all predators except weasels and snakes, and no weasels were caught in that area at any time during a previous 2-year live-trapping study adjacent to the pens (Wolff et al. 1996).

Self-regulation

The self-regulation hypothesis asserts that some aspect of social interactions at high density causes behavioural stress, which ultimately affects reproduction, fecundity, and juvenile recruitment (Krebs 1978, 1996). In our 0.2 ha enclosures, vole populations typically peak at 60 to 100 voles/enclosure (300 to 500 voles/ha; Table 1) with little, if any, indication of density-dependent effects on reproduction or social spacing (see also Wolff, this volume). In one experiment in which we removed 70% of the vegetation, mean population densities in the remaining 30% of the habitat ranged from 1056 to 2880 voles/ha (Wolff et al. 1997). Female gray-tailed voles are territorial, but they were not able to defend space or prevent intrusion from animals immigrating from the areas where vegetation was removed. Even at the highest densities, 37–48% of females were reproducing and juvenile recruitment was 0.5 recruits/female (Wolff et al. 1997).

Disease

The impact of disease on rodent declines has not been well studied, but considerable data are available from an intensively studied population of montane voles, *Microtus montanus*, from Oregon during a peak population in 1957–58 that may be relevant to the 1999 decline of gray-tailed voles. In the winter of 1957–58, montane voles in the Pacific Northwest, and especially the Klammath Basin area of south-central Oregon exhibited the largest irruption of a vole population ever reported in North America (Vertrees 1961). The vole population peaked in November at estimates ranging from 500 to 10,000 voles/ha and as many as 75,000 burrow entrances and 370 nests/ha (Vertrees 1961). By March, voles had all but disappeared from the landscape. Overall, populations were estimated to have declined by >90% and pregnancy rates declined from 80% to near 0% from January to April.

Most deaths were associated with disease. Large numbers of undamaged vole carcasses were found lying on the ground, under hay piles, in drainage ditches, along roadways, and in open fields (Jellison et al. 1958, 1961). Laboratory tests showed that dead voles were infected with the bacterium *Pasteurella tularensis* that causes tularemia. In additional samples from other areas, 30–40% of voles were infected with tularemia. Approximately 30% of voles brought into the laboratory died within 25 days—all were infected with tularemia. Infection rates increased in one wild population from 14% to 39% from the beginning to the end of December suggesting that the disease could have been transmitted at a high rate. In samples from throughout the irruption area, *P. tularensis* was isolated from 28 of 30 voles near Klammath Lake, and 66 of 89 and 54 of 56 from other areas of southern Oregon (Jellison et al. 1961). Infection rates of about 40% persisted through February and March and by spring and summer, all tests were negative. By summer, vole populations in fields that had been associated with tularemia epizootics were at a subnormal level (Kartman et al. 1961).

The decline of gray-tailed voles in western Oregon exhibited signs similar to those reported for the decline of montane voles in 1958. The 1999 decline was associated with a record rainfall in December–February that raised the level of the watertable, filling drainage and irrigation ditches and flooding much of vole habitat. The Willamette Valley is flat and during heavy rains, thousands of hectares of agricultural and vole habitat are flooded and interconnected by waterways that could distribute waterborne pathogens rapidly over large areas. Pathogens in the 1957–58 vole decline were transmitted in water. Water readily flows through and among our enclosures via a tile line that runs underground through the middle of our enclosure facility. In 1999, 19 of our 24 enclosures contained standing water. Interestingly, rainfall during the 1957–58 epidemic and vole decline was 2.1 times higher than average, similar to that in our vole decline in 1999. However, rainfall in itself does not appear sufficient to cause vole declines, in that winter rainfall in 1995 was 1.6 times greater than average and in 1996 it was 2.3 times greater than average with no measurable effect on vole dynamics. Average daily minimum temperatures were comparable for all months from 1991–1999 (unpublished data) so it is unlikely that weather directly caused the vole decline. The characteristics of the decline in 1999 are similar to those of 1958 in which a rapidly transmitted pathogen, tularemia, was associated with vole deaths. Although tularemia may be the pathogen that contributed to the vole decline, other pathogens should not be discounted (H. Henttonen, pers. comm.).

Conclusions

Gray-tailed vole numbers in western Oregon declined precipitously in open-field and protected, enclosed populations in spring 1999. We were not able to obtain data to discern among the standard alternative hypotheses for population declines in voles experimentally, rather we used indirect evidence from 8 years of research to address each hypothesis. The food limitation, predation, and self-regulation hypotheses were not supported by results from open-field data, previous experimental studies of enclosed populations, and several lines of indirect evidence (additional hypotheses such as senescence and kin selection were also rejected but not discussed here). Although we have no data on vole diseases associated with this decline, the wide scale and rapid decline followed by low survival through summer and into autumn are consistent with an epidemic, rapidly transmitted disease. Characteristics of the decline are similar to those of a 1958 decline of montane voles in south-central Oregon that was associated with an epizootic outbreak of tularemia. Based on the data currently available, the disease hypothesis is a plausible explanation for the decline of voles in western Oregon and should elicit future research.

Acknowledgments

Our studies of voles in the Willamette Valley were supported by the United States Environmental Protection Agency and the National Science Foundation. Numerous field assistants and several graduate students assisted with data collection for these studies. L. Hansson, H. Henttonen, T. Manning, L. Hinds, G. Singleton, H. Leirs, and B.J. Verts provided helpful comments on an earlier draft of this manuscript. This is manuscript 11,664 of the Oregon Agricultural Experiment Station.

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Pathogen study of house mice on islands reveals insights into viral persistence in isolated populations

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Abstract. Studies on island populations of house mice and their viruses can reveal insights into viral persistence in isolated communities, while allowing hypotheses to be developed with respect to local adaptation to insular environments. We compared the seroprevalence of antibodies to 14 murine viruses from house mice inhabiting three islands near Australia. House mice sampled from arid Thevenard Island were seropositive to only one virus, murine cytomegalovirus (MCMV), while mice on Boullanger Island were seropositive to two viruses—MCMV and epizootic diarrhoea of infant mice. On subantarctic Macquarie Island, house mice were seropositive for five viruses—MCMV, lymphocytic choriomeningitis virus, mouse parvovirus, epizootic diarrhoea of infant mice, and Theiler's murine encephalomyelitis virus. The diversity of antiviral antibodies is lower among populations of house mice on islands than those inhabiting mainland Australia. The diversity of viruses in island populations of house mice poses interesting questions about viral persistence in isolated and remote locations.

Introduction

The house mouse (*Mus domesticus* or *Mus musculus*) is well adapted to survival across a variety of islands worldwide, with populations extending from the northern Lofoten Islands and Iceland (Saemundsson 1939) to the southern islands of the subantarctic (Berry et al. 1978). Studies of these insular populations have investigated their genetic structure (Berry and Peters 1975), diet and food preferences (Copson 1986), population demographics and reproduction (Pye 1984), and parasites (Pisanu et al. 2001). There have been very few studies that have investigated the viruses that infect insular populations of house mice (Moro et al. 1999).

Past serosurveys of murine viruses on the Australian mainland have been conducted in the agricultural regions, where house mice were found to be seropositive to 8 of 14 viruses (Smith et al. 1993). Seroprevalence to some murine viruses, including mouse hepatitis virus, minute virus of mice, mouse adenovirus, and murine cytomegalovirus, was related to the density and breeding condition of house mice (Smith et al. 1993). Subsequent research on viral epidemiology has focused on house mice inhabiting these regions (Singleton et al. 2000), with investigations focusing on the reduction of population numbers by fertility control (Chambers et al. 1999; Singleton et al. 2002). Island populations of house mice that experience irregular or rare immigration events have been rarely studied.

Offshore or oceanic islands offer an experimental and natural geographical location to study viruses in populations of house mice. Island populations have been found to have few viral pathogens, partly because of the small number of founders that initiated the population, or the population has remained too low for the virus to be maintained (Dobson 1988). Furthermore, the isolation of islands often precludes viruses from entering the host population unless an infected host is introduced from elsewhere. Island populations may therefore harbour fewer viruses than non-island populations by virtue of their remoteness. For viral pathogens that occur in island environments, seroprevalence will reflect those viruses that are well adapted to persist (or remain latent and reactivate) at low host population densities (Black 1975).

In this review, we describe the incidence of antiviral antibodies of free-ranging house mice inhabiting islands off Australia, and compare their seroprevalence with those on mainland Australia to understand whether seroprevalence varies across geographically remote (island) populations of house mice.

Materials and methods

Study sites and species

House mice (*Mus domesticus*) were collected from three islands comprising geographical extremes (Figure 1):

Thevenard Island (21°28'S, 115°00'E), Boullanger Island (30°18'S, 115°02'E), and Macquarie Island (54°30'S, 158°57'E).

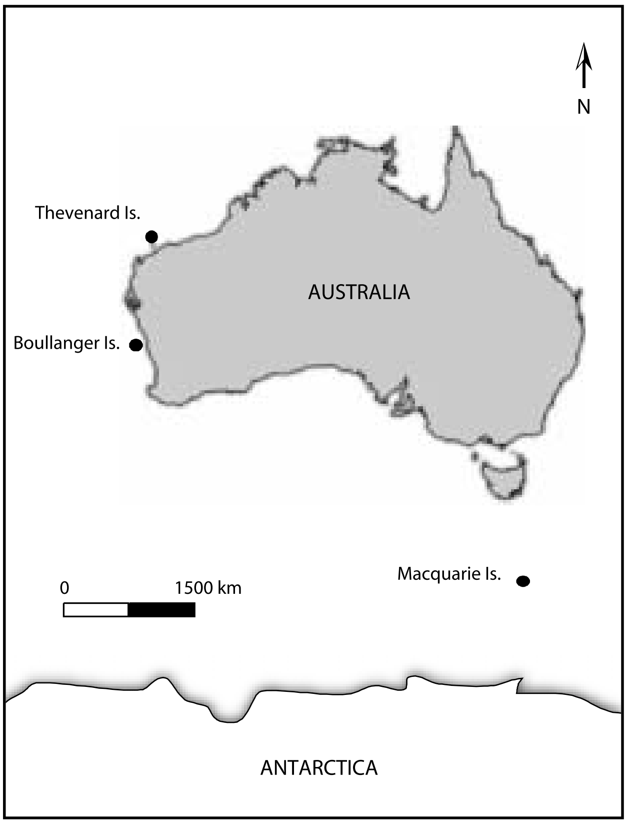

Figure 1. Location map showing sites where house mice were sampled for antiviral antibodies. Island sizes are not to scale.

Thevenard Island (550 ha) is a semi-arid sand cay situated 20 km offshore from mainland Australia. The region experiences an arid subtropical climate. Rainfall is seasonal, falling mostly between January and June, but is also influenced by tropical cyclones that pass through the area each year. Boullanger Island (25 ha) is also a semi-arid island situated 4 km offshore. The island occurs in a region that experiences cool wet winters and hot dry summers, with most rain falling between June and August. Both Thevenard Island and Boullanger Island have no areas where free water is available, except following rains. Macquarie Island (12,800 ha) is subantarctic and situated 1500 km south of Australia. The climate is cold and wet year round, with snow settling across the mid-year months.

House mice were introduced accidentally on Thevenard Island some time during the late 1980s following seismic operations from mining companies. No information is available to identify the introduction of house mice to Boullanger Island. House mice were first reported from Macquarie Island in 1890 (Cumpston 1968), though their introduction to the island could have been from shipwrecks as early as 1812, or with cargo and provisions by sealers using the island as a base for their activities (Cumpston 1968). Thevenard Island and Boullanger Island are nature reserves, and Macquarie Island is a listed World Heritage site. Quarantine measures on Thevenard Island and Macquarie Island are enforced by the agencies that function on these islands, so it can be assumed that further introductions of house mice were either rare or absent.

Serum collection and viral serology

House mice were captured using Elliott live-capture traps, and information on body mass, sex, age, and breeding condition were noted. Trapping occurred from 1994–1996 on Thevenard Island, once during 1998 and 2001 on Boullanger Island, and once during 2000 on Macquarie Island.

In a laboratory, approximately 240 µL of blood was drawn into heparinised, microhaematocrit tubes (Fortuna, Bildacker, Germany) from the infraorbital blood sinus of each mouse. Only adult mice were bled because of the volume of blood required for serum assays for viral antibodies. Blood samples were immediately centrifuged at 8000 rpm for 5 min. Blood haematocrit was measured for each individual sample, and the serum was separated into autoclaved microcentrifuge tubes that were sealed and frozen at –80°C. Tubes were transported in liquid nitrogen to laboratories in Western Australia for later analysis of viral antibodies.

Sera were primarily tested by enzyme-linked immunosorbent assay (ELISA) for antibody directed against the following 14 viruses: murine cytomegalovirus (MCMV), lymphocytic choriomeningitis virus (LCMV), mouse hepatitis virus (MHV), minute virus of mice and mouse parvovirus (combined test using recombinant antigen, PARV), pneumonia virus of mice (PVM), reovirus type 3 (REO), epizootic diarrhoea of infant mice (ROTA), sendai virus (SEND), vaccinia virus (ECT, used to test for ectromelia virus antibody), mouse adenovirus strains FL and K87 (MadV), encephalomyocarditis virus (EMCV) and Theiler’s murine encephalomyelitis virus (TMEV). ELISA procedures followed those of Lawson et al. (1988), with modifications described in Moro et al. (1999). Equivocal or suspect samples were re-tested by immunofluorescence assay (Smith et al. 1993).

Results and discussion

Of 14 antiviral antibodies surveyed, only antibodies to MCMV were detected in the sera of house mice from Thevenard Island (Table 1). On Boullanger Island, two antiviral antibodies were identified, MCMV and ROTA. On Macquarie Island, house mice were seroprevalent to five viruses, though only one individual of 92 sampled was seropositive for LCMV. Although sample sizes for house mice sampled from Boullanger Island and Macquarie Island are lower than those collected elsewhere, power analysis predicts that a minimum sample size of 25 house mice will provide a 95% probability of detecting at least one seropositive mouse in a population with an expected prevalence of 10% (Canon and Roe 1982). There were no statistical differences between seropositivity to any one virus and sex or breeding condition. TMEV was only recorded from Macquarie Island, and occurred in 50% of the sampled population. It is the only record of this murine virus from Australian territories. These results on island house mice are interesting when compared to the serologic surveys of house mice inhabiting Australia (Smith et al. 1993); seroprevalence was higher among mainland sites, with six to eight antiviral antibodies identified depending upon the location of the survey.

There are two hypotheses for the observed impoverishment of murine viruses observed on Thevenard Island, Boullanger Island and Macquarie Island, and these hypotheses are inherently linked to the recruitment and population dynamics of the host species (McCallum et al. 2001).

Viral diversity may reflect the origins of founders of hosts (house mice) to an island. This simple hypothesis implies that differences observed in seroprevalence to murine viruses between islands are chance events, and is dependent upon which virus the host transfers to the island ecosystem.

Viral diversity may also be dependent upon those viruses that can persist during periods of low population density. Seroprevalence to MCMV is influenced by the density of house mouse populations (Smith et al. 1993; Moro et al. 1999; Singleton et al. 2000). These environmental changes that impose continuous bottlenecks to the mouse population may explain the (lack of) diversity of virus in remote and isolated areas. Mouse populations on mainland Australia also undergo periods of boom and bust (Singleton et al. 2002). Biotas on some arid islands undergo periods of boom and bust in response to periods of drought and rains; for example, on Thevenard Island, seroprevalence to MCMV changed in response to population crashes of house mice following the passage of cyclones near the island (Moro et al. 1999). It is common for islands to harbour fewer mammal species than an equally-sized piece of the mainland (Lawlor 1986), and for pathogens dependent upon their host, such as murine viruses, this phenomenon seems no exception.

A small host population may preclude the survival of murine viruses, which could not establish persistent infection. Evidence for the low seropositivity of murine virus among populations of house mice on Thevenard Island, Boullanger Island and Macquarie Island raises interesting questions about the persistence of virus in remote locations. It is known that measles virus shows dependency upon a human population that is above a threshold of approximately 500,000 people (Black 1966). In contrast, varicella zoster virus can survive in small

Table 1. Seroprevalence to antiviral antibodies in house mice sampled from three insular locations around Australia. Comparative information for house mice sampled across south-eastern Australia is also presented (+ = <20% of sampled house mice; ++ = 20–50%; +++ = >50%; NT = not tested).

Pathogen[a]	Island location				
	Thevenard Island	Boullanger Island	Macquarie Island	Australia[b]	Australia[c]
n	309	27	92	269	267
MCMV	+++	++	+++	+++	+++
ROTA	–	+	+	+++	+++
LCMV	–	–	+	–	+
PARV	–	–	+	NT	NT
REO	–	–	–	++	++
MadV	–	NT	NT	++	++
MHV	–	–	–	+++	+++
MVM	NT	NT	NT	+	++
TMEV	–	–	++	–	–
SEND	–	–	–	–	+
ECT	–	–	–	–	–
PVM	–	–	–	–	–
EMCV	–	NT	NT	NT	NT
HANT	NT	NT	NT	–	–
Total no. of virus antibodies	1	2	5	6	8

[a] MCMV = murine cytomegalovirus, ROTA = epizootic diarrhoea of infant mice, LCMV = lymphocytic choriomeningitis virus, PARV = minute virus of mice and mouse parvovirus (combined test using recombinant antigen), REO = reovirus type 3, MadV = mouse adenovirus strains FL and K87, MHV = mouse hepatitis virus, MVM = minute virus of mice only, TMEV = Theiler's murine encephalomyelitis virus, SEND = sendai virus, ECT = vaccinia virus (ECT, used to test for ectromelia virus antibody), PVM = pneumonia virus of mice, EMCV = encephalomyocarditis virus, and HANT = Hantaan virus.

[b] Information source: Singleton et al. (1993).

[c] Information source: Smith et al. (1993).

human populations by establishing latent infection (Black 1966). Since MCMV can establish latent infection in mice from which reactivation is known to occur (Osborn 1982), providing continuing opportunities for transmission, it is likely that this virus could persist in small populations such as those found on the three islands sampled. Consequently, viral persistence in areas experiencing large changes in host density will also be influenced and restricted to those viruses that can persist at low host densities (but see McCallum et al. 2001).

On subantarctic Macquarie Island, however, although climate is cold, the annual variation in climatic conditions is not as extreme as that experienced on arid islands, such that mouse densities (as reflected in trap success) remain stable across the year (Berry and Peters 1975). The larger area of Macquarie Island relative to the other two islands may also support a larger population of house mice and so a higher population threshold for viral pathogens. A greater area, together with a higher, more stable density of mice, may allow a higher diversity of viruses to persist on Macquarie Island relative to the other two arid islands.

Further support for the hypotheses identified will follow if sampling for murine viruses is undertaken on a suite of other islands worldwide.

Conclusion

Serosurveys for murine viruses on islands have recorded fewer murine viral antibodies when compared to house mouse populations inhabiting mainland Australia. Although serology is not an optimal test to screen for murine viruses, it does serve as a benchmark and certainly reveals the history of viral activity. In addition, the diversity of antiviral antibodies was lower on arid islands than one subantarctic island. These results raise questions about viral persistence in house mice isolated in remote locations.

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Helminths of the rice-field rat, *Rattus argentiventer*

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Abstract. We studied the helminths in liver and digestive tracts in rice-field rats in West Java during the 1997/98 planting season in lowland irrigated rice fields. Six species of helminths were recorded: *Capillaria hepatica*, *Taenia taeniaeformis*, *Nippostrongylus brassiliensis*, *Viktorocara* sp., *Vampirolepis diminuta* and *Echinostome* sp. For helminths of the digestive tract, the highest prevalence and intensity was found for *N. brassiliensis*. This helminth may be promising for use as a biological agent to control populations of rice-field rats. For helminths of the liver, *C. hepatica* had the highest prevalence. The intensity of infection for *C. hepatica* was bimodal with many light and heavy infections and few infections of medium intensity.

Introduction

The rice-field rat, *Rattus argentiventer*, is the major pre-harvest pest in rice crops in Indonesia, causing damage in every planting season (Singleton and Petch 1994). They also attack secondary crops and other agricultural commodities. Generally, Indonesian farmers practise methods of rodent control that rely on heavy use of chemicals (rodenticides) (Sudarmaji, Singleton et al., this volume), or physical methods of control that are labour-intensive. However, apart from promising experimental results from using a trap–barrier system associated with an early-planted crop (Singleton et al. 1999), these management methods have low efficacy. Control of rodent pests using a biological control agent is a prospective technology that could be economic and environmentally friendly. Parasites can have both direct and indirect effects on host reproduction—indirect effects include abnormal growth, delayed sexual maturity and a decrease in the time that the rodents are physiologically capable of reproducing (Scott 1988). Modelling studies support the potential for microparasites and macroparasites to regulate populations of mammals (Anderson and May 1979). Laboratory studies confirm this potential (Scott 1987; Spratt and Singleton 1986), but strong evidence from field studies is lacking.

The current study aimed to identify and then monitor the prevalence and intensity of infection with macroparasites in the gastro-intestinal tract and liver of the rice-field rat for 8 months in 1997/98 in Sukamandi, West Java, in an effort to determine the potential of macroparasites as biological control agents for the rice-field rat.

Materials and methods

The study was conducted at the Indonesian Institute for Rice Research field station in Sukamandi, West Java in April–December 1997. Rats were sampled from one permanent trap–barrier system consisting of a rectangular plastic fence with eight multiple-capture live-traps (Lam 1988). We visually screened liver, stomach, small and large intestine, and caecum for helminths. Prevalence (percentage of rats infected) and intensity of infection (number of individual helminths per rat) were determined for each parasite species.

Results and discussion

We removed 199 rats (87 males and 112 females). Six species of helminths were detected: *Capillaria hepatica, Taenia taeniaeformis, Nippostrongylus brassiliensis, Vampirolepis diminuta, Viktorocara* sp. *and Ehinostome* sp. (Table 1). In the digestive tract, *N. brassiliensis* had higher prevalence and intensity of infection than *V. diminuta*, *Viktorocara* sp. and *Echinostome* sp. (Table 1). Potentially high prevalence is required if a parasite is to be used to manipulate the density of its host on the population level. *N. brassiliensis* helminths consume lipids of their host's body, hence disturbing food uptake in the host (Cheng 1986). If this has a negative impact on reproduction or increases mortality in the rice-field rat, it may be useful for population control. This needs to be tested further. The occurrence of *Echinostome* sp. was usually associated with inflammation of the small intestine. This may severely reduce food uptake in infected rats.

In the liver, *C. hepatica* had higher prevalence than *T. taeniaeformis* (Table 1). The high prevalence of *C. hepatica* in rice-field rats is similar to house mice where prevalence can reach >50% (Singleton and Chambers 1996). According to Baker (1979) and Singleton and Spratt (1987), *C. hepatica* is transmitted through cannibalism in house mice. This may also have been the case in rice-field rats.

Table 1. Prevalence and intensity of helminth infection in *Rattus argentiventer* during 8 months in 1997/98 in Sukamandi, West Java.

Species (infection site)	Prevalence (mean ± se) (*n* = 199)	Intensity (mean ± se) (*n* = 199)
Capillaria hepatica (liver)	26.0 ± 5.9	–
Taenia taeniaeformis (liver)	5.6 ± 2.8	1.4 ± 0.6
Nippostrongylus brassiliensis (small intestine)	82.1 ± 8.3	43.4 ± 12.1
Vampirolepis diminuta (small intestine)	24.4 ± 2.2	2.6 ± 0.6
Viktorocara sp. (stomach)	9.8 ± 4.7	2.8 ± 1.3
Echinostome sp. (small intestine)	34.2 ± 3.7	13 ± 9.5

The intensity of *C. hepatica* infections seemed to be bimodially distributed (Table 2). About two-thirds of rats had light infections and about one-third had extremely heavy infections. Heavy infection of one or two lobes or moderate infection of all lobes was rare. The high percentage of rats heavily infected with *C. hepatica* was surprising. It could be a result of immigrating rats from populations with different levels of *C. hepatica* infections during the post-harvest migration.

Table 2. Intensity (%) of *Capillaria hepatica* infection in the liver (and number of lobes involved) in infected *Rattus argentiventer* (*n* = 57) during 8 months in 1997/98 in Sukamandi, West Java.

Light (1–2 lobes)	Light (>2 lobes)	Heavy (1–2 lobes)	Moderate (all lobes)	Extremely heavy
17.5	45.6	3.5	5.3	28.1

Conclusion

It is clear that further work on the assessment of helminths as potential biological control agents is warranted. It is important to know whether the two species of helminths, which are prevalent, affect the reproductive success of the rats.

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Occurrence and pathomorphological observations of *Cysticercus fasciolaris* in lesser bandicoot rats in India

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Abstract. The infection intensity, main characteristics of the hepatic capsules, and pathomorphological observations of *Cysticercus fasciolaris* (the larval stage of adult tapeworm, *Taenia taeniaeformis*, of cats and related carnivores) were studied in livers of naturally-infected lesser bandicoot rat, *Bandicota bengalensis*. The prevalence of infection in all rats was 25.7%. The capsules, single or multiple (4–15 mm in diameter), were embedded on the surface and deep in the liver parenchyma and contained a well-defined wall. The larvae were found neatly coiled in the capsule. Morphological features of the strobilocercus were similar to the adult tapeworm, having segmentation but without genital organs. Histopathologically, inflammatory reaction was seen in hepatic parenchyma with mononuclear cell infiltration adjoining immature capsules. Severe fatty change was seen in the liver. Inflammatory reaction adjoining the connective tissue capsule was not seen in mature *C. fasciolaris* cysts. The finding of live motile larvae inside the fibrous tissue capsule indicates that infected rats are a potential source of infection for cats and other carnivores.

Introduction

Cysticercus fasciolaris is the larval stage of the helminth parasite *Taenia taeniaeformis*, the commonly occurring intestinal tapeworm of cats and related carnivores. Rodents serve as intermediate hosts and are infected by ingesting the ova in contaminated food and bedding materials (Jithendran and Somvanshi 1998). The larval stages or metacestodes occur in the liver as a chronic infection. This paper describes the infection intensity, main characteristics of hepatic capsules, and pathomorphological observations of *C. fasciolaris* in the liver of free-living, naturally-infected lesser bandicoot rats, *Bandicota bengalensis*.

Materials and methods

Thirty-five lesser bandicoot rats, *B. bengalensis*, were live-trapped using both single and multiple-catch rat traps during April to June 2001 from highly infested fields of moong crop. Rats were sexed, weighed and kept individually in laboratory cages with free access to food (cracked wheat, powdered sugar and groundnut oil in a ratio of 96:2:2) and water. All the animals were killed under deep ether anaesthesia and livers showing parasitic larval capsules were removed and collected in warmed normal saline solution for further preservation in 10% formal saline. The number and condition (size and surface etc.) of capsules and gross and histopathological changes in the liver were recorded. Morphology of the larvae was studied for their identification after dissecting the capsules from the freshly collected samples before preservation in formal saline. The capsules were opened through a small slit to release the parasites. Representative liver samples with capsules in situ were embedded in paraffin and 4–5 µm thick sections were cut, processed routinely and stained with haematoxylin and eosin (H&E) for examination.

Results and discussion

At necropsy, all organs except the liver were normal. Nine out of 35 (25.7%) rats of either sex and different age groups contained pea-sized, whitish, single or multiple (1–3) capsules from 4–15 mm in diameter in the liver (Figure 1). The capsules were embedded on the surface and deep in the liver parenchyma, causing considerable tissue damage. A well-defined wall surrounded the capsules. Each capsule contained a single characteristic larva called a strobilocercus. The majority of adult rats had capsules while young rats had none. After opening the capsule, live motile larvae were found neatly coiled in the connective tissue cavity. The larvae measured 30–92 mm in length and looked like a small tapeworm. Cheng (1991) observed that larvae can reach a length of 20 cm. The morphological features of the strobilocercus were consistent with those of *T. taeniaeformis* worms, but without genital organs (Bowman 1999).

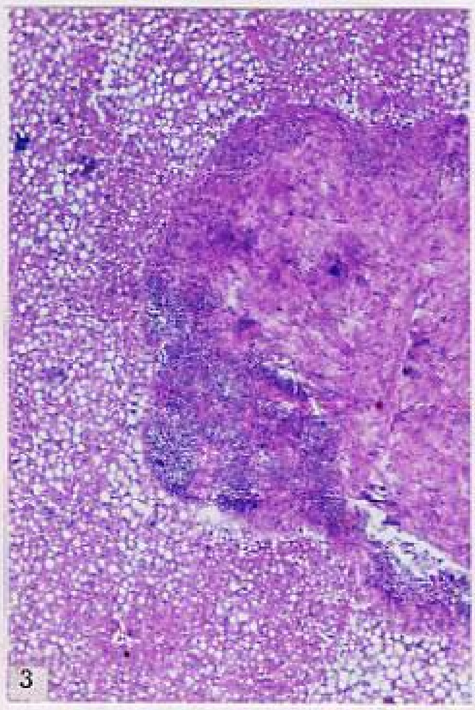

Figure 1. Livers of *Bandicota bengalensis* showing pea-sized or slightly larger, whitish cysts of *Cysticercus fasciolaris*.

Figure 2. The rostellum of *Cysticercus fasciolaris* armed with a row of long hooks and a concentric row of short hooks (×70).

Figure 3. Moderate fatty change with granulomatous inflammation with prominent infiltration of mononuclear cells in adjoining parenchyma of liver to *Cysticercus fasciolaris* cysts (haematoxylin and eosin staining; ×70).

Figure 4. Strobilocercus of *Taenia taeniaeformis* encysted in liver of *Bandicota bengalensis*. Fatty change and fibrous tissue encapsulation is seen around the mature *Cysticercus fasciolaris* larvae (haematoxylin and eosin staining; ×14).

The larvae were unique in that the scolices were not invaginated into the bladder but were attached to it by a long segmented neck, which measured several centimetres in length as described by Shadduck and Pakes (1978). The rostellum of the larvae was armed with two rows of small and large hooks (Bowman 1999) (Figure 2).

Histopathologically, inflammatory reaction was seen in the hepatic parenchyma around the capsule with newly-formed, loose, fibrous connective tissue and a thick cuffing zone of mononuclear cells (predominantly lymphocytes) (Figure 3). In what were assumed to be older or mature *C. fasciolaris* capsules, inflammatory reaction was encapsulated by connective tissue and inflammatory reaction in the liver parenchyma adjoining the connective tissue capsule was not observed (Figure 4). The connective tissue capsule consisted of few fibroblasts and abundant collagen fibres. Segments of larvae were seen inside the fibrous tissue capsule. The tegument of the metacestode appeared as a thick, homogenous, non-cellular layer supported by a basal membrane. The two zones of muscle fibres observed in the body parenchyma were typical of adult tapeworm segments. Thus, the matrix—a parenchymal meshwork of loosely arranged cells—is divided into distinct outer and inner portions by a system of longitudinal and transverse fibres (Figure 4).

The liver showed degenerative changes, mainly severe fatty change. The host connective tissue capsule may give rise to sarcomas in older animals typically 12–15 months post-infection (Kohn and Barthold 1984; Hanes 1995). In the intermediate host, hepatic function may be disrupted by excessive development of the cysticerci and degenerative fatty changes, and thus the animal may die. In South Bohemia, this parasite is the main cause of death in muskrat (Janssen Animal Health 2002). However, natural cysticercus infection in clinically asymptomatic rats is considered harmless (Jithendran and Somvanshi 1998). Further, it may lead to misinterpretation of results for biological experimentation (Tirina 1953).

Conclusions

The present study revealed a high prevalence (25.7%) of *C. fasciolaris* in lesser bandicoot rats, *B. bengalensis*. The presence of capsules in the liver was asymptomatic, yet caused fatty change of hepatic tissue and local infiltration with mononuclear cells around *C. fasciolaris*. The finding of live motile metacestodes inside the fibrous tissue capsule indicates that rats are a potential source of infection for cats and other carnivores.

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SYMPOSIUM 2: CONSERVATION

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Rodents on islands: a conservation challenge

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Abstract. Rodent species endemic to islands account for 18% of the more than 2050 known species. Despite this high species richness, and the high extinction rate of island rodents (caused by habitat destruction, overhunting and the introduction of alien species), little attention has been drawn to these animals by conservationists. This paper reviews the current conservation status of threatened endemic rodents on islands, the spread of alien rodents (*Rattus exulans*, *R. rattus*, *R. norvegicus* and *Mus musculus/domesticus*) to islands and their impacts on native biota (including endemic rodents). Eradication attempts against invasive alien rodents are also briefly reviewed and discussed.

Introduction

Islands have attracted the special attention of biologists since the time of Darwin and Wallace. In the modern world, the high endemism rates of insular animals and plants and their vulnerability to the introduction of alien species make insular biotas among the top conservation priorities. The high number of rodent species (more than 2050) and the high rate of endemism of rodent orders among mammals, coupled with lack of information on population status and often still questionable taxonomy, emphasise the priority for research on these animals. Scant attention has been paid to the conservation of rodents in general. This is particularly worrying when we consider island species which are particularly threatened.

The purpose of this paper is to define the current status of threatened rodent taxa on islands and to consider the threats posed by introduced rodents to endemic species. Alien rodent species threaten many endemic island taxa such as birds, reptiles and plants, but we emphasise that they also have impacts on endemic rodent species.

Current status of endemic island rodent taxa

There are 355 rodent species endemic to islands (Wilson and Reeder 1993; Alcover et al. 1998; Nowak 1999), representing 18% of all rodent species. According to data in Hilton-Taylor (2000) 37.6% of all island endemic rodent species are threatened (27 critically endangered, 40 endangered, 60 vulnerable), representing 33% of all threatened rodent species. Many other island endemics are known to have very small geographical ranges and for others there are insufficient data about their status.

Rodent species endemic to islands include several that occur on islands very close or connected in the past to the mainland. For a fuller appreciation of the differentiation of rodent taxa on islands it is useful to consider endemism at the genus level. Eighty-one genera are restricted to islands, comprising 194 species of four families—Sciuridae, Muridae (Murinae, Nesomyinae, Sigmodontinae, Arvicolinae), Capromyidae (Capromyinae and Isolobodontinae) and Gliridae—representing 17% of all rodent genera. According to Amori and Gippoliti (2001) 28 island genera are threatened (i.e. they have all extant species listed by the International Union for Conservation of Nature and Natural Resources (IUCN) (Hilton-Taylor 2000) in one of the three higher categories of threat) and 8 are potentially threatened (i.e. they have all extant species listed in other IUCN categories of threat). The islands with the highest number of endemic rodent genera are the Philippines (20), New Guinea (19), Sulawesi (12) and Madagascar (9).

According to MacPhee and Fleming (1999), 79 rodent species endemic to islands have become extinct and 36 of these did so during the last 500 years and a further 4 are suspected to have recently become extinct (Table 1). Of these, *Nesoryzomis swarthi* (Galapagos, Santiago), listed by McPhee and Fleming (1999) as a suspected extinct species, has been removed from the list following its rediscovery (Dowler et al. 2000). However, we have added *Oryzomys galapagoensis* (Galapagos, San Cristobal), *Nesoryzomys indefessus* (Galapagos, Baltra) (Dowler et al. 2000) and *Solomys salamonis* (Solomons), which were considered extant by MacPhee and Fleming (1999) but classed as extinct by IUCN (Hilton-Taylor 2000).

If we consider also those species found by the first human settlers on oceanic and oceanic-like islands, the list of extinct endemics would be extended. It should also include *Malpaisomys insularis* (Canary Islands) (which probably became extinct in the last 800 years due to competition from introduced *Mus domesticus*), *Papagomys theodorverhoeveni*, *Spelaemys florensis*, *Solomys spriggsarum*, *Coryphomys buhleri*, and *Melomys spechti* (Wilson and Reeder 1993; Alcover et al. 1998). *Microtus* (*Thyrrenicola) henseli* and *Rhagomys orthodon* (Sardinia and Corsica) also became extinct during Roman times, presumably due to the progressive introduction of alien species that started at the beginning of the Neolithic Period (Vigne 1992).

Table 1. Recently extinct island rodent species (source: MacPhee and Fleming 1999).

Rodent species	Geographic range	Date of extinction (if known)
Malpaisomys insularis	Canaries	
Rattus macleari	Christmas Islands, Indian Ocean	1903
Rattus nativitatis	Christmas Islands, Indian Ocean	1903
Noronhomys vespuccii[a]	Fernando de Noronha (Brazil)	
Megaryzomys sp. undescribed	Galapagos (Isabela)	
Nesoryzomys indefessus	Galapagos (Baltra)	1929
Nesoryzomys two spp. undescribed	Galapagos (Isabela)	
Nesoryzomys darwini	Galapagos (Santa Cruz)	<1940
Megaoryzomys curioi	Galapagos (Santa Cruz)	
Oryzomys galapagoensis	Galapagos (San Cristobal)	1835
Geocapromys tropicalis	Little Swan (Carribean Sea)	1950[b]
Oryzomys nelsoni	Maria Madre (Gulf of California)	1897
Pharotis imogene	Papua New Guinea	1890
Crateromys paulus	Philippines (Ilin)	1953[b]
Peromyscus pembertoni	San Pedro Nolasco Isl. (Mexico)	1931
Uromys porculus	Solomons (Guadalcanal)	1887
Uromys imperator	Solomons (Guadalcanal)	1960[b]
Nyctimene sanctacrucis	Solomons (Santa Cruz)	<1892
Solomys salamonis	Solomons (Florida)	?
Oryzomys sp. undescribed	West Indies (Barbados)	
Oryzomys hypenemus	West Indies (Barbuda and Antigua)	
Megalomys audreyae	West Indies (Barbuda)	
Geocapromys sp. undescribed	West Indies (Cayman Brac)	
Capromys sp. undescribed	West Indies (Cayman Isl.)	
Geocapromys columbianus	West Indies (Cuba)	
Brontomys offella	West Indies (Cuba)	
Brontomys torrei	West Indies (Cuba)	
Geocapromys sp. undescribed	West Indies (Gran Cayman)	
Isolobodon portoricensis	West Indies (Hispaniola and Puerto Rico)	
Brotomys voratus	West Indies (Hispaniola)	
Isolobodon montanus	West Indies (Hispaniola)	
Plagiodontia ipnaeum	West Indies (Hispaniola)	
Quemisia gravis	West Indies (Hispaniola)	
Hexolobodon phenax	West Indies (Hispaniola)	
Rhizoplagiodontia lemkei	West Indies (Hispaniola)	
Oryzomys antillarum	West Indies (Jamaica)	1877
Megalomys desmarestii	West Indies (Martinique)	<1894
Oligoryzomys victus	West Indies (Saint Vincent)	1892
Megalomys luciae	West Indies (St. Lucia)	<1881

[a] Carleton and Olson (1999).

[b] Suspected to be extinct.

Extinct endemic rodent island genera (19), comprising those that survived until the Neolithic Period, are reported in Table 2. This list does not include the monotypic *Paulamys* (Flores Island), described from subfossil records, which some authors consider to be closely related to *Bunomys* (Sulawesi). *Spelaeomys florensis* (Flores) is known from subfossil records (3000–4000 years BP), but possibly still lives on other nearby islands. *Hypnomys* (*H. morpheus* and *H. mahonensis*) (Balearic Islands), considered sometimes as a synonym of *Eliomys*, became extinct about 4000–5000 BP. The islands of the West Indies are especially affected by extinctions in endemic genera (8 genera and 14 species). Among others, a whole endemic family (Heptaxodontidae) comprising 4 genera and 5 species has vanished from this area (Woods 1990).

Overall, it is too early to make a complete assessment of the human impact on insular rodent species, because the original fauna and palaeontology of many islands are poorly known, and in many cases more accurate genetic research is needed to distinguish species. However, it is clear that the main reasons for extinction of insular endemic rodent species are habitat loss, intense hunting and the introduction of alien species. The patterns of body size of recently extinct insular rodent species lead us to suggest that the smaller species became extinct mostly because of competition with introduced rodent species, whilst the larger species were probably more affected by overhunting and habitat destruction.

Introduced rodents, their impacts and eradication attempts

Impacts of alien rodents

A few rodent species are human commensals and have been introduced (mostly accidentally) to many islands around the world as humans have visited or colonised them. These commensal rodents include *Rattus exulans*, *R. norvegicus*, *R. rattus* and *Mus musculus/domesticus*, all of which not only damage crops and stored foods, but also are invasive alien species that threaten the native biodiversity of islands to which they are introduced. The three species of *Rattus* have colonised at least 82% of the 123 major island groups of the world (Atkinson 1985). In addition to preying on vulnerable fauna (their most obvious impact), they also consume the leaves, seeds and fruits, flowers, bark and stems of many endangered plants. By impeding regeneration and destroying seedlings, they can modify entire plant communities, and thereby also affect the associated native fauna (Clark 1981). Because they exhibit important ecological differences, the three widespread species of alien rats have had slightly different impacts on island biodiversity (Atkinson 1985; Lever 1994).

Rattus exulans was probably the first rodent species to become widely distributed on islands outside its native range. It is native to Southeast Asia, but has been dispersed throughout the Pacific by humans over the past few thousand years (Matissoo-Smith et al. 1998). It now

Table 2. Recently extinct genera of island rodents.

Rodent genus	Rodent family	Geographic range	Number of species
Noronhomys	Muridae	Fernando da Noronha (Brazil)	1
Megaoryzomys	Muridae	Galapagos	1
Microtus (*Thyrrenicola*)	Muridae	Sardinia and Corsica	1
Rhagamys	Muridae	Sardinia and Corsica	1
Coryphomys	Muridae	Timor	1
Malpaisomys	Muridae	Canary Islands	1
Canariomys	Muridae	Canary Islands	1
Hypnomys	Gliridae	Baleary Islands	2
Megalomys	Muridae	West Indies (St Lucia, Martinique, Barbuda)	3
Brotomys	Echimyidae	West Indies (Hispaniola)	2
Boromys	Echimyidae	West Indies (Cuba)	2
Heteropsomys	Echimyidae	West Indies (Puerto Rico)	2
Puertoricomys	Echimyidae	West Indies (Puerto Rico)	1
Hexolobodon	Capromyidae	West Indies (Hispaniola)	1
Rhizoplagiodontia	Capromyidae	West Indies (Hispaniola)	1
Quemisia	Heptaxodontidae	West Indies (Hispaniola)	1
Elasmodontomys	Heptaxodontidae	West Indies (Puerto Rico)	1
Amblyrhiza	Heptaxodontidae	West Indies	1
Clidomys	Heptaxodontidae	West Indies (Jamaica)	2

occurs on almost every tropical Pacific island and on several temperate ones, from the Asiatic mainland, south to New Guinea and New Zealand, and east to Hawaii and Easter Island. *R. exulans* not only causes damage to crops, but also has been blamed for the extinction of many native invertebrate, amphibian, reptile and bird species (Crook 1973; Atkinson 1978). Most of the extinctions caused by *R. exulans* probably occurred hundreds of years ago, as these rats were spread across the Pacific by human colonists to many islands that were previously free of land mammals (Steadman 1985). Some modern studies have revealed the continuing effects of this invasive rodent, which is capable of having significant impacts as a predator. For example, on Kure Atoll, *R. exulans* has been observed killing Laysan albatrosses, great frigate birds, red-tailed tropic birds, sooty terns, common noddies and Bonin Island petrels (Kepler 1967). On Henderson Island, rat predation on Murphy's petrel is so severe that the colony probably persists only through immigration from the nearby rat-free islands of Oeno and Ducie (Lever 1994). In New Zealand, *R. exulans* (introduced by Polynesian voyagers hundreds of years before any other rodents arrived) are implicated in the decline or extinction of many endemic species, including large flightless insects, frogs, reptiles, birds and bats (Atkinson and Moller 1990).

Rattus norvegicus probably originated in China and spread westwards to Europe from the 16th–18th centuries (even if some records from Germany dated back to Middle Ages). For many decades it was the most common shipboard rat and was accidentally distributed around the world to many islands (from the tropics to polar regions) by early European explorers and colonists (Atkinson 1985). The species has largely terrestrial habits, especially favouring coastal or waterside habitats, and preys on birds, reptiles and invertebrates. It is particularly significant as a predator of ground-nesting birds, including seabirds. Twenty-seven of the 53 bird species that Atkinson listed as prey of *R. norvegicus* are seabirds. The species is undoubtedly responsible for many extinctions on islands around the world, but is often present along with other introduced rodent species, or predators such as cats, so its specific impacts may be difficult to distinguish. Nevertheless, some examples show that the impacts on native biodiversity are typically disastrous. The invasion of Whenuakura Island in New Zealand by *R. norvegicus* in 1982 led to the elimination of the entire local population of tuatara (*Sphenodon punctatus*) (Newman 1988). The recovery of native fauna on islands from which *R. norvegicus* have been removed can be dramatic: on Breaksea Island (New Zealand) large insects (beetles, weta, harvestmen) have recovered following rat eradication and it has been possible to reintroduce threatened birds such as saddlebacks (*Philesturnus carunculatus*) in the absence of rat predation (B.W. Thomas, pers. comm.).

Rattus rattus was the prevalent shipboard rat on vessels originating from Europe from the mid-1800s onwards and has been accidentally distributed (like *R. norvegicus*) to many islands. It is arguably the most damaging invasive rodent on islands worldwide, because it has arboreal as well as ground-feeding habits, so has widespread impacts on native faunas as a predator. King (1985) pointed out that rats have been implicated in 54% of the recent bird extinctions attributed to predators and stated that "of the three species which have shared the blame for this record of predation…*Rattus rattus* has been the most serious problem". Atkinson (1985) stated that "on a few islands, the proportion of bird species that have become extinct following the introduction of *R. rattus* is so great that the term catastrophe is appropriate". Perhaps the best documented example of the impacts of this single rat species on native biodiversity is the sequence of events following the arrival of *R. rattus* on Big South Cape Island (New Zealand) in the early 1960s. Nine native landbird species declined and five of these became extinct, along with the last known population of the greater short-tailed bat (*Mystacina robusta*) and at least one species of flightless weevil. *R. rattus* was the only introduced mammal on that island, so all effects were unequivocally caused by it. Other extinctions specifically attributed to *R. rattus* have occurred on Hawaii, Lord Howe Island and Midway Island, among many others (Innes 1990). As with other alien rodents, the long-term effects of their presence in island ecosystems are unknown. Palmer and Pons (1996) investigated the impact of *R. rattus* on the insect fauna of 51 islets of the Balearic Islands. Five endemic beetles showed a consistent smaller number of presences within infested islets than expected and only two non-endemic beetle species seemed to benefit from the presence of rats. This again raises the question of how many unknown changes have occurred in the animal and plant communities of islands where alien rats have been present for a long time (e.g. the Mediterranean islands).

The fourth common rodent that has been accidentally introduced to many islands around the world is the house mouse (*Mus musculus* or *Mus domesticus*). This small commensal rodent is now probably more widely distributed than any other mammal, apart from humans. Its global spread to oceanic islands is mostly relatively recent, dating from the period of European exploration and colonisation. The impacts of mice as alien predators are generally regarded as less severe than those of rats, but this may reflect our ignorance of their impacts. They are known to prey extensively on invertebrates and to kill lizards, but they also consume large amounts of seeds and may have consequent effects on plant regeneration. Like other alien rodents, they may also contribute indirectly to declines of vulnerable native fauna, by forming the prey base for other introduced predators, such as mustelids or cats (Murphy and Pritchard 1990).

A common consequence of rodent introductions to islands is the subsequent deliberate introduction of predators such as cats, mongoose (*Herpestes* spp.) and snakes to control the rodent pests. These predator introductions often cause further negative impacts on native fauna, and typically fail to prevent the damage caused by the introduced rodents.

Impacts of alien rodents on native ones

Alien rodents can also cause negative effects on native mammals, including native rodents. These impacts are probably mostly through competition, although direct predation by alien species on native ones is also possible.

Goodman (1995) drew attention to the negative effects of competition from introduced *R. rattus* on the native rodent fauna of Madagascar (endemic subfamily Nesomyinae). *R. rattus* has invaded even remote forested areas, replacing endemic rodents. Control or eradication of the alien rats is made especially difficult because trapping techniques and rodenticides that are available also affect native rodents. The same conclusions were reached by Lehtonen et al. (2001) who suggest protecting primary forest from logging as a possible way of preventing the spread of *R. rattus*. The invasion of Madagascar by introduced rodents (also including *R. norvegicus* and *M. musculus*) may date back to 800–900 BP.

R. rattus now occurs in all vegetated habitats of the seven islands of the Galapagos and is thought to be responsible for the extinction of four species of endemic rice rats (Brosset 1963). The extinction of *Nesoryzomys darwini* and *N. indefessus* from Santa Cruz Island occurred relatively recently; the last specimens being collected in 1929/30 and 1934, respectively (see also Table 1). These extinctions are almost certainly a result of competition by *R. rattus*, introduced by early sailors or pirates (Dowler et al. 2000). Darwin collected *R. rattus* on Santiago Island in 1835, so this alien species has been in the Galapagos for some time.

Eradication of alien rodents

Only 25 years ago, it was deemed virtually impossible to remove rodents from islands where they had established. However, with the advent of ‘second generation’ anticoagulant rodenticides in long-life, palatable baits, it has proved possible to permanently remove rats and mice from increasingly large islands, if operations are carefully controlled. On the many islands that have no native mammals, it is now feasible to eradicate entire populations of alien rodents in only a few days (although a period of planning is also required), usually by distributing toxic baits from the air, but sometimes by using ground-based bait stations. These approaches to rodent eradication have been developed especially in New Zealand, but have been used on many other islands around the world, from the arctic to the subantarctic (Veitch and Clout 2002). For example, in New Zealand, *R. norvegicus* was apparently eradicated in 2001 from 11,000 ha Campbell Island with a single airdrop of toxic bait. *R. exulans* and *R. norvegicus* were similarly eradicated from 1960 ha Kapiti Island, *M. musculus* from 800 ha Enderby Island, and *R. rattus* from a number of islands of up to 200 ha. Another recent example is the eradication of *R. norvegicus* from Fregate Island, Seychelles (Thorsen et al. 2000).

Eradication is, however, much more of a challenge when native, non-target mammals are present, especially when these include native rodents, because methods used to eradicate alien rodents are also likely to threaten native ones. For this reason, the preservation of habitats and prevention of further invasions by alien rodents (or other introduced species) remain the best strategies for the conservation of endemic rodents on islands.

Conclusion

It is clear from the statistics presented here that many endemic taxa of rodents on islands are vulnerable to extinction. To prevent their extinction, we make some recommendations and suggest actions to be followed.

Firstly, research should be focused on islands that may host relict populations or species known only from specimens from the type locality or from the holotype. This should facilitate the discovery of species whose existence is in doubt and help to determine the status of populations that are poorly known. Systematic investigations, with the aim of understanding phylogenetic relationships among populations and species, are fundamental for the refinement of current taxonomy and systematic affinities. This is needed even for common and widespread genera such as *Rattus*. For example, *Rattus everetti* probably contains more than one species and seems unrelated to other species of *Rattus* endemic to the Philippines (Musser and Heaney 1992).

Secondly, monitoring the effects of changing ecological conditions on threatened species is another important priority. For example, Sommer and Hommen (2000) constructed a predictive model for *Hypogeomys antimena*, a Malagasy threatened rodent, considering ecological and population parameters, that led to negative predictions for the future of this species. Similar exercises would be valuable for other threatened species, but ecological conditions are often poorly monitored.

Thirdly, strategies to prevent further invasions, monitoring systems to detect alien species, and improved capacity for prompt eradication responses when needed are all urgently required to safeguard native biodiversity from invasive rodents. Invasions of alien rodents threaten island biodiversity in general, but they are also strongly correlated with declines and extinctions of several endemic rodent species on islands. Eradication of invasive rodents from islands is increasingly feasible, generally leading to the recovery of threatened species, but monitoring of the full range of ecological consequences is all too rarely done. Species eradications from islands constitute major ecological experiments, which present unique research opportunities to improve our understanding of ecosystem function.

Finally, we urge the creation of protected areas on islands to benefit the conservation of endemic rodents, the establishment of captive breeding colonies of threatened rodents, and a growing involvement of conservationists and the general public to maintain all current rodent lineages. Rodents represent a significant proportion of mammalian diversity and rodents that are endemic to islands are especially threatened.

Extinction is a natural phenomenon, but we should try to avoid increasing its natural rate of occurrence.

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Positive effects of rodents on biota in arid Australian systems

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Abstract. This study investigates the beneficial effects of Australian desert rodents on other vertebrates and vascular plants. Observations of rodent burrows confirmed that they are used opportunistically by at least 17 other vertebrate species. One species, the lesser hairy-footed dunnart, *Sminthopsis youngsoni*, does not dig, and at times uses rodent burrows extensively for shelter. Detailed censuses around the complex burrow systems of the long-haired rat, *Rattus villosissimus*, showed that plant cover, plant and seed species richness are greater on the disturbed soil near burrows than at sites where soil has not been disturbed. In other experiments, exclusion of all rodent species from fenced plots led to increased cover of spinifex grass, *Triodia basedowii*, relative to control plots, but also to depressed activity of two species of lizards. Positive effects can be biotic, if they occur between interacting species, or environmental, if one species modifies resources that can then be used by a second species. Both kinds of interactions occur between rodents and other organisms in arid systems in Australia and elsewhere, and may be more prevalent than is often suspected.

Introduction

Due to the pioneering work of James Brown, Michael Rosenzweig and their colleagues on heteromyids in the deserts of the south-western United States, desert rodents are often viewed as model organisms for the study of ecological processes. In North America, as well as in Asia and Africa, much attention has focused on identifying the biotic interactions that structure desert rodent communities. Competition has emerged as an important organising force; pattern analyses and removal experiments suggest that this process commonly shapes body size, resource use and community composition (Brown 1975; Shenbrot et al. 1994). Predation also has emerged as a pervasive structuring process, but indirect interactions such as bioperturbation (soil disturbance by animals) may also be important (Whitford and Kay 1999).

In Australia, by contrast, most studies have emphasised the role of weather in shaping the population and species dynamics of desert rodents (Dickman et al. 1999). The effects of rodents on each other and on other biota have been little studied; where they have, a primary concern has often been to manage the impact of pest species on grain and other dryland crops (Pech et al. 1999). Yet, some evidence is beginning to emerge that Australian desert rodents can have subtle effects on the abundance, resource use and local diversity of a wide range of plants and animals (Dickman 1999). Moreover, while some of these effects are mutually depressive (i.e. competition), many interactions involving desert rodents appear to be positive.

In this paper, I describe some observations and experiments carried out in the Simpson Desert of central Australia that demonstrate positive effects of rodents on other vertebrates and vascular plants. I recognise two general kinds of effects: *biotic*, where effects occur directly or indirectly between interacting species; and *environmental*, where one species modifies the quality or amount of resource that then becomes available to a second species. More detailed discussion of kinds of interactions and terminology is given in Dickman (1999).

Materials and methods

Study site and animals

Field work was carried out on Ethabuka station, north-eastern Simpson Desert, western Queensland. The Simpson is classified as a hot desert; maximum daily temperatures average 38°C in summer, minima average 7°C in winter. Rainfall at the study site averages <200 mm a year. The Simpson Desert is characterised by long parallel sand dunes up to 8 m high and ~1 km apart that may run for many kilometres. Spinifex, *Triodia basedowii*, predominates on sandy soil in the valleys and on the slopes between the dunes, while gidgee, *Acacia geor-*

ginae, trees occur on clay. Perennial shrubs occur throughout the dune fields, and herbs and ephemeral grasses are abundant after rain.

Rodents and other small terrestrial vertebrates were live-captured in pitfall traps, marked and released 3–6 times a year between 1990 and 2002. Some individuals were tracked to identify burrows and foraging patterns using radio-tags, cotton spools or fluorescent pigments. The trapping and tracking protocols are described in detail elsewhere (Predavec and Dickman 1994; Dickman et al. 1999).

Four species of rodents were captured frequently. The long-haired rat, *Rattus villosissimus* (140 g), was abundant in 1991 and 1992 after heavy summer rains in 1990 and 1991, but was seldom captured at other times. The spinifex hopping-mouse, *Notomys alexis* (30 g), and sandy inland mouse, *Pseudomys hermannsburgensis* (12 g), also were abundant in 1991 and 1992 but scarce for the next 7 years. Both species then erupted in 2001 following heavy rains the previous year. The final species, the desert mouse, *Pseudomys desertor* (25 g), was present sporadically for the first 10 years of the study, but erupted synchronously with *N. alexis* and *P. hermannsburgensis* in 2001. All species are omnivorous but take considerable amounts of seed in the diet, with *R. villosissimus* taking relatively more green plant material than the other species. All the rodents also dig burrows of varying complexity.

Effects of rodents on biota

Three sets of observations and experiments were established over the course of the study, as described below.

Environmental effects of burrows

Tracking allowed identification of the burrows constructed by each species of rodent. Between 1990 and 1992, two sets of observations were made of the use of these burrows by other organisms. Firstly, opportunistic observations were made of burrow use by other vertebrates, including dasyurid marsupials, reptiles and frogs. Results are expressed simply as tallies of observations; although burrows provided at least temporary shelter for other taxa, it was not possible to quantify the effects of burrow use on their population sizes. Secondly, in 1990 and 1991, intensive tracking using radio transmitters and fluorescent pigments was carried out on one common species of dasyurid, the lesser hairy-footed dunnart, *Sminthopsis youngsoni* (10 g). Animals were collected from pitfall traps soon after dark, and either fitted with a single-stage ‘wren’ tag (0.5 g) glued between the shoulders, or dusted with fluorescent pigment. Tracking began 1–4 h after the release of animals near the point of capture. Radio fixes were obtained hourly at night and once or twice by day for up to 7 days, while pigment trails were followed until they had faded. Several habitat components were scored at point locations where animals were active, but here I summarise only the data on burrow use.

Environmental effects of soil movement

Long-haired rats constructed both simple and complex burrows, the latter having radii up to 3 m, up to 14 burrow entrances and comprising some 20 m of underground tunnels (see Predavec and Dickman 1994 for a detailed reconstruction of a complex burrow). Because these burrows result in much soil being deposited on the ground surface, as well as general disturbance, areas near complex burrows have different edaphic conditions to adjacent, undisturbed areas. To evaluate the effect of such soil disturbance on plant cover and species richness, a single 2×2 m^2 quadrat was placed at a randomly-chosen point on each of 10 rat burrow complexes and at a further 10 undisturbed sites at least 50 m distant from the nearest burrow system. Overall ground cover was estimated as a percentage, by eye, for each quadrat, and each plant species identified. To evaluate the effect of soil disturbance on plant seeds, I collected three samples of surface sand ($5 \times 5 \times 2$ cm deep) from within each of the 20 quadrats used for plant samples, and then sifted seeds out using a 0.5 mm gauge mesh strainer. Seed species were identified, and the cumulative number of species per quadrat recorded. Field sampling was carried out in June 1992 when the abundance of long-haired rats was high (during ‘plague’), and again in November 1992 when the population was in decline (Predavec and Dickman 1994). Differences in plant cover, plant and seed species richness were compared between rat burrow complexes and undisturbed sites using analysis of variance. Plant cover data were arcsine-transformed before analysis.

Biotic effects of seed predation

Consumption of seeds by rodents may have a negative short-term impact on plant populations, but depletion of the seed bank could affect animals by leading to longer-term alterations of habitat structure. This possibility was investigated by establishing rodent-proof exclosures. Eighteen exclosures, each 3×3 m^2, were established in April 1994, and comprised six experimental, six fence control and six open control fences. The exclosures were all ≥250 m apart, and located on the lower-mid dune slopes. The experimental exclosures were constructed from 0.5 cm wire mesh with sides 145 cm high and with 15 cm buried in soil at the base. The fence controls were similar, but the mesh was not dug into the soil and thus permitted access by rodents underneath, while the open controls consisted simply of corner posts. Spinifex and total plant cover was estimated as a percentage, by eye, for each exclosure in April 1997. Casual observations suggested initially that lizards showed differential activity among the exclosures, and these were subsequently quantified. In April 1997 and March 1999, direct observations were made for 5 minutes at each exclosure, once during the morning (0930–1100 h), once during the afternoon (1530–1700 h), and once in the early evening (2030–2200 h) over 3–4 consecutive days. Counts were made of all individual lizards within the exclosures. Separate analyses of variance were computed for the day and night counts, and for the two yearly censuses, and mean counts across the exclosure types were compared. To avoid temporal pseudoreplication, exclosures were used as the units of replication. Thus, the two sets of day counts were averaged over the number of days of observations, and the single set of night counts was averaged in the same way. All analyses were carried out after checking for homogeneity of variances using Cochran's test.

Results

Environmental effects of burrows

In general, the three smaller species of rodents occupied deep (0.8–1.0 m) and steeply sloping burrows in summer, and shallow (0.2–0.4 m), superficial burrows in winter. Long-haired rats were tracked to both simple and complex burrows in all seasons, with the simple burrows more likely to be occupied for brief periods at night. All burrow types were used by other taxa, including four species of dasyurid marsupials (*Ningaui ridei*, *Planigale tenuirostris*, *Sminthopsis crassicaudata* and *S. youngsoni*), three species of agamids (*Ctenophorus isolepis*, *C. nuchalis* and *Pogona vitticeps*), three species of varanids (*Varanus brevicauda*, *V. eremius* and *V. gouldii*), four species of skinks (*Ctenotus helenae*, *C. lateralis*, *C. pantherinus* and *Egernia inornata*), two species of geckos (*Heteronotia bynoei* and *Nephurus levis*) and one species of frog (*Notoden nichollsi*). Thirty of 35 burrow observations were made by day; two were made of geckos by night, as well as one observation each of a dasyurid, a varanid, and a frog. Both disused and active rodent burrows were used by other taxa—on at least nine occasions dasyurids, agamids or skinks were known to be in the same burrow complex at the same time as the resident rodents.

In 1990, rats were absent from the study site and smaller species of rodents were uncommon. Pigment tracking showed that *S. youngsoni* occasionally used rodent burrows (8 of 55 observations, 14.5%), but primarily rested in burrows constructed by the agamid *Ctenophorus nuchalis* (26 observations, 47.3%), other lizards or invertebrates. There was no evidence that this species dug burrows of its own. Radio-tracked animals moved 1.8 ± 0.7 km (mean ± sd, $n = 6$) each night, often moving between the dune valleys and crests, with some individuals travelling up to 3 km (Dickman et al. 1991). In 1991, by contrast, when all species of rodents were relatively abundant, *S. youngsoni* used rodent burrows more frequently (25 of 37 observations, 67.6%) than in the previous year ($\chi^2_{\text{corr}} = 24.8$, $P < 0.001$). Radio-tracked animals moved 1.1 ± 0.5 km each night, and appeared to focus activity near to the burrow complexes of long-haired rats in the dune valleys and slopes. Although difficult to quantify, burrows appear to have been relatively more available in 1991 than in 1990, and appear to have been more fully used by *S. youngsoni* in 1991 than previously.

Environmental effects of soil movement

There was no difference in plant cover around rat burrows compared with sites away from burrows when rats were in plague, but cover on burrows increased dramatically when rat numbers subsided (Figure 1a). Plant species richness also was similar on rat burrows and away from them during plague, but was more than double around burrow complexes than away from them when the rat population had fallen (Figure 1b). In contrast, the richness of seed species in soil samples around rat burrows was more than double that in more distantly collected samples both during and after the plague of long-haired rats (Figure 1c). Inspection of the raw data suggested that there were considerable differences in both the plant and seed species composition between rat burrow complexes and sites away from them, with annual grasses and herbs being most abundant around the burrows.

Biotic effects of seed predation

Two species of lizard were observed frequently enough to evaluate their use of the exclosures. In both 1997 and 1999, the diurnal military dragon, *Ctenophorus isolepis*, was more active in the open and fence control exclosures than in the experimental exclosures (Figure 2a). A similar pattern of activity was observed in the nocturnal panther skink, *Ctenotus pantherinus*, (Figure 2b). Plant cover, especially of spinifex, *T. basedowii*, was greater in the experimental exclosures (38.7 ± 9.2%) than in either the open or fence control exclosures (22.4 ± 10.8%, pooled cover; $F = 5.2$, df = 1,16, $P < 0.05$). Both species of lizard appeared to move preferentially across open sand or to skirt the edges of shrubs and spinifex hummocks, suggesting that their activity was reduced by the greater plant cover in the experimental exclosures.

Discussion

The results suggest that other organisms benefit from the environmental and biotic activities of rodents in the Simpson Desert. The diggings and surface disturbances created by long-haired rats appeared to favour increased plant cover and were associated with locally-enriched hotspots for some species of grasses, herbs and plant seeds. Digging may bring deeply buried seeds to the surface, allow easier penetration of water into the soil profile, or create a rough ground surface that traps organic debris and returns nutrients to the soil. These environmental effects would facilitate germination and help to promote seedling establishment in the vicinity of rodent burrows. In addition, a rough ground surface may simply act as a seed trap, concentrating wind-blown seeds in pockets of soil and providing the conditions for mass germination when conditions are favourable. The engineering effects of rodents have been shown to facilitate seed germination and plant growth in other arid systems (Alkon 1999).

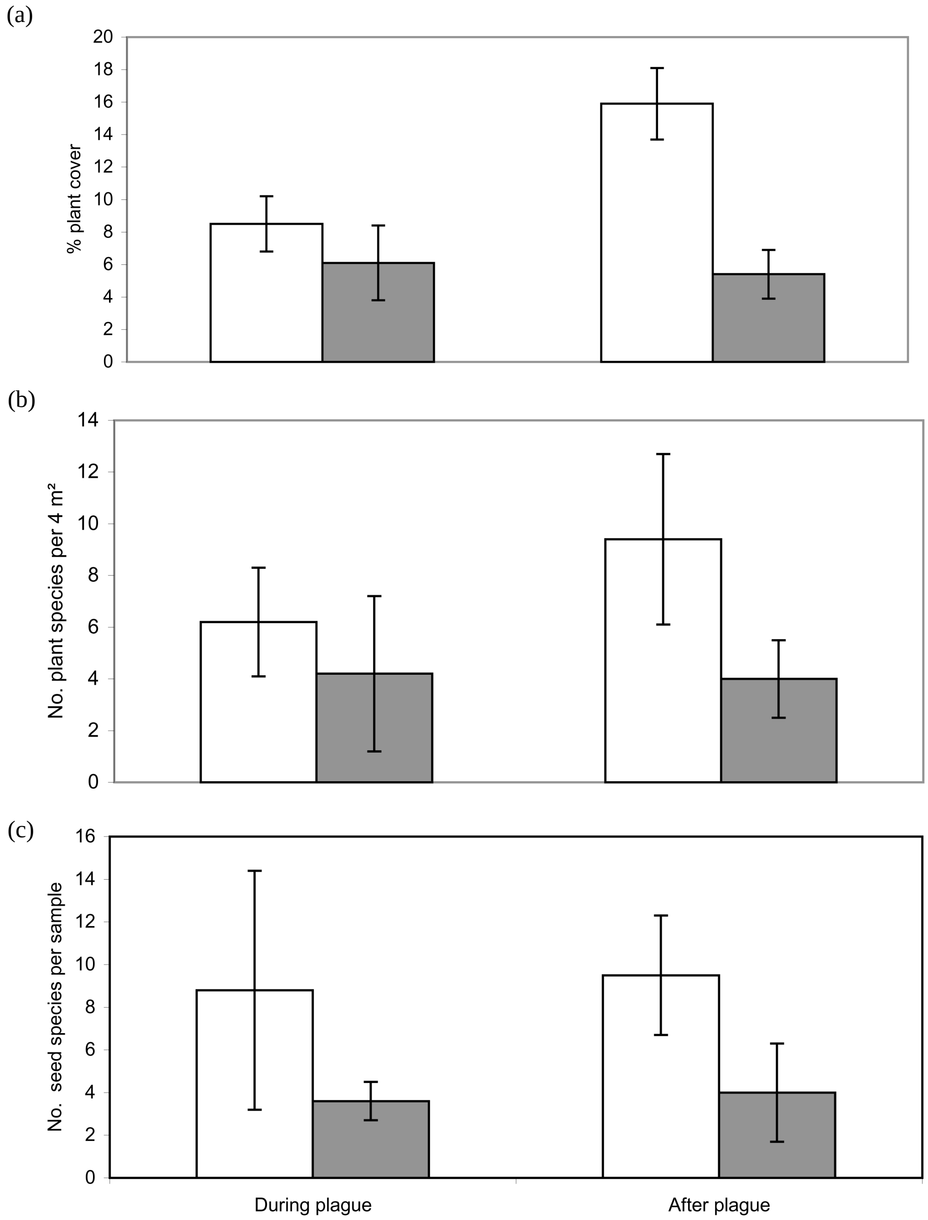

Figure 1. Effects of the long-haired rat, *Rattus villosissimus,* during and after plague conditions on (a) % plant cover, (b) plant species richness, and (c) seed species richness in the Simpson Desert, Queensland. Means are shown ± standard deviations. White bars represent samples taken on burrow complexes, black bars represent samples taken from undisturbed sites >50 m away. Analyses of variance were significant for all comparisons made after the rat plague and for seed species richness during the plague (*F*-values range from 6.5–22.8, df = 1,18, $P <$ 0.05), but not for % plant cover and plant species richness during plague ($F < 2.1$, df = 1,18, *P* = not significant).

There is some evidence that fungi, including mycorrhizae, also are more abundant in the disturbed soil around rodent burrows (Hawkins 1996), and it is possible that such fungi assist in the establishment of vascular plants. Interestingly, positive effects of rat burrows on plant cover and plant species richness in the present study did not become obvious until rat numbers had declined. This suggests that the positive effects of the rodents may be lagged, or that there is a trade-off between enhanced germination and establishment around burrows and direct predation by rodents of young plant shoots.

A further environmental effect of rodent burrowing is the creation of underground shelters for other organisms. Although this study showed that at least 17 other taxa of vertebrates opportunistically used rodent burrows, it is not clear what effect this may have on their population sizes. Nor is it clear that burrows were in short supply when observations were made. Nevertheless, the association of lesser hairy-footed dunnarts with long-haired rat and other rodent burrows, and their switch to using rodent burrows more heavily when the burrows were available, provides some support for the view that the burrows represent a valuable resource.

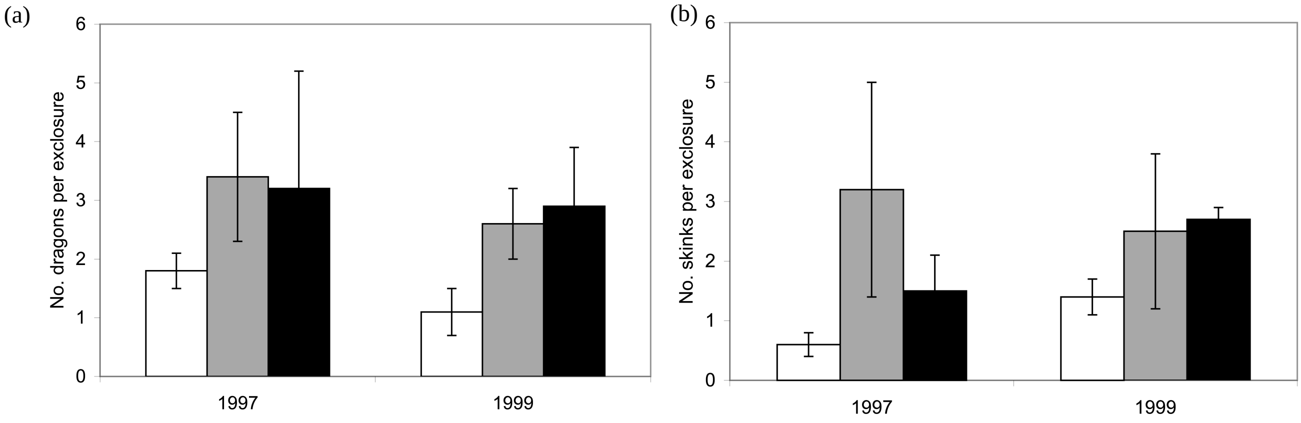

Figure 2. Effects of experimental exclusion of rodents in two years on numbers of (a) military dragons, *Ctenophorus isolepis*, and (b) panther skinks, *Ctenotus pantherinus*, within fenced plots in the Simpson Desert, Queensland. Means are shown ± standard deviations. White bars represent experimental exclusion plots, grey bars represent fence control plots, and black bars represent open control plots. Analyses of variance were significant for all comparisons: dragons 1997 ($F = 4.7$, df = 2,15, $P < 0.05$), 1999 ($F = 6.1$, df = 2,15, $P < 0.05$); skinks 1997 ($F = 7.5$, df = 2,15, $P < 0.01$), 1999 ($F = 6.4$, df = 2,15, $P < 0.01$).

Except for the carnivorous mulgara, *Dasycercus cristicauda*, none of the dasyurid species in the Simpson Desert dig their own burrows—all depend critically on the burrows created by other species. In the absence of any other apparent interactions between these marsupials and rodents, it is likely that dasyurids derive net benefit from using the shelter resources that rodents create.

Exclusion of rodents from small experimental areas led to declines in the activity of two species of lizard. In contrast to the results for plant cover around long-haired rat burrows, plant cover increased in the experimental plots in the absence of rodents, and it was this increase in cover that appeared to depress foraging activity in the lizards. Rodents show some preference for fresh spinifex seed in captivity (Murray and Dickman 1997), and may diminish its establishment by depredating its seeds in the field. It is unlikely that spinifex seed requires undisturbed soil conditions for germination, as seedlings have been observed in highly disturbed cattle pads and near vehicular tracks (unpublished observations). If this is so, the results can probably be interpreted as an indirect biotic interaction, in which seed predation by rodents depresses spinifex cover and in turn increases the foraging opportunities for lizards in open areas. Similar experimental evidence suggests that foraging by kangaroo rats suppresses the cover of grass and facilitates open foraging areas for granivorous birds; if the heteromyids are removed, grass cover increases and bird numbers fall (Thompson et al. 1991).

These preliminary results show that rodents can have positive effects on a range of taxonomically unrelated organisms in arid systems. It is premature to conclude that such effects are as important as competition, predation, weather or other processes that have received more extensive study, but the elucidation of positive interactions between rodents and other species clearly warrants further research. Establishing the relative importance of positive biotic and environmental effects should be a profitable line for further research; so too should be carefully planned experimental work that documents the magnitude of positive effects at the population level of interacting species.

Acknowledgments

I thank Gayle McNaught, Fiona Qualls, Bobby Tamayo and many others for assistance in the field, David and Paula Smith for hospitality at Ethabuka, Mathew Crowther for commenting on the manuscript, and the Australian Research Council for funding.

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Feasibility of non-lethal approaches to protect riparian plants from foraging beavers in North America

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Abstract. Beavers in North America will occupy almost any wetland area containing available forage. Wetland restoration projects often provide the resources necessary for dispersing beavers to create desirable habitats. Their wide distribution and ability to disperse considerable distances almost assure that beavers will establish themselves in new wetlands. Although beavers are a natural and desirable component of a wetland ecosystem, their foraging behaviours can be destructive. Fencing may be a feasible approach to reduce damage to small, targeted areas, and textural repellents may provide some utility to protect established trees. However, these non-lethal approaches will be marginally effective when beaver populations become excessive. Beaver populations need to be maintained at levels that permit viable colonies while still permitting plant communities to flourish. This will require a better understanding of beaver movements, site and forage selection, and reproductive characteristics. This is particularly true when management objectives and regulations prohibit beaver removal from project sites.

Introduction

Beavers (*Castor canadensis*) occupy wetlands throughout most of North America (Hill 1982; Miller and Yarrow 1994). Pristine range for these aquatic mammals included almost any site containing a continuous water source and winter forage (Hill 1982). However, trapping pressure during the late 1800s caused a significant decline in beaver numbers. Populations estimated at 60 million before European arrivals were nearly exterminated by 1900 (Seton 1900). Over the past century, beaver populations have rebounded primarily because of trapping regulations and translocation programs conducted by wildlife agencies (Hand 1984). At present, beavers are once again established throughout their original range and some dispersing animals have invaded previously unoccupied sites (Wilson and Ruff 1999).

Beavers often modify environmental attributes (Rutherford 1955). Given a water source, beavers are probably the most capable species, except humans, at creating suitable habitats for themselves (Hand 1984). Beavers dams and resultant ponds have benefited riparian restoration projects (Albert and Trimble 2000). Beaver ponds create standing water, which increases vegetation diversity and edge effects, and reduces erosion (Hill 1982). These attributes generally benefit other wildlife species (Rutherford 1955). Although beavers are a natural and desirable component of a wetland ecosystem, their behaviours can be destructive. Reduced water flow is detrimental to some fauna, and high beaver populations can negatively impact on native plant communities (Hill 1985). Extensive foraging can destroy plant restoration projects (Nolte 1998). Beavers have severely hampered efforts to establish vegetation to improve salmon habitat in the Pacific Northwest (DuBow 2000).

Excessive beaver activity was credited for destroying vegetation established by the Tres Rios Riparian Restoration Project, near Phoenix, Arizona, United States of America (USA). This project converts treated city waste water into wetland areas. Tres Rios has established small wetland habitats occupied by a variety of flora and fauna. Although animal foraging on plant materials is a natural component of a balanced ecosystem, beaver activity at these sites became destructive. Some areas were rendered barren of aquatic plants because of heavy foraging by beavers. Numerous trees, primarily cottonwood (*Populus deltoides*) and willow (*Salix* spp.), were cut or girdled, and extensive burrowing undermined dikes and islands. Visual signs, including burrows, clipped vegetation, and runways, all indicated high beaver numbers. Spotlight-surveys counted 14 animals within a single evening. A prior study indicated that spotlight-surveys reveal approximately 33% of actual beaver densities (unpublished data). Thus, beaver populations on these sites were estimated to be between 34 and 50 individuals on the 4.5 ha site. Further, a nearby river serves as a continuous source for additional animals to invade the site. Beavers may be coming from the river to forage on vegetation surrounding the demonstration sites. Roads surrounding demonstration ponds were marked by beavers dragging cut trees across them, and evidence suggested beavers were using the demonstration ponds as corridors to reach and cut larger trees.

Although the Tres Rios group recognised that beaver activity had to be suppressed, they did not consider lethal removal a viable option. Capture and removal also was not possible because beavers already occupied the desirable habitat in Arizona. Placing additional animals in these areas would have only made new animals vulnerable to starvation, or caused displacement of existing animals. The only alternative options were to exclude beaver from desirable plants, or reduce desirability of plants or the site. Objectives of this study were to assess the: (1) efficacy of fencing and frightening devices to protect aquatic vegetation; (2) efficacy of fencing, frightening devices, and textural repellent to reduce gnawing of cottonwood trees; and (3) impact of these non-lethal approaches on other wildlife species.

Study area

The Tres Rios Project is located in Maricopa County, Arizona. The area is approximately 14.8 km in length and 1.6 km wide and encompasses approximately 2,250 ha. The Salt River flows into the Gila River just upstream of the 115th Avenue crossing. The Aqua Fria River flows into the Gila River near the demonstration end of the study area. Elevations vary from about 285 to 310 m. Irrigation channels crisscross the surrounding area—otherwise, standing water is scarce. Mean annual precipitation is less than 20.5 cm. The potential evapotranspiration is slightly less than precipitation during January, and greater during all other months. Ecological communities within the vicinity of the project area have been broadly assigned to three categories: desert wash or riparian, desert outwash plain, and desert upland.

The study was implemented on the Tres Rios demonstration plots. These plots consist of approximately 4.5 ha emergent marsh and free-water surface wetlands. Cobble and Hayfield sites each contained two ponds similar in size, approximately 0.8 ha on the Cobble and 1.2 ha on the Hayfield. Terrestrial plots (4 × 4 m) were established along the perimeters of these ponds, in areas known to have been frequented by beaver. Plot corners were marked with a metal T-post. A minimum interval of 8 m separated plots.

Materials and methods

The study indirectly measured beaver response to control measures by monitoring amount of damage inflicted to cottonwood stems and aquatic plants. Beaver numbers were unknown, but attempts were made to establish each experimental replicate within separate beaver colony territories. Replicate independence, however, was most likely compromised because of pond size and beaver movements.

Aquatic treatments

An aquatic replicate was established at each end of the two Hayfield ponds. Three treatments and an untreated control were randomly assigned among the four plots established within each of these four replicates. Treatments implemented to protect aquatic vegetation were an electronic frightening device, an electro-shocking device, and fence. The electronic devices were located in the centre of the plot, and the fence encircled the plot perimeter. Electronic frightening devices were created by attaching a CritterGitter (AMTEK, San Diego, California) to each side and 5 cm from the bottom of a 10.2 × 10.2 cm post. A flashing light (Enhancer Model EH/ST-1) was attached immediately above each CritterGitter. A 5 cm hole centered through the post core permitted the frightening device to be installed over a metal T-post. The device was set atop and secured to a flotation platform that maintained the motion detectors a few centimetres above water level. An electro-shocking device, previously developed by the National Wildlife Research Center scientists for beaver dispersal in water, was modified to be triggered by the frightening device. Therefore, this device was the same as the frightening device, except the surrounding water received a low electrical current when activated. This current causes a tingling sensation at the perimeter of the electrical field or a mild shock at the central post. The perimeter radiated approximately 2–3 m around the central post. A switch operated by remote control activated the device. The fence exclosures were constructed with 2 m metal T-posts set at plot corners, and a 0.95 m high, woodland-green vinyl-coated, 5 cm mesh, 0.095 core 9 gauge chain-link fence. Untreated plots were marked by installing T-posts at each corner of the plot. Equipment status was recorded and repaired at 1-week intervals if necessary.

Four 4 m line-transects were used to monitor changes in aquatic vegetation. Transects ran parallel to the bank. A transect was stretched from a randomly selected point to the same point on the opposite plot side within each quarter (1 m) of a plot, to stratify placement. Species composition and cover were determined by recording the intercept distance for each species that crosses a line-transect. Vegetation was monitored when the trials were implemented and then at 2-week intervals for 4 months. A photographic record was kept for each plot at the same 2-week intervals.

A one-factor analysis of variance with repeated measures was used to determine whether aquatic plant cover varied among treated plots over time. Plant cover was the dependent variable. The treatment factor had four levels and bi-weekly monitoring was the repeated measure (eight levels).

Terrestrial treatments

Two terrestrial replicates were established on islands within ponds on the Cobble sites and two replicates were placed along the banks of the Hayfield ponds. Each replicate consisted of four plots containing nine cottonwood stem segments (8–20 cm diameter) at 1 m intervals and 1 m from the plot edges. These stems were collected from a stand near the Tres Rios demonstration plots. Each 2 m stem segment was buried upright to a depth of approximately 1 m, leaving 1 m of the stem exposed above ground. Three treatments and an untreated control were randomly assigned to one of the four plots established along each pond. Treatments in this trial were an electronic frightening device, a textural repellent, and a fence. The electronic frightening device was the same as described above except set at ground level. Textural repellent was a simple mixture of 70 mil sand and alkyd paint (140 g/L). The mixture was kept well mixed until painted evenly on cottonwood stems. A fence was constructed as described for the aquatic treatments. Untreated plots were marked by installing a metal T-post at each corner of the plot.

Damage to the cottonwood stems inflicted by beavers was recorded when the trials were implemented and then at 1-week intervals for 4 months. Damage intensity was scored from 0 to 7 for each stem by visual estimation: 0 = no damage; 1 = tooth marks; 2 = <10% bark removed; 3 = 10–25% bark removed; 4 = 25–75% bark removed or stem gnawed less than 25% through; 5 = 25–75% bark removed or stem gnawed between 25 and 50% through; 6 = >75% bark removed or stem gnawed between 50 and 75% through; 7 = stem gnawed through. Damaged stems were not replaced. Equipment status was recorded and, if necessary, repaired at 1-week intervals.

A one-factor analysis of variance with repeated measures was used to determine whether damage inflicted to cottonwood stems varied among treatments over time. Damage scores were the dependent variable. Treatment was the comparative factor (four levels) and weekly recordings were the repeated measures (16 levels).

Plot observations

An observational point overlooking all four plots within each replicate was identified where activity could be observed with minimal disturbance for most native fauna. Bird and mammal activity was observed from these points on each pond for 30 minutes on a fixed schedule: dawn (–1 to +1 hour of sunrise); mid-morning (+2 to + 4 hours post-sunrise); late afternoon (–4 to –2 hours before sunset); and dusk (–1 to +1 hours post-sunset) once every 2 weeks. Night (+3 to + 8 hours post-sunset) observations were made once every 4 weeks. Observation order was counter-balanced among replicates, and all observations for a specific fortnight were made within a 4-day period. Species present and activity (e.g. swimming, perched) were recorded for each plot at 1 m intervals. Vegetation surrounding terrestrial plots inhibited similar observations. However, species or an indicator observed while conducting other activities were recorded.

Species sighted and individual responses were recorded and summarised. Statistical comparisons among treatments were not conducted.

Results

Aquatic plant cover increased over time (*P* < 0.0001) regardless of treatment (*P* > 0.35; Figure 1). Overall plant cover increased by approximately 60% during the study. Mean cover within a plot at the start of the study was 420 cm, and mean cover by the end of the study was 713 cm. There was no interaction between treatment and time (*P* > 0.35).

Damage to the cottonwood stems also increased over time (*P* = 0.0014), but was not significantly different among treatments (*P* > 0.35; Figure 2). No beaver activity was observed on the Hayfield site. Therefore, the analysis was repeated using only replicates with activity recorded on at least one plot. Results were similar—damage increased over time (*P* = 0.0018) with no differences detected among treatments (*P* > 0.35). There were no interactions (*P* > 0.35). Overall, beavers inflicted minimal damage to cottonwood stems during the study. However, mean damage scores collected during the last survey were probably indicative of the potential efficacy for each treatment. The mean damage score for control plots was 1.95 (se = 1.90). The mean damage score was higher for plots with the electronic frightening device (2.39, se = 1.03) and

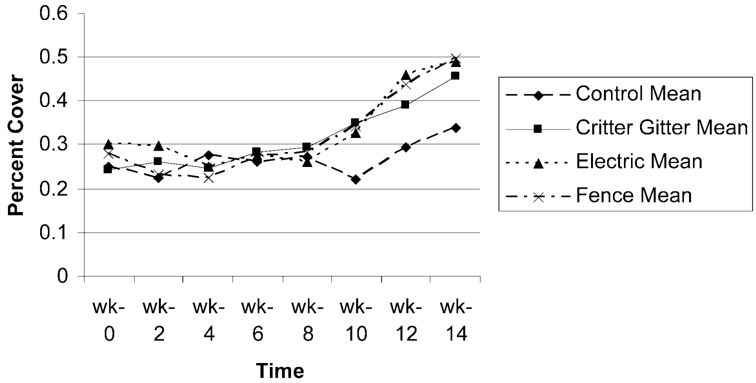

Figure 1. Mean percentage plant cover on plots with fencing, a frightening device, an electro-shocking device, or an untreated control at the start and at 2-week intervals throughout the study.

lower for stems treated with the textural repellent (0.89, se = 0.78). There was no evidence that beaver entered fence plots, which was reflected in the mean damage score (0.0, se = 0.0).

Numerous birds (70 species), mammals (10 species), and reptiles/amphibians (5 species) were observed at the Tres Rios site during the study. Other than during the first few hours, the electronic devices appeared to have minimal impact on target or non-target species. Some waterfowl developed nests within a few metres of the devices. Fences appeared to have impeded mammal movements and restricted swimming birds. Birds were observed perching on the fences and American coots (*Fulica americana*) constructed nests inside the exclosures.

Discussion

Minimal beaver activity was observed during the study. Beavers were frequently observed the year before and their impacts on aquatic vegetation and nearby trees were considerable. Why beaver activity declined is unknown. Increasing human activity may have contributed to the demise of beavers. Although hunting is prohibited, humans may have had a negatively impact on beaver populations on developed property, thus creating a sink for animals to disperse and greatly limiting a source for invading animals. However, if humans contributed or caused a decline in beaver numbers, then a rebound in the beaver populations can be anticipated. Human activity will decline as the project progresses and better protective measures are implemented. It also is possible that manipulating the mineral content of effluent discharged into the wetlands rendered the water less desirable to beavers. Natural predators most likely account for some beaver mortality, but predation pressure has likely not changed over the past year.

Regardless, the Tres Rios wetlands provide optimum beaver habitat and beavers will continue to occupy these sites. Beavers should be considered a desirable component of these wetland habitats. A high beaver population, however, can be a destructive force (Miller and Yarrow 1994). Aquatic vegetation may once again decline and mature trees will likely disappear. Eventually, existing vegetation will be replaced by less palatable and highly competitive species, such as salt-cedar. As a result, beaver populations can be expected to decline once habitat quality declines. Thus, a natural ‘balance’ between beavers and vegetation components of the system will eventually be achieved. Beavers are the primary, non-human force determining wetland habitat conditions (Hill 1982). Unfortunately, vegetation status in ‘balance’ with high beaver activity can be anticipated to be well below current or desirable status, such as an extensive wetland and riparian flora supporting a diverse fauna.

Although minimal damage occurred, the study did provide insight into the feasibility of the non-lethal approaches tested. The electronic frightening device was ineffective for any prolonged period. Beavers and muskrats were observed swimming along plots protected by these devices. Activated devices appeared to have minimal impact on their behaviour. Further, cottonwood stems protected by these devices were frequently damaged. These results are similar to reports of attempts to apply frightening devices to deter other species. Frightening devices (e.g. artificial light, automatic exploders, pyrotechnics) rarely work for more than a few days or at most a week (Koehler et al. 1990). Incorporating the shocking device as implemented in this study did not appear to improve efficacy in deterring animals. Efficacy could probably be improved by increasing electrical current. However, associated potential hazards may render this device unacceptable for use in publicly accessible areas. A positive attribute was that non-target species did not appear to be negatively impacted by either device. Species observed and behaviours exhibited did not vary among treatments. Regardless, these devices have minimal long-term utility for deterring beavers. They may work well, however, if installed in stream channels to inhibit beavers from repairing dams for a few days, permitting short-term water drainage.

Effective repellents render a plant less attractive to foraging animals. An animal may select one plant over another because it is attracted to the first or because it is avoiding the alternative (Galef 1985). Thus, the likelihood

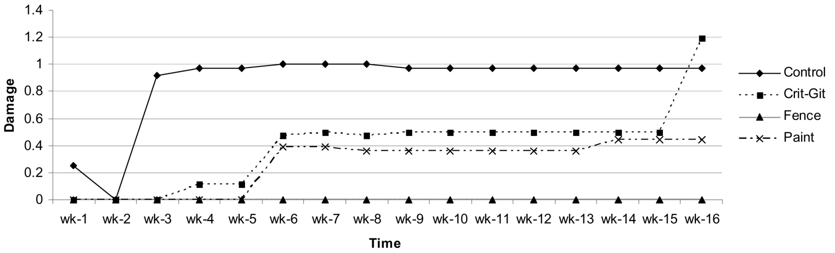

Figure 2. Mean damage scores for plots containing cottonwood stems treated with fencing, a frightening device, a textural repellent, or untreated controls at 1-week intervals throughout the study. A damage score of 0 indicates none of the stems were damaged, while a score of 7 indicates all stems were cut down by beavers.

of a particular plant being eaten depends on its own palatability, and availability and desirability of alternative foods (Nolte and Mason 1998). Chemical repellents have limited utility to reduce gnawing by beavers (unpublished data). However, chemical repellents can reduce damage when applied directly to foliage consumed by beavers (DuBow 2000). Label restrictions may severely restrict applying chemical repellents in riparian zones. Textural repellents may offer an alternative. Cottonwood stems painted with the textural repellent were damaged less than control stems or stems planted near frightening devices. Textural repellent, however, did not totally impede gnawing. A few trees were cut and others were stripped of bark. These results were less supportive than pen trials assessing efficacy of textural repellents to reduce beaver gnawing on cottonwood stems (unpublished data). Untreated stems or stems painted with untreated paint were severely damaged during this 2-week trial, while treated stems received minor damage. Eight of ten beavers completely avoided stems treated with 30 mil sand, and gnawing by the other two beavers was very limited. Painting cottonwood stems in this study did not adversely affect vigour of the stems. Buds sprouted through the paint and new foliage appeared.

Beavers did not penetrate fences installed on aquatic or terrestrial plots. Fencing is a feasible approach to reduce foraging pressure while plants are established. Beavers do not climb, so fences need not be constructed very high. Fences installed for this study were not visually obtrusive because they were relatively short, often protruding above water less than 0.5 m and their green colour-coated vinyl blended with vegetation. Extensive fencing, however, will be expensive and probably require considerable maintenance. The small fenced plots used in this study had minimal impact on non-target species, probably because animals could easily move around the perimeter. However, extensive fencing would impede movements of some species. Aquatic mammals also are less likely to circumvent a large fenced area. Beavers are capable of burrowing beneath a fence, thus regular monitoring for tunnels would be necessary—a rather difficult task for fences installed in murky waters.

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Balancing rodent management and small mammal conservation in agricultural landscapes: challenges for the present and the future

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Abstract. Rodent conservation poses special challenges, especially where the separate imperatives of small mammal conservation and pest rodent management meet and potentially collide in an agricultural landscape. Rodent management or control actions can have potentially deleterious impacts on small mammals and other wildlife, especially where non-selective methods such as poisons are applied. However, without rodent pest management, native species may be at risk from aggressively invasive species such as the black rat, Rattus rattus, and from novel pathogens carried by the pest rodents. Our ability to identify and mitigate these potential impacts is currently limited by a lack of knowledge in a number of key areas. In some parts of the world, for example across much of South and Southeast Asia, we are presently unable to say which species are 'native' and which are recently 'introduced' or 'naturalised'. Additionally, there is often little hard evidence to say which rodent species cause significant damage to crops and which may bring ecological benefits that outweigh any crop losses. Finally, the nature of interactions between pest rodents and other small mammals (including non-pest rodents) are poorly understood, such that it is difficult to predict the outcomes of not acting to control pest rodents in areas of shared agricultural and natural heritage value. Where agriculture and conservation meet, rodent control strategies need to be developed in a broad systems framework.

Introduction

Rodents hold the dubious distinction of being one of a small number of vertebrate groups where the effort put into eradication and control vastly outweighs that put into conservation. The bad public image of a small number of rodent species undoubtedly contributes to the relative lack of effort put into rodent conservation (Amori and Gippoliti 2000). This situation is made less palatable by the fact that 384 species of rodents are currently classified as 'vulnerable', 'endangered' or 'critically endangered' (IUCN 2000); and even more so by the undeniably important role that many rodent species play in maintaining ecosystem functions (Dickman 1999).

Rodent pests represent a significant constraint to production in many agro-ecosystems, and especially so in grain-producing systems (Meehan 1984). Globally, estimates of pre-harvest losses to rodent typically fall between 5–15% in rice, wheat and maize production systems, with more extreme, episodic losses in systems that experience irruptive rodent outbreaks, driven either by climatic fluctuations or by pulsed environmental resources (Singleton and Redhead 1990; Douangboupha et al., this volume). In many areas, the scale of chronic crop losses to rodents is said to have increased in recent decades. This is sometimes attributed to intensification within the crop production system as a consequence of the 'Green Revolution', however, in some cases, it is also clearly linked to changes in market systems (Singleton, Kenney et al., this volume). Post-harvest losses in some areas match or even exceed the pre-harvest damage.

Rodent pest management by traditional methods often targets specific habitats and therefore specific taxa, even where the methods themselves (e.g. snaring) are non-selective (Singleton et al. 1999a). However, more recent developments, especially the trend towards increasing reliance in many countries on various categories of rodenticides, have brought to the fore major concerns regarding the wider conservation implications of rodent management (Buckle 1999; Singleton et al. 2002). The emergence of ecologically based rodent management (EBRM) as a general philosophy is a positive development in this regard (Singleton et al. 1999b). However, there are a number of important but largely unexplored issues that revolve around the sometimes competing requirements of rodent pest management and small mammal conservation in agricultural landscapes. This paper represents an initial step towards exploring some of these issues.

We begin by discussing how to distinguish true pest rodents—species that we might wish to control or even eradicate—from non-pest rodents that we might wish to conserve and even propagate in the local environment. We then focus attention on some of the key biological and biogeographical factors that individually, and in combination, pose the major threats to the survival of small mammal populations in agricultural landscapes. And finally, we will attempt to identify some of the present and future challenges for the successful integration of rodent pest management with small mammal conservation. Our illustrative examples will be drawn primarily from three contrasting agro-ecosystems in which we have conducted field research, namely: (i) the wheat-producing belt of southern Australia; (ii) the intensive rice-production systems of the Mekong and Red River Deltas of Vietnam; and (iii) the zone of shifting cultivation in the uplands of Lao PDR (Laos).

Pest and non-pest rodents

In the Australian context, the terms 'exotic' and 'pest' are virtually synonymous when applied to rodents, despite the fact that there are more than 60 species of native rodent, a majority of which are not pests. Across southern Australia, the three rodents that might be regarded as 'pests' were all introduced after European colonisation. These are the house mouse (*Mus domesticus*), the black or ship rat (*Rattus rattus*) and the Norway rat (*R. norvegicus*). Of these species, the house mouse is far and away the largest agricultural pest. This species undergoes periodic and spectacular irruptions in parts of the grain-growing country of southern and eastern Australia (Singleton and Redhead 1990). *R. rattus* is a pest in orchards and vegetable crops (White et al. 1998), but there are few quantitative data on the scale of damage inflicted. All three species are also significant urban pests—both *Rattus* species do considerable structural damage in buildings (Meehan 1984) and pose a significant, albeit as yet poorly documented, human health risk (Singleton, Smythe et al., this volume).

In northern Australia, a number of native rodent species are agricultural pests: *Rattus sordidus* and *Melomys burtoni* in cane-growing systems (McDougall 1947); *Rattus colletti* and *Rattus* sp. cf. *villosissimus* in the rice-growing areas around Kununurra in north-western Western Australia (Watts and Aslin 1981); and *Rattus* sp. (an undescribed member of the *sordidus* group) in a wheat-growing area of central Queensland (G. Gordon, pers. comm.). Local control activities are carried out against each of these taxa, with the most intensive and widespread campaigns being waged against *R. sordidus*.

In the Southeast Asian context, the distinction between 'pest' and 'non-pest' species and 'native' and 'introduced' species, is far from straightforward. Some species, including the house mouse and the Norway rat, are generally found only around the major towns and these are universally regarded as exotics. However, once we move out into the agricultural landscape, confusion soon replaces consensus. This confusion derives from two sources—uncertainly over exactly which species are responsible for damaging crops; and uncertainty over the 'indigenous' versus 'exotic' status of each species in any given region.

One species about which there is general agreement, at least in regard to culpability, is the rice-field rat, *Rattus argentiventer.* This species can attain extremely high population densities in lowland rice-growing areas of Indonesia, Malaysia and Vietnam, and is regarded as a major cause of crop damage in these countries (see Singleton and Petch 1994) but not, for as yet unexplained reasons, in Thailand (Boonsong et al. 1999). The wider distribution of the rice-field rat extends from Thailand to the southern Philippine Islands and the far-eastern Indonesian province of West Papua. Musser (1973) noted that this species is always reported from anthropogenic habitats and is unknown in the wild state. He attributed the more easterly parts of its range to human-assisted dispersal, but was otherwise unsure of its original or 'native' distribution. Studies of the mitochondrial cytochrome b gene so far reveal little or no variation in *R. argentiventer* samples from across a large part of its range (H. Suzuki and A. Chinen, pers. comm.). This suggests a recent, rapid phase of range expansion—by implication, the rice-field rat is probably not 'native' across most parts of its current range.

Some other species that fit the same general profile are the Pacific rat, *R. exulans*, the lesser rice-field rat, *R. losea*, the black rat, *R. rattus*, and the giant bandicoot, *Bandicota indica* (Aplin, Chesser and ten Have, this volume). Each of these species has a broad geographical range, each is most often encountered in anthropogenic habitats, and each is reported to cause damage to particular crops. Moreover, for each of these species, significant doubts have been expressed previously regarding the 'original' geographical range of the species.

The Pacific rat occurs from Bangladesh and the Andaman Islands in the west, to New Zealand and Easter Island in the east. It is everywhere closely associated with human activities. Musser and Newcomb (1983, p. 523-524) remarked on the morphological uniformity of *R. exulans* across its range and postulated a possible origin somewhere in mainland Southeast Asia. As reported by Aplin, Chesser and ten Have (this volume), *R. exulans* occurs in the 'wild state' (i.e. living in montane forest, far away from any villages or agricultural activity) in the central highlands of Indonesian Timor. However, the Timorese archaeological record appears to document the arrival of *R. exulans* within the last few thousand years, along with the disappearance around the same time of a suite of endemic rodents (Glover 1986). The history of *Rattus* on Timor may represent a good instance of 'naturalisation' of exotic species (a form of *R. rattus* also lives in the montane forests), either contributing to, or perhaps consequent upon, the extinction of a native fauna. We will return to this point below.

The lesser rice-field rat is a significant agricultural pest across all or most of its range. However, unlike *R. argentiventer*, it does show some geographical patterning in both morphology and in cytochrome b variation (K. Aplin, T. Chesser and J. ten Have, unpublished data). It is also known from 'natural' habitats, as high as 900 m in China, Vietnam, Laos and Thailand. Nevertheless, within some parts of its range, *R. losea* is clearly associated with rice fields and there can be little doubt that it has undergone a substantial increase in geographical range and in local population densities. Perhaps for this species we can be confident that it is regionally 'native'; however, at a local scale its status remains equivocal.

The black rat group presents an even more complex picture. This group probably comprises three or more distinct species (Aplin, Chesser and ten Have, this volume), each of which has almost certainly moved around in company with people for many thousands of years. For example, one of two very distinct East Asian species is widespread, ranging at least from Japan to Bangladesh, yet there is no indication of geographical substructuring in the cytochrome b gene. In a growing number of localities, two distinct forms of *R. rattus* are known to be living side by side, with some instances of hybridisation reported. Across Southeast Asia, members of the *R. rattus* group are typically found in and around villages. However, in parts of the Philippines, in the uplands of Laos and in Thailand east to parts of the Indian subcontinent, the local variants of the *R. rattus* population are found in rice fields where they can wreak substantial havoc (Khamphoukeo et al., this volume). In Laos, *R. rattus* also occurs in forest habitats, but whether these populations are viable without replenishment from the agricultural landscape is not known. In our experience, the only true 'wild' population of *R. rattus* is that encountered by K. Aplin in remote montane forest at 1500 m elevation in Indonesian Timor; as noted above, this population is almost certainly 'exotic' but 'naturalised'.

As a final example, *Bandicota indica* is perhaps the epitome of uncertainty. This species, if indeed it is only one (Aplin, Frost et al., this volume), has a huge geographical range that extends across most of India, Sri Lanka, Nepal, Bangladesh, Myanmar, Thailand, Laos, Cambodia, Vietnam and southern China. The giant bandicoot was introduced historically to Taiwan and the Kedah and Perlis regions of the Malay Peninsula (Musser and Brothers 1994), and possibly prehistorically to Sumatra and Java (Musser and Newcomb 1983). At least within Southeast Asia, this species is closely associated with anthropogenic habitats and it never seems to extend very far into forest. Despite this seemingly classic commensal pattern, there is evidence of some genetic diversity within the group (K. Aplin, H. Suzuki, T. Chesser and J. ten Have, unpublished data). However, for the present we cannot rule out the possibility that this diversity was introduced in original stock from different localities. Finally, there is some uncertainty as to just how much damage *B. indica* really does in the rice-growing systems (Aplin, Frost et al., this volume). The species often digs its burrows in and around the rice-field habitat and its trackways can be seen leading into the rice crop. However, its preferred diet probably consists of various rice-field invertebrates, including snails and crabs, and there are indications that breeding activity is not linked to the availability of rice crops. Although these data are admittedly incomplete, there are certainly grounds to question whether *B. indica* might not, in some circumstances at least, be doing more good than harm in the rice-field environment through predation on insects, crabs and other potential crop pests. The same question might be asked of other supposed pest species, including the various species of *Mus* (e.g. *M. caroli* and *M. cervicolor*) that occur in the agricultural landscapes of Southeast Asia.

These examples illustrate some of the difficulties involved in deciding whether an agricultural rodent species is 'native' or 'exotic' and also whether or not it is technically a 'pest'. Many other examples could be cited from South Asia and from other parts of the world—anywhere, in fact, where there has been a long history of landscape modification and either deliberate or accidental movement of rodents.

One way of testing whether a species preserves any vestige of its original distribution pattern is to examine its phylogeographical structure, that is the geographical pattern of genetic variation (Arbogast and Kanagy 2001). In general, where genetic patterning contains a strong geographical signal, there is a good chance that the distributions are partly original. The next step is to then look at the distribution of genetic variability—populations with high variability are likely to be within the original source area, while populations with very low variability are more likely in areas where the species is invasive and derived from the introduction of a few individuals. Of course, other explanations might be found to explain differences in genetic variability, hence this kind of analysis may produce equivocal results.

A second approach is to seek information on the 'original', preferably pre-agricultural, rodent fauna of an area. This would usually come from analysis of bones and teeth from ancient owl-pellet accumulations. Archaeological collections, the remains of ancient food items, are also potentially informative. In Australia, remains of this kind have been of fundamental importance in reconstructing the original fauna of many areas. Very few studies of this kind have been undertaken for mainland Asia.

There is far less ambiguity for rodents that have their major distributions in natural vegetation. However, the examples cited above of introduced *Rattus* species living in montane forests of Timor can be matched by similar examples of 'naturalised exotics' from elsewhere in the world (e.g. Madagascar; Lehtonen et al. 2001). Such occurrences are admittedly in the minority, nevertheless they urge caution in the classification of any population as being in a 'wild state' and thus within its 'natural range'.

The importance of habitat disturbance and heterogeneity

Habitat disturbance in its various forms (outright destruction, alteration or simplification, fragmentation) is the single greatest threat to global biodiversity (Ehrlich and Ehrlich

1981). However, this simple observation belies a complex set of biological and biogeographical phenomena that are manifest in various ways and over contrasting time scales in different parts of the world, and which have combined to produce highly variable outcomes (Soulé 1995).

In some parts of the world, e.g. in Australia and across much of the Americas, the transformation of natural to agricultural landscapes is a comparatively recent phenomenon, intimately linked to the short periods of European occupation. In these areas, the impact on native fauna and flora typically has been catastrophic, resulting in the extinction of many native animals, especially mammals, and in some areas, the virtual disappearance of entire ecosystems (Saunders et al. 1987). While these changes have had catastrophic impacts on regional biodiversity, especially in Australia, the recency of the events also means that even relatively small patches of vegetation can retain significant conservation value. In the Australian grain-growing country, for example, many small to medium-sized patches of remnant vegetation support native birds, reptiles and amphibians, and sometimes even mammals. In the long term, each of these isolated populations is non-viable and bound for extinction. Accordingly, in Australia and elsewhere, a substantial proportion of conservation effort is directed, not only at maintaining the quality of the remnant vegetation itself, but also in the establishment of corridors that allow recolonisation and gene flow to occur (Saunders and Hobbs 1991).

In contrast, crop production in many parts of the ‘Old World’ has a far longer pedigree. In parts of China, this extends over eight millennia (Diamond 1997). However, more typically, the major agricultural landscapes of South and Southeast Asia, Europe and Africa have developed over the last 2–5 millennia. In most areas, this development occurred slowly at first, with a relatively recent acceleration of forest clearance and wetland conversion related to the recent escalation in population growth. For example, on the island of Java in Indonesia, agricultural activity probably began more than 5000 years ago, yet large parts of the island were still covered in primary rainforest until the onset of rapid population growth in the early years of the 20th century. Similarly, large areas of the highly productive Mekong Delta of Vietnam were first cleared of natural forest cover and turned over to broadacre rice cultivation only during the last 50 years, facilitated in part by canal construction during French colonial times (Brocheux 1995). Today, the Mekong River Basin represents Vietnam’s major area of rice production. In other parts of Southeast Asia, the process is more immediately ongoing, especially in parts of Kalimantan, Sumatra and southern Vietnam, where the rate of new forest clearance for agriculture rivals that of the more widely publicised Amazonian situation (Achard et al. 2002). As described above for Australia, small remnants of original vegetation may support remnant populations of native mammal species. One example is the survival of the squirrel *Callosciurus finlaysoni* in remnant *Melaleuca* forests in the Mekong Delta province of Kien Giang (Tam et al., this volume). Alternatively, native mammals may become adapted to the agricultural landscape and might even benefit from the increased food production. However, in the case of Kien Giang province, Tam’s results (Tam et al., this volume) suggest otherwise; only four rodents were captured during the rodent survey, the other three being widespread commensals.

Agricultural landscapes by definition are structurally simple and contain relatively low biotic diversity. At the extreme, such landscapes can be a virtual monoculture, with the only variability related to crop production cycles. However, more commonly, the cropping areas are broken up by other habitat types, including canals, roads, fencelines, rock outcrops or other areas of topographical relief, and human habitations (e.g. Figure 1). Small to medium-sized patches of remnant native vegetation sometimes punctuate the agricultural landscape. In areas under less-intensive forms of cultivation, such as ‘slash-and-burn’ or swidden agriculture, the landscape usually supports a more complex mosaic of habitat types. In such environments, the cropping area usually consists of active and abandoned fields in various stages of fallow. Moreover, the cropping area itself is often in close proximity to areas of primary vegetation along streams and on the steeper, slopes and ridgelines (Figure 2). In the uplands of Laos, villages are also located in close proximity to cropping areas.

The existence of heterogeneity within an agricultural landscape may have very different implications for rodent management and conservation. In the Australian context, fenceline and roadside habitats appear to be important refuge habitats that ensure the survival of populations of the house mouse (*Mus domesticus*) through fallow periods and allow rapid recolonisation of cropping systems after replanting (Mutze 1991). The same is possibly not true for larger patches of remnant vegetation. These are often blamed as a ‘source’ of mouse plagues, but one recent study showed that mouse populations in these patches only increased and commenced breeding after an upsurge in mouse numbers and breeding activity in the surrounding cropping areas (Singleton, Kenney et al., this volume). This important finding suggests that the larger patches of remnant vegetation may actually represent ‘sink’ habitats for the house mouse in this type of landscape; and further, that the biodiversity value of these remnants is therefore not likely to be compromised through the presence of exotic rodents.

In lowland grain-growing areas of South and Southeast Asia, the most common refugial habitats are levee banks of irrigation systems, elevated village complexes and small areas of ‘upland’ habitat; the latter may be uncultivated or may support alternative crop types (e.g. fruit trees, vegetables). These areas commonly show active or abandoned rodent burrows and animal trackways leading into adjacent crop production areas. In rice fields, small rodent species such as species of *Rattus* and *Mus* also dig breeding burrows in the low bunds used to demarcate fields and to control water flow. To date, these small-scale ‘refugial’ habitats have not been found to support populations of any small mammals other than ‘pest’ species of rodents. In part, this may reflect the much longer histories of modification of these landscapes.

Figure 1. A typical cereal-producing landscape in south-eastern Australia. Broad expanses of crop are broken by small patches of remnant vegetation and by other refuge habitats along fencelines and roads.

Figure 2. A typical rural landscape in the uplands of Laos. The village habitat is surrounded by active and abandoned gardens, with remnant forest on the upper slopes and ridgelines.

In the uplands of Laos, areas under shifting cultivation often support a rich variety of small mammals that includes both ‘pest’ and unambiguous ‘non-pest’ species (Khamphoukeo et al., this volume). The major pest species in all crop types (typically rice, maize and vegetables) is a member of the *R. rattus* complex and the same species is abundant also in villages. Interestingly, this species is also present in forest habitats, at least where these adjoin the agricultural landscape. Other ‘pest’ species commonly encountered within this landscape include *B. indica* and one or more species of *Mus*. Unambiguously ‘native’ rodents are most commonly caught in the forest habitat, but they also utilise the regrowth habitat and may enter traps set in upland fields, especially where these abut forest or mature regrowth. Such captures may be largely accidental, however it is not improbable that the native species are being attracted into the field by the readily available foods. One group of native rodents in particular, the rattan rats (*Leopoldamys* spp.), have been caught in sufficient numbers in upland cropping areas in Sekong province of southern Laos to suggest that they are making specific use of these areas as part of regular foraging territories. Although *Leopoldamys* species are known to be good climbers, nothing is recorded of their nesting requirements (Marshall 1977).

One group of native species that sometimes has burrow systems located within the cropping areas are the bamboo rats, members of the family Rhizomyidae. These highly distinctive rodents, comprising a minimum of four species in two genera, are found across much of Southeast Asia. As their name suggests, bamboo rats are often found in proximity to groves of bamboo and they probably all feed primarily on the rhizomes and young shoots—Marshall (1977, p. 392) noted some damage caused to cultivated tapioca and sugar cane. In the uplands of Laos, bamboo rat burrows, both active and abandoned, are frequently observed in and around active fields. However, farmers in Luang Prabang province reported that the burrows are constructed exclusively in areas of forest or regrowth, and come to be located in garden areas only when theses areas are subsequently cleared for cultivation.

The dynamics of the rodent communities that occupy the complex agricultural landscape of the Lao uplands are still poorly understood (Khamphoukeo et al., this volume). Rat population densities in the cropping areas clearly fluctuate through the year in response to the availability of food resources, with a decline to very low resident populations through the dry season. Village populations may be more stable and there is good evidence from several provinces in Laos that *R. rattus* breeds more or less continuously within the village habitat. There are strong grounds to suspect that that village acts as a ‘source’ habitat for *R. rattus*, with dispersal out into the fields once the cropping cycle is under way. Unfortunately, much less is known about population dynamics in the forest habitat, however it is at least possible that this habitat also acts as a source area for *R. rattus*. Alternatively, the forest may be a ‘sink’ that absorbs individuals at the end of the cropping cycle but supports little, if any, subsequent breeding.

These contrasting biological scenarios have quite different implications for rodent management in the upland cropping systems (Khamphoukeo et al., this volume). If the upland villages represent the major source habitat for the *R. rattus* population that attacks the crops, then a vigorous rodent control campaign in the villages just before the onset of the wet season might serve to reduce subsequent crop damage in the fields. This could be conducted without fear of non-target impact on native rodents, none of which have been trapped immediately around the villages. On the other hand, if the field population of *R. rattus* is derived in part or whole from the forest habitat, proactive rodent control might be very difficult without inflicting considerable harm on native species. One alternative might be to apply the trap–barrier system plus trap crop (TBS+TC) that has been successful in controlling rodent damage in lowland irrigated rice systems (Singleton et al. 1999a). However, there are significant technical challenges to be overcome before this system can be applied in the upland cropping environment.

The impact of introduced competitors and pathogens

There are major conservation issues related to the potential impact of *R. rattus* and other potentially invasive commensals on the forest small mammal communities including native rodents. Two aspects need to be considered: first, the potential direct impact of invasive species on native species through competition for resources; and second, the potential indirect impact of the introduction of novel pathogens into naïve native mammal populations.

Introduced competitors

In Australia, most attention has been given to the impact on native wildlife of introduced predators such as the cat and fox. Ecological studies of the three introduced rodents suggest that they compete poorly against native rodents in natural vegetation but are able to colonise heavily disturbed habitats such as recently burnt or cleared areas (e.g. Fox and Pople 1984). Provided populations of native rodents survive the disturbance processes, these will eventually rebuild and displace the introduced species, usually after 5–6 years. However, in areas where native rodents have declined to extinction for other reasons (e.g. predation), populations of *M. domesticus* and *R. rattus* can be found living in areas of mature natural vegetation (Menkhorst 1995). The close link between invasive success and intensive disturbance regimes is mirrored in many other groups of organisms (Hobbs and Huenneke 1992).

Little is known of the ecology of *R. exulans* in Southeast Asia. In Papua New Guinea, this species is most abundant in anthropogenic grassland, with smaller populations in villages, active and abandoned gardens, and areas of secondary or heavily disturbed forest (Flannery 1995). Areas of *Imperata* grassland in New Guinea also support smaller populations of two small-bodied, scansorial native rodents, *Melomys lutillus* and *M. rufescens* (Flannery 1995). These species have smaller modal litter sizes than *R. exulans* (Dwyer 1975) and it is possible that they may have declined following the prehistoric introduction of the Pacific rat.

In New Zealand, there is compelling evidence that the recently introduced black and Norway rats have displaced the earlier-introduced *R. exulans* across most of its original range (Roberts 1991). Indeed, the latter species generally only persists on smaller islands that have not been reached by the larger *Rattus* species, or where colonisation has been unsuccessful.

R. rattus was evidently introduced to Madagascar some time before the 11th century but it has only become pervasive over the last century (Goodman 1995). Today, it can be trapped in both secondary and primary forest (Lehtonen et al. 2001), even in the presence of native rodent species. The local abundance of *R. rattus* in Madagascar is clearly related to the level of habitat disturbance—it is most common in areas of heavily logged secondary forest. Goodman (1995) expressed fears regarding the future of Madagascar's endemic nesomyine rodents, many of which might be progressively displaced by the invader, especially as more and more original forest is logged or cleared for shifting cultivation.

The extent to which the various forms of *R. rattus*, or indeed any other commensal rodent species, might pose a similar threat to native mammals including rodents in Southeast Asia is currently unknown. At present, *R. rattus* appears to be more or less confined to anthropogenic habitats in Laos (Francis 1999), as it is in Thailand (Marshall 1977). However, the annual increase of rodent populations to high densities in the upland cropping areas of Laos, combined with frequent disturbance of adjacent forest habitats, represents an ideal context for more pervasive invasion by *R. rattus*, at least on a local scale. Detailed ecological studies are urgently needed to document its current pattern of habitat use and to identify those circumstances that might lead to any deleterious impact on native small mammals.

Introduced pathogens

Ecologists generally underrate the role of pathogens in regulating vertebrate populations and in potentially influencing community structure. This is somewhat surprising, given the obvious role that pathogens such as trypanosomes and malaria have played historically in limiting the ability of humans to exploit large parts of the globe before medical prophylaxis (Diamond 1997). On the other hand, there is a growing acceptance of the potential impact of 'emerging infectious diseases' on naïve wildlife populations (Daszak et al. 2000).

Rodents are known to serve as hosts for at least 60 zoonotic diseases (Hugh-Jones et al. 1995) and there are presumably many more diseases that could be transmitted between rodents or between rodents and other small mammal species. The high level of transfer of both ecto- and endo-parasites (and presumably microbial pathogens) that can occur between native and introduced rodents was clearly demonstrated by Roberts (1991) study of the parasites of *R. exulans*, *R. rattus* and *R. norvegicus* in New Zealand and other Pacific Islands.

Most attention has naturally been given to those diseases with the greatest potential impact on humans, including the hantaviruses and arenaviruses, leptospirosis and plague (*Yersinia pestis*). In the case of plague, there is also considerable evidence of its regulatory and deleterious impact on small mammal communities. Biggins and Kosoy (2001) argued that the Americas were plague-free until the time of the third pandemic (late 19th century – early 20th century) and noted that more than one-half of the North American rodent species of conservation concern are found within the range of enzootic plague in western North America. Numerous North American rodents are known to be highly susceptible to plague, although some species show evidence of increased resistance in areas of repeated epidemics (Cully and Williams 2001).

Y. pestis has a remarkably broad host range (>200 species of mammals; Poland and Barnes 1979) and has pathogenic impacts on many species including most rodents. Most Southeast Asian murids are highly susceptible to plague, but *R. norvegicus*, *R. rattus* and *Bandicota* species may be sufficiently resistant to serve as primary or enzootic hosts (Cully and Williams 2001). Among other groups of mammals, canids (dogs and their relatives) are generally quite resistant to plague, while felids (cats) and mustelids (ferrets, otters etc.) appear to be considerably less so. Smaller felids and mustelids remain moderately abundant in upland forest in Laos (Duckworth et al. 1999) and they presumably come into regular contact with commensal rodents along the garden–forest interface.

The status of plague as a wildlife disease is poorly documented in other areas to which it has been recently introduced. However, the possibility that this disease has contributed to the decline of native rodents in Madagascar and elsewhere, following its introduction during the third pandemic, certainly warrants further consideration.

Rodent pest management and conservation—an emerging partnership?

Previous commentaries on the relationship between rodent management and conservation have focused almost exclusively on the potentially negative impacts of non-target impacts of rodent management activities including rodenticide use (Buckle 1999) and direct culling methods (Singleton et al. 2002). In this review, we have tried to take a step back from such considerations in order to take a broader ecological view of conservation in agricultural landscapes. The search for understanding at this broader level is not an isolated endeavour—on the contrary, it is merely one part of a much larger attempt to find a viable partnership between sustainable agricultural production and conservation (Craig et al. 2000).

Our review of this broad topic has been necessarily selective and regionally focused. Nevertheless, we have identified what we believe are a number of significant issues that warrant further consideration and, in some cases, specific field studies and experimentation.

The first major point is that we are currently uncertain, at least in the Southeast Asian context, as to which species we should be trying to control, and which ones we should be trying to conserve. For each of the species that we might regard as ‘major pests’ there are strong grounds to suspect that they have undergone major range expansions in comparatively recent times. In many areas, these species are probably not strictly ‘native’, although they might be regarded as ‘naturalised’ or perhaps ‘commensal’ in a broader sense that implies an obligate association with human landscapes rather than just human dwellings. However, each of these species is presumably also native to at least some part of its current range and we might wish to think carefully before instigating broad-scale lethal control.

A second level of uncertainty relates to the actual ‘pest’ status assigned to some of these commensal rodents. For the rice-field rat this status is not in doubt—on the contrary, for this species we have sufficient high-quality population and behavioural data to unequivocally link this species to crop damage on a large scale. On the other hand, for each of the remaining ‘major pest’ species, we know little or nothing about population cycles, diet and behaviour, or else what we do know comes primarily from peri-urban contexts (e.g. *R. rattus*, *Bandicota* spp.). Additionally, while it is true that traditional farmers often have detailed knowledge of the timing and extent of rodent damage in their crops, this is rarely if ever linked back to specific rodent species, if these are indeed recognised at all (Frost and King, this volume; K. Aplin and G. Singleton, personal observations). In making this point, we do not wish to imply that all of the other commensal species are innocent—on the contrary, the majority, if not all, of these species probably do inflict a certain level of damage to standing crops or to stored produce. However, we do wish to pose the question as to whether, in some cases, these species might also play other, beneficial roles in the rice-field or garden ecosystems. For example, heavy predation by *Bandicota* spp. on crabs in rice fields might reduce the level of direct damage inflicted on growing rice tillers by the crabs themselves. The important point is that we currently do not know enough about the ecology of most agricultural ‘pest’ rodents, at least in Southeast Asia, to know whether or not such potential benefits might outweigh the costs of direct crop losses. The same is probably true in many other parts of the world.

The second major point to emerge from our review is that agricultural pest species such as members of the *R. rattus* complex may themselves pose a considerable threat to native rodents and other small mammals. In complex cropping environments such as exist in the uplands of Laos (and similar habitats exist throughout many parts of the world), the annual dramatic increase in populations of the black rat in the cropping areas can be seen as a constant source of invasive pressure on adjacent forest habitats. In Laos, we do not know to what extent the black rat has penetrated these habitats, or what kind of impact it might have on populations of other mammal species if it did. However, the invasion of forest habitat by *R. rattus* in other parts of the world, most notably in Madagascar, gives genuine cause for concern in this regard. Importantly, the risks associated with invasive rodent species are not limited to active competition between invaders and endemics, but also extend to the potential impact on naïve endemic mammals of novel pathogens spread by *R. rattus* and other invasive species.

In such contexts, proactive rodent management activities might be beneficial not only for humans through reduced crop losses and human health risks, but also for native wildlife and natural ecosystems through reduced risks of invasion by exotics and their pathogens. To our knowledge, this potential benefit of rodent control has not previously been factored into cost–benefit scenarios. To do so would be challenging and would require more information on the ecology of the potential invaders and the natural habitats than we currently possess.

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Conservation and management of hydromyine rodents in Victoria, Australia

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Abstract. Of the 15 species of native rodents recorded from Victoria, Australia, six became extinct within 70 years of European settlement, and two of the remaining nine are classified as 'threatened' and four are classified as 'near threatened'. Thus, only three species are considered to be adequately conserved. This represents one of the most dramatic mammalian species declines recorded in Australia. All the threatened species belong to the subfamily Hydromyinae, the Australian 'old endemics'. Of the extinct species, four were recorded only from the semi-arid north-west of the state and two from dry woodlands in the central and southern regions. The two endangered species are the smoky mouse, which has a disjunct distribution from near-coastal to sub-alpine habitats, and the New Holland mouse, which is the most geographically restricted species. Discovered in Victoria only in 1970, it has become extinct at several locations and is the subject of a major recovery program that includes captive breeding and reintroduction. Conservation protocols and practices for Victoria's native rodents are implemented under state legislation, but lack of basic ecological information makes their conservation a difficult task.

Introduction

Sixty-six species of native rodents, all in the Family Muridae, were extant at the time of European settlement of Australia in 1788. Of that total, 9 (13%) are now considered to be extinct, a further 11 (17%) are threatened, 13 (20%) are in need of additional information and only 33 (50%) are considered secure. All of the species of conservation concern are in the subfamily Hydromyinae, the Australian 'old endemics' (Lee 1995).

Of the 15 native species of rodents recorded in Victoria, six (40%) were extirpated within 70 years of European settlement, and two of the remaining nine (22%) are classified as threatened ('critically endangered', 'endangered' or 'vulnerable') and four (44%) are considered to be 'near threatened' (Table 1) (Seebeck and Menkhorst 2000; IUCN 2001). This level of population decline represents one of the most dramatic mammalian species declines recorded in Australia (Bennett et al. 1989). In the following accounts, the International Union for Nature and Natural Resources (IUCN) 2000 category (published by IUCN in 2001) refers to the species' status in Victoria; several species are still extant elsewhere in Australia, and we thus applied the IUCN (2001) criteria at the regional level following the guidelines of Gardenfors et al. (1999). These assessments have been made by J.H. Seebeck and P.W. Menkhorst as part of our state legislative responsibility.

In this paper, we deal only with the subfamily Hydromyinae. The two representatives of the subfamily Murinae, both in the genus *Rattus*, are secure and ranked of 'least concern' under IUCN criteria. We present an overview of the conservation status of the species under consideration and follow this with a case study of one endangered species, the New Holland mouse. Key locations discussed in the paper are shown in Figure 1.

Species accounts

Species extinct in Victoria

White-footed rabbit-rat, *Conilurus albipes*

The white-footed rabbit-rat is extinct. Its decline in Victoria was alarmingly rapid; it was last recorded in the 1860s, despite having been reported as being "the common rat of the country" by settler John Cotton in 1846. It is perhaps more than coincidence that the first reported *Conilurus* from Victoria (in 1839) was captured by a settler's cat! Despite the paucity of records of the white-footed rabbit-rat as a living animal (only four can be given a reliable provenance), the species was seemingly widespread, occurring in south-western and central Victoria and in Gippsland in the east (Menkhorst 1995; Seebeck and Menkhorst 2000). Its habitat was open forest and grassy woodland. **IUCN 2000 category: extinct**

Lesser stick-nest rat, *Leporillus apicalis*

Now extinct, the lesser stick-nest rat was collected only from the far north-west of the state, by the Blandowski expedition in 1856–57. It was apparently common in the riverine environments along the Murray River, where it occupied hollow limbs and built domed stick nests. The species may have survived until the 1920s in the Murray mallee. Descriptions of large rodents and the stick nests they inhabited in mallee vegetation near Yungera, 100 km south-east of Mildura, during the late 1920s (Menkhorst 1995) most likely refer to this species. **IUCN 2000 category: extinct**

Table 1. Species of native rodents recorded from Victoria in the modern era, and their current status, using International Union for Conservation of Nature and Natural Resources (IUCN) 2000 categories (IUCN 2001).

Common name	Species	Status
Subfamily Hydromyinae		
White-footed rabbit-rat	*Conilurus albipes*	Extinct
Water rat	*Hydromys chrysogaster*	Least concern
Lesser stick-nest rat	*Leporillus apicalis*	Extinct
Greater stick-nest Rat	*Leporillus conditor*	Regionally extinct
Broad-toothed rat	*Mastacomys fuscus*	Not threatened
Mitchell’s hopping mouse	*Notomys mitchellii*	Not threatened
Silky mouse	*Pseudomys apodemoides*	Not threatened
Plains mouse	*Pseudomys australis*	Regionally extinct
Bolam’s mouse	*Pseudomys bolami*	Regionally extinct
Desert mouse	*Pseudomys desertor*	Regionally extinct
Smoky mouse	*Pseudomys fumeus*	Endangered
New Holland mouse	*Pseudomys novaehollandiae*	Endangered
Heath mouse	*Pseudomys shortridgei*	Not threatened
Subfamily Murinae		
Bush rat	*Rattus fuscipes*	Least concern
Swamp rat	*Rattus lutreolus*	Least concern

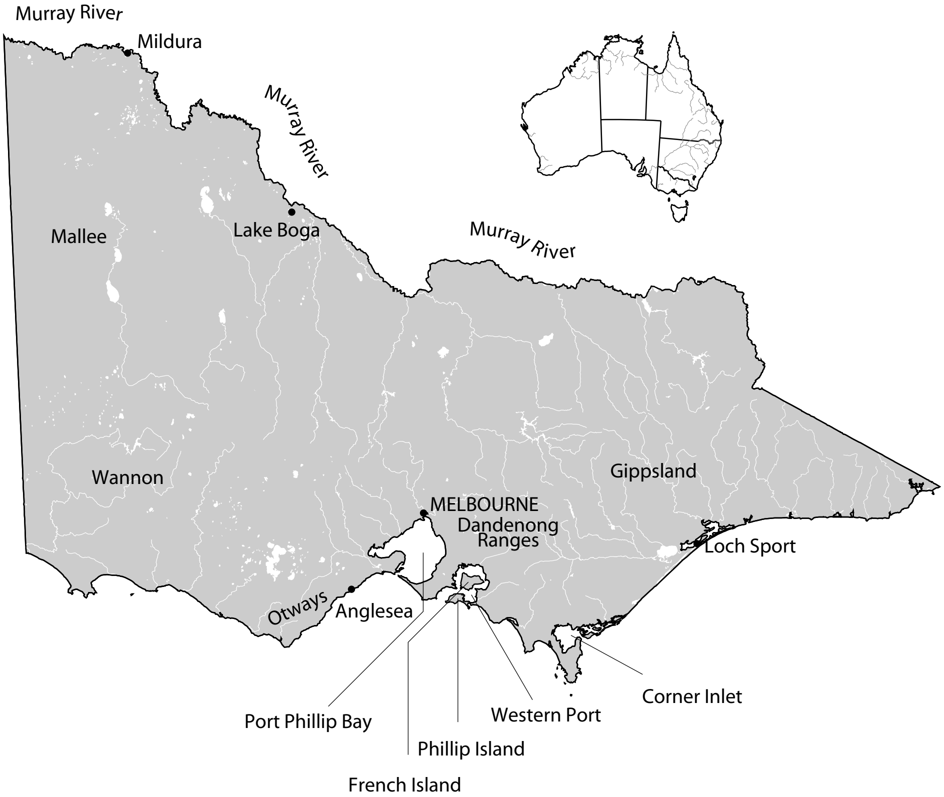

Figure 1. Key locations discussed in the text with regard to rodent species in Victoria, Australia.

Greater stick-nest rat, *Leporillus conditor*

In his report on the fauna collected during the Blandowski expedition of 1856–57, Krefft (1866) observed that this species had been abundant in the Murray River area “not many years ago”, but that only empty nests were found. There are no other records of this species for Victoria. **IUCN 2000 category: regionally extinct**

Plains mouse, *Pseudomys australis*

The post-European occurrence of *Pseudomys australis* in Victoria is equivocal (Menkhorst 1995) as, indeed, is its taxonomic identity (Watts and Aslin 1981; Lee 1995). Present in Pleistocene and Holocene fossil deposits in western Victoria, no specimens from the modern era have been collected. However, anecdotal records have been interpreted to refer to this species’ presence in the 1840s (Seebeck and Menkhorst 2000). Its habitat was grasslands and grassy woodlands. **IUCN 2000 category: regionally extinct**

Bolam’s mouse, *Pseudomys bolami*

Bolam’s mouse was collected in Victoria only by the Blandowski expedition in 1856–57 (Krefft 1866). Widespread and common in the ‘Murray scrub’ at that time, there is a slight possibility that the species still exists in the chenopod shrublands and grassy woodlands of the lower Murray River flood plain (Menkhorst 1995), but it was not found during extensive fauna surveys conducted in the late 1980s (Robertson et al. 1989). **IUCN 2000 category: regionally extinct**

Desert mouse, *Pseudomys desertor*

Another of the species recorded only by the Blandowski expedition, little is known about the occurrence of the desert mouse in Victoria (Menkhorst 1995). Krefft (1866) noted that they were “in large numbers” and over 20 were taken as museum specimens. Favoured habitat is hummock grassland, but this species has not been found in areas carrying this kind of habitat in Victoria (Robertson et al. 1989). **IUCN 2000 category: regionally extinct**

Species currently found in Victoria

Water rat, *Hydromys chrysogaster*

The water rat, the first native rodent to be described from Australia, in 1804, is widespread in waterbodies throughout Victoria. It is found in fresh, brackish and saltwater wetlands, including sheltered coastal zones in Port Phillip Bay. Four island populations are reported—French Island, Phillip Island, Sunday Island and a complex of islands centred on Swan Island. These latter populations are possibly part of local populations in Corner Inlet and Swan Bay, respectively. Locally abundant in northern Victoria, they are uncommon in Gippsland (Seebeck and Menkhorst 2000). **IUCN 2000 category: least concern**

Broad-toothed rat, *Mastacomys fuscus*

Although described from Tasmania in the 1880s, *Mastacomys fuscus* was not discovered in Victoria until the 1920s. It occurs in higher rainfall areas of southern and eastern Victoria, from coastal grassy/shrubby dunes to alpine snowfield heaths—an altitude range between sea level and 1800 m. It is generally rare and localised, but may be locally common in appropriate habitat such as sedge-fields or sub-alpine heaths. The species persists at several sites in the Dandenong Ranges close to Melbourne and may be present in parts of coastal East Gippsland (Seebeck and Menkhorst 2000). **IUCN 2000 category: near threatened**

Mitchell’s hopping mouse, *Notomys mitchelli*

Victoria’s only hopping mouse is found in the drier west and north-west of the state (Menkhorst 1995). It occurs in plant communities such as mallee scrub and tall mallee heath developed on deep sands. Although most of its remaining habitat is protected in nature reserves, its range has been greatly reduced through clearing for agriculture. For example, it is no longer found within 100 km of Lake Boga, from whence it was first collected, by Sir Thomas Mitchell, in 1836. **IUCN 2000 category: near threatened**

Silky mouse, *Pseudomys apodemoides*

Pseudomys apodemoides was only recognised as part of the Victorian fauna as late as 1963, when specimens were incorrectly identified as the similar *P. albocinereus* of Western Australia; at the time, the two species were lumped together. *P. apodemoides* was itself not recognised as a separate species until 1932. It is widespread within its geographical limits in the drier west and north-west, in Lowan Mallee south of the Sunset Country and in the northern part of the Wannon region (Menkhorst 1995). *P. apodemoides* is widespread within the Big Desert and Little Desert and is not considered particularly rare. Most of its dry heath and brown stringybark scrub habitat is reserved, and it is likely that *P. apodemoides* is far more common and widespread than its desert associate, *N. mitchelli*. **IUCN 2000 category: near threatened**

Smoky mouse, *Pseudomys fumeus*

Considered to be endemic to Victoria until 1985, when it was discovered in the Australian Capital Territory, the smoky mouse was first found in the Otway Ranges of south-western Victoria in 1933, and was rediscovered in the early 1960s in the Grampians, some 180 km to the north-west. The distribution of the smoky mouse is disjunct in four widely separated areas (Menkhorst 1995), where it inhabits a variety of vegetation alliances, ranging from coastal heaths to sub-alpine heaths and dry forest or woodland. It has also been occasionally found in fern gullies in wet forest. It is rare, and the isolated populations require careful monitoring. Recent surveys suggest that populations have declined significantly at some locations. **IUCN 2000 category: endangered**

New Holland mouse, *Pseudomys novaehollandiae*

Considered to be extinct for 80 years, the New Holland mouse was rediscovered in 1967, in New South Wales, and first recorded in Victoria in 1970. This species is the most geographically restricted *Pseudomys* in Victoria. It is considered critically endangered and is the subject of special conservation measures. It was present in four discrete population centres but is now extinct at one of these. It occurs in a variety of coastal heath, heathy woodland and coastal scrub habitats. In coastal heath, optimum habitat occurs in vegetation actively regenerating two to ten years after fire. The greater floristic diversity in regenerating heath ensures that a range of seeds will be available year-round. Consequently, fire management of its habitat is required at appropriate intervals (Wilson 1991; Seebeck et al. 1996). **IUCN 2000 category: endangered**

Heath mouse, *Pseudomys shortridgei*

The heath mouse is restricted to two areas in south-western Victoria. Since its discovery in Victoria in 1961, it has been found to be widespread within this region and locally common at some sites. Taxonomic studies of the Victorian form and the Western Australian nominate form, described in 1907, are required to establish the relationship between eastern and western populations. Heath mice inhabit dry heath, and woodland and forest with a heathy understorey, and prefer relatively immature, floristically-rich low heath (Menkhorst 1995; Seebeck and Menkhorst 2000). **IUCN 2000 category: near threatened**

Conservation protocols

All species are legally protected under the *Wildlife Act 1975*, and penalties apply to the illegal handling or possession of the species. In addition, some species are given further protection under the *Flora and Fauna Guarantee Act 1988*, which provides a legislative framework for the conservation of Victoria's biota. Species that are considered threatened may be *listed* under the Act, and this guarantees a conservation commitment by the state. A consequence of listing is the preparation of an Action Statement, a document that provides a detailed series of actions to be implemented to ensure conservation of the listed species. The following species are listed: *P. fumeus*, *P. novaehollandiae* and *P. shortridgei*. *Leporillus apicalis* and *Pseudomys australis* are included in an Action Statement that concerns species extinct in Victoria, while *Conilurus albipes* is included in an Action Statement that concerns species now wholly extinct.

Conservation practices

Some populations of all extant species are nominally protected in conservation reserves such as National or State Parks, Wildlife Reserves or Coastal Reserves. Within these reserved areas, habitat management, and predator and competitor control are carried out, although the intensity of such actions varies with location and resources available. For species listed under the *Flora and Fauna Guarantee Act*, implementation of conservation actions may be more particularly applied. Populations outside conservation reserves may not be especially managed.

Flora and Fauna Guarantee Action Statements may recommend the establishment of a Recovery Program, usually directed by a Recovery Team consisting of representatives of relevant agencies and the community.

Case study: the New Holland mouse

Described in 1843, the New Holland mouse was thought to be extinct, having not been collected since before 1887. It was rediscovered in New South Wales in 1967, first recorded from Victoria in 1970, from Tasmania in 1976 and from Queensland in 1996. In New South Wales, it occurs in a number of coastal locations in addition to more inland, higher altitude records that may represent a separate taxon; this same taxon may include the animals that are known from south-eastern Queensland. In Tasmania, it is found on the north and east coasts and on Flinders Island in Bass Strait. In Victoria, it has been recorded from eight disjunct sites on the coastal plains east of Melbourne, and at Anglesea to the west, on the eastern Otway coastal plain. Populations at a number of these sites are now extinct, the most recent being at Anglesea, from whence the last remaining animals were removed to captivity in 1999.

The habitat in which the species occurs in Victoria includes heathland, woodland with heathy understorey, open forests and vegetated sand dunes. The preference is for habitats with soft sandy substrates (necessary for burrow construction), floristically rich vegetation and low vegetative cover, although sand dunes may be floristically and structurally simpler. Nocturnal, it is principally a granivore (particularly legumes) but includes insects and other invertebrates, leaves, flowers and fungi in its diet. Female New Holland mice live for up to 2 years in the wild. Breeding is seasonal and reproductive productivity is related to habitat quality and hence food abundance and quality. New Holland mice are closely tied to habitat succession resulting from fire regimes, although natural senescence may also play a role. In many areas, the optimal habitat age is 2–3 years after fire, but this pattern is not universal. As the vegetation ages, population densities decline and populations may not persist. It is not known whether this is due to loss of plant species diversity, loss of particular plant species, reduction in low vegetation cover, or a decline in vegetation productivity.

Threats to the species' conservation include: alteration and increased fragmentation of habitat, often linked to inappropriate fire regimes; weed invasion; alienation of habitat for human development; infection of habitat by cinnamon fungus, a root pathogen that reduces floristic diversity and structure; predation by introduced carnivores; and, potentially, competition from introduced rodents.

Conservation management under the Flora and Fauna Guarantee commenced with the initiation of a series of actions directed by a multi-skilled Recovery Team, consisting of staff from the Department of Natural Resources and Environment, Parks Victoria, universities and community groups. Studies on habitat and habitat requirements, diet, population dynamics, predation, and response to disturbance have enabled the development of more detailed management strategies, particularly related to fire management. Genetic studies demonstrated that each population was genetically distinct, and that Anglesea animals were demonstrably different from Gippsland animals—perhaps as a consequence of their long genetic isolation. The rapid decline of several populations, especially that at Anglesea, prompted the establishment of a captive colony and an investigation of captive breeding, with a view to reintroduction. Population modelling is used to determine population viability for both wild and captive populations.

Studies at Anglesea have determined the relationship of New Holland Mouse habitat to landscape and other environmental variables, and a geographical information system (GIS) based predictive model of habitat capability was consequently produced (O'Callaghan 1999). The habitat model identified 3252 ha of the area as suitable habitat. The species occurred only on tertiary lateritic materials of quartz sands, carbonaceaous clayey silt and clayey sand, and areas of ferruginous clayey quartz sand at elevations between 43 and 110 m and slopes of 0.1–10%. The model highlighted the importance of factors such as soil, topography and aspect to the habitat suitability for the New Holland mouse. The model identified areas of potentially suitable habitat for reintroductions. This gives the opportunity to reintroduce the species to a number of areas spread across the landscape, thus spreading risk of extinction from stochastic factors such as wildfires.

Initially, a captive colony was established at Deakin University, and protocols for maintenance and breeding were devised. Subsequently, the colony was transferred to Melbourne Zoo. The intent has been to maintain as high a level of the Anglesea genotype possible to enable the reintroduction of the species to that location. Release sites were chosen on the basis of habitat suitability, especially relating to age since burning, and other factors identified by habitat evaluation and modelling. Selected sites within the area have been subjected to environmental burning to prepare them for future reintroductions. Sufficient animals had been produced in the captive colony by 2001 to carry out an experimental release into purpose-built enclosures on-site. Further experimental releases have been carried out during 2002. Animals placed into the enclosures are fitted with radio-collars and their movements and activity monitored daily.

Two areas have been selected as release sites and an acclimatisation (predator-proof) enclosure has been constructed at each site. Three trial releases of small numbers of animals (3–5) have been conducted, with mixed results. Radio-collars have not been successful, with animals either dying or losing their collars. Techniques to improve future releases have been formulated and rodent-specific radio-collars have been purchased from Canada for use in further trials.

The ongoing colony at Melbourne Zoo currently holds 30 Anglesea/Loch Sport hybrid animals and 23 pure Anglesea animals. Breeding success has been higher in the hybrids than the pure Anglesea animals, possibly indicating some level of inbreeding depression.

It is too early yet to be confident that the reintroduction will be successful, but the habitat is at an appropriate seral stage, other environmental factors are equivalent to sites at which the mouse has been previously recorded and, initially, potential predation is controlled.

Conclusions

Of the seven extant hydromyine rodents in Victoria, only one, the water rat, is of 'least concern'. Four are considered to be 'near threatened' and the remaining two are 'endangered'. The key to conservation of these two species, and most of the 'near threatened species' is habitat management through an appropriately designed environmental burning regime and management of introduced predators. Because so little is known about the precise ecological requirements of most species, habitat manipulation by fire, in their highly flammable heath environments, can only be experimental at best. Habitat fragmentation and the consequent lack of gene exchange between disjunct populations is also of concern and may require strategic translocation of individuals to maintain genetic diversity.

The rodents of Victoria have been affected more than any other group of native mammals by the changes wrought by European settlement and their continued conservation is of great concern. While the ecological requirements of most species remain poorly understood, we cannot plan appropriate habitat management nor respond to natural or human-induced perturbations, and conservation of many species thus becomes a game of chance, and the continuing presence of all rodent species in Victoria cannot be assured.

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The use of small mammal community characteristics as an indicator of ecological disturbance in the Korannaberg Conservancy

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Abstract. Small mammals were sampled over four seasons in four different habitats inside the Korannaberg Conservancy in South Africa and in one habitat on its border. Small mammal density, species richness, the relative abundance of the component species, and diversity differed significantly between habitats, but not seasons. The high number of species, high diversity and evenness in the four habitats within the conservancy, the presence of 'specialists', as well as the relatively low contribution of indicator species, such as *Mastomys coucha*, are indicative of a healthy and relatively 'stable' ecosystem. In comparison, the fifth habitat, on the border of the conservancy, housed very few species, showed low diversity and evenness, the absence of 'specialists', and *M. coucha* completely dominated the nocturnal small mammal component. This study therefore showed the possible role that conservancies play in the conservation of small mammals and the survival of complete ecosystems.

Introduction

Little has been published on small mammal diversity in Free State province habitats (Avenant 2000) or on its association with biotic and abiotic features in southern Africa (see Els and Kerley 1996), and almost nothing on small mammal community structure as an indicator of habitat integrity (see Avenant 2000; Avenant and Kuyler 2002; Avenant and Watson 2002). In many systems, the highest species richness and biodiversity have been observed at an intermediary level of disturbance because "relatively few ruderal species [those species that are found in heavily disturbed areas] dominate when disturbances are frequent, and relatively few highly competitive species dominate when disturbances are rare; intermediate levels of disturbance allow succession to proceed but limit the ability of competitive species to dominate the community" (Valone and Kelt 1999). This reasoning has also been used in interpreting the typical hyperbolic pattern that small mammal species richness and diversity show after disturbances such as drought and fire. Where veldt recovery has not been allowed, as under conditions of constant heavy trampling and over-utilisation by domestic stock, very low small mammal species richness and diversity have been reported (Joubert and Ryan 1999). Avenant (2000; Avenant and Kuyler 2002; Avenant and Watson 2002) reasoned that the monitoring of small mammals is a relatively quick and cheap method of indicating healthy or unhealthy ecosystem functioning. Small mammal monitoring should also add to our knowledge of small mammal habitat preferences, correlation with plant communities, whether and under what circumstances species function as ecosystem engineers, keystone species or indicator species, as well as the method which should be used to sample small mammals effectively. Such studies are, therefore, essential for the conservation and regulation of small mammal biodiversity and terrestrial ecosystems.

While some authors stress the importance of continuously gathering and reviewing biodiversity data and species lists, others refer to the lack of it in South African nature reserves. The biodiversity value of conservancies has not been recognised. Conservancies are groups of farms on which owners and managers practice cooperative nature conservation and are potentially of enormous importance for the conservation of habitats and the survival of complete ecosystems. Within the conservancy, a specially-appointed 'ranger', or well-trained farm worker, frequently patrols the total conservancy and its fences, cribs and water pumps. He removes snares, reports mortalities and stray dogs, prevents unlawful hunting, game and cattle theft, and practises proper problem-animal control measures over a large area. Although often praised, South Africa's provincial and national nature reserves are also criticised for being relatively small and isolated. As c. 80% of South Africa's total surface area is in private hands, conservancies are expected to play an invaluable role in the conservation of our ecosystems. Today the 99 agricultural conservancies in Free State province already add c. 5000 km^2 to the total area of only c. 1065 km^2 in the province's proclaimed nature reserves.

This study was initiated to report on small mammal diversity, distribution, relative abundance and evenness, and therefore small mammal community structure, in specific habitats in the Korannaberg Conservancy. It is also aimed to explore the concept that more species are present in more even numbers (and therefore higher diversity scores) in more pristine areas, while the indicator species *Mastomys coucha* tends to dominate at disturbed sites (Avenant 2000; Avenant and Kuyler 2002; Avenant and Watson 2002; N.L. Avenant and P. Cavallini, unpublished data).

Study area

Korannaberg Conservancy, established in 1985, was the first conservancy in Free State province. This conservancy is situated on a part of Korannaberg Mountain (28°55'S, 27°15'E) and covers an area of c. 114 km2. Altitude ranges between 1500 m and 1881 m. Mean annual rainfall in this summer rainfall area exceeds 700 mm. Mean daily maximum and minimum temperatures range from c. 27.9°C and 12.5°C in January to c. 16.3°C and –0.7°C in July. The vegetation of the mountain plateau is represented by 'highveld sourveld'[1] to *Cymbopogon–Themeda* veldt transition and the surrounding plains by *Cymbopogon–Themeda* veldt. The interactions of environmental factors, such as altitude, topography, geology, soil types, climate, fire, grazing, trampling and ploughing, are responsible for the considerable number of different habitats on the mountain and the rich species diversity. To date, 115 plant families, comprising 385 genera and 769 species, and 277 bird species have been identified.

Cattle had access to the habitats studied here and none of the transects has burnt during the period of field work or during the 36 months before the study.

Materials and methods

Small mammals were surveyed with snap-traps over four different seasons during 1996 and 1997 and specimens later included in the National Museum collection. During each season, a fixed number of traps (see Table 1) were put out on four trap-lines (transects) in the conservancy and a fifth on the border of the conservancy (Table 1). Trap lines were moved c. 200 m every season and were never closer than c. 75 m to any previous lines on the same transect (habitat). These trap-lines in homogenous habitats (see Avenant 2000) covered the major untransformed habitat types present on and around Korannaberg. Traps were spaced 5 m apart and left open for c. 92 hours (four nights and roughly four days). They were checked and re-baited (with a mixture of peanut butter, rolled oats and marmite) at sunrise and just before sunset. The term 'trap night' is used to describe one trap, which was set for a 24 h period. The relative abundance or evenness of the component species was determined as E_{var} (Smith and Wilson 1996). Trap success (or percentage success) is the number of small mammals captured/100 trap nights. Species richness (variety) is the number of species collected, and the Shannon diversity index ($H' = -\Sigma p_i \ln p_i$) is a measure of both the number of species and equality of representation of the individuals of all species (Magurran 1988). The computer program Statistica for Windows (Statsoft Inc., 1995) was used to do the statistical analyses. Kruskal–Wallis tests were used to detect inter-group differences. The 95% level ($p < 0.05$) was regarded as statistically significant for all tests.

Table 1. A description of the transects on which small mammals were caught at the Korannaberg Conservancy during winter and spring 1996, and summer and autumn 1997.

Transect number	Habitat	Plant community	Number of traps used per season
1	Rock bed, shallow soil, bushes	Fynbos[a]	100
2	Shallow sandy soil, grass	Koperdraadgras[b]	200
3	Clay soil, loose stones, trees	Southern slope	200
4	Clay soil, loose stones, bushes	Northern slope	200
5[c]	Deep sandy soil, grass	Grassy plain	200

[a] Vegetation similar to macchia (Spain) or chaparral (USA).
[b] An unpalatable, pioneer grass species.
[c] This transect was on the border of the conservancy.

Results

Nine small mammal species (298 individuals) were trapped in a total of 13,801 trap nights (Table 2). Total trap success in the various habitats ranged from 0.72 to 4.11 captures/100 trap nights, species richness from two to seven, diversity from 0.292 to 1.837, and evenness from 0.394 to 0.865 (Table 2).

The four measures, namely, trap success ($H_{4;15}$ = 11.89, $p < 0.001$), species richness ($H_{4;15}$ = 11.77, $p < 0.001$), Shannon diversity ($H_{4;15}$ = 11.94, $p < 0.001$) and evenness ($H_{4;15}$ = 5.64, $p < 0.01$) all showed that the small mammal community structure differed between the habitats sampled. Table 3 shows how these measures changed over seasons. Trap success, species richness and diversity were almost consistently highest and lowest in the Fynbos (transect 1) and the grassy plain (transect 5) habitats, respectively. *Mastomys coucha* was present on four of the five transects, but was the only nocturnal species present on transect 5.

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[1] Highveld' is the highest part of the southern African central plateau (high in altitude). 'Sourveld' describes an area with high annual precipitation—salts have been washed from the soil, and therefore the veldt is relatively 'sour' (acidic).

Discussion

Small mammal community structure and species richness have been related to variables such as habitat structure and complexity, area, rainfall, productivity, predation, trampling and grazing, surrounding landscape and the distance between similar habitats, maturity of the habitat/succession of the vegetation, and the presence of exotics (see Avenant 2000). The differences in mammal composition, trap success and diversity observed between habitats in this study were, therefore, expected. The relatively high small mammal species richness, diversity and evenness in the four habitats inside the Korannaberg Conservancy make this area very special for Free State province (Avenant 2000). This high diversity and species richness (Wootton 1998; Hastwell and Huston 2001) and the relatively low contribution of indicator species, such as *M. coucha* (Avenant 2000; Avenant and Kuyler 2002; Avenant and Watson 2002; N.L. Avenant and P. Cavallini, unpublished data) are an indication of a healthy and relatively stable ecosystem (Cardinale et al. 2000; Chapin et al. 2000; Johnson 2000; Loreau 2000; McCann 2000; Petchey 2000; Fonseca and Ganade 2001). The fact that two relatively 'scarce' species, *Dendromus melanotis* and *Mus minutoides*, were trapped in relatively large numbers on transects may be a further indicator of ecosystem health in the conservancy.

In comparison, the fifth habitat, transect 5, housed only one nocturnal (*M. coucha*) and one diurnal (*Rhabdomys pumilio*) species. Smaller numbers of species are expected in such more-uniform habitats (see Kerley 1992; Els and Kerley 1996). In this instance, however, only two out of six species expected were collected (other species expected being *Mystromys albicaudatus*, *Dendromus melanotis*, *Tatera brantsii*, and *Mus minutoides*). The low small mammal species richness, diversity and evenness, and the fact that the indicator species *M. coucha* completely dominated the nocturnal small mammal fauna, all suggest that this habitat was the most disturbed of the five habitats sampled. This greater degree of disturbance was not necessarily due to trampling and grazing of domestic animals (transect 2 is also frequently grazed by these animals), but probably primarily due to differences in the small to medium-size predator component affecting the whole ecosystem. Transect 5 is the only transect below the mountain and therefore more accessible to people and dogs. The absence of natural predators and the presence of dogs have been mentioned as factors that may decrease mammal diversity and, therefore, indirectly lead to an overall decrease in biodiversity (see Avenant 2000).

Although this study did not correlate one specific habitat type to various degrees of disturbance, such as measured by the percentage presence of pioneer plant species (Avenant 2000; Avenant and Kuyler 2002; Avenant and Watson 2002) or ecological value of the veldt (N.L. Avenant and P. Cavallini, unpublished data), it does not reject the hypothesis that more species are present in more even numbers (and, therefore, higher diversity scores) in more pristine areas, while the indicator species *M. coucha* tends to dominate at disturbed sites. This study also showed the possible role that conservancies play in the conservation of small mammals and the survival of complete ecosystems.

Table 2. The total number of different small mammals trapped, trap success, species richness, Shannon diversity, and evenness on five transects when data for four seasons were pooled during the 1996/97 small mammal survey at the Korannaberg Conservancy.

Species	Transect number				
	1	2	3	4	5
Mastomys coucha	14	6	0	5	10
Rhabdomys pumilio	16	31	4	2	107
Elephantulus myurus	5	0	10	15	0
Aethomys namaquensis	11	0	6	15	0
Dendromus melanotis	0	9	0	0	0
Graphiurus murinus	0	0	1	0	0
Mus minutoides	6	7	1	0	0
Crocidura cyanea	5	0	0	1	0
Myosorex varius	6	5	0	0	0
Total	63	58	22	38	117
Number of trap nights	1533	3067	3067	3067	3067
Trap success[a]	4.11	1.89	0.72	1.24	3.81
Species richness[a]	7	5	5	5	2
Diversity[a]	1.837	1.325	1.304	1.251	0.292
Evenness[a]	0.865	0.747	0.539	0.452	0.394

[a] Indicates a significant ($p < 0.01$) difference between transects.

Table 3. The trap success, species richness and diversity of small mammals on five transects during the 1996/97 seasonal small mammal survey at Korannaberg Conservancy (TN = transect number; TS = trap success; SR = species richness; DI = diversity; E = evenness).

TN	July 1996				October 1996				January 1997				April 1997			
	TS	SR	DI	E	TS	SR	DI	E	TS	SR	DI	E	TS	SR	DI	E
1	4.70	7	1.754	0.772	4.96	6	1.430	0.587	3.65	5	1.433	0.719	3.13	5	1.474	0.784
2	0.52	2	0.562	0.813	2.22	4	1.232	0.681	1.57	3	0.824	0.602	3.26	5	1.185	0.569
3	0.91	3	0.956	0.803	0.39	2	0.637	0.924	0.52	3	1.040	0.932	1.04	3	0.974	0.782
4	1.43	2	0.474	0.672	1.83	3	0.980	0.866	0.65	3	1.055	0.932	1.04	4	1.321	0.901
5	3.91	2	0.451	0.634	3.26	2	0.440	0.617	2.61	2	0.199	0.275	5.48	1	0.000	0.000
Means of transects																
	2.29	3.2	0.839	0.739	2.53	3.4	0.944	0.735	1.80	3.2	0.910	0.692	2.79	3.2	0.991	0.607
Transects pooled																
	2.03	8	1.549	0.399	2.26	8	1.544	0.334	1.59	7	1.350	0.436	2.75	8	1.228	0.369
Transects and seasons pooled																
	2.16	9	1.530	0.328												

Acknowledgments

I thank M.J. Strydom, H. Keyter, and the Council and Directors of the National Museum, Bloemfontein, for permission to carry out the project on the farms Maermanshoek, Mooimeisieshoek, and Merrimietzie. Gratitude is expressed towards J.P. Eksteen, I. Sekhuni and J. Senoge for their contribution in the field. J.P. du Preez (University of the Free State) made valuable comments during this project and helped with the selection of the habitats that were sampled. James Brink kindly proofread the manuscript.

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Activity range and den trees of the brush-tailed rabbit-rat on Cobourg Peninsula, Northern Territory, Australia

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Abstract. Activity ranges and den-tree characteristics of 41 brush-tailed rabbit-rats (*Conilurus penicillatus*) were studied in two different habitats (sites) on the Cobourg Peninsula, Northern Territory, Australia. Activity ranges were found to be larger for males, and did not differ significantly between the two habitats. Rabbit-rats in tall eucalypt forest used den trees with a significantly larger diameter than rabbit-rats in low eucalypt forest. Animals from both grids showed a preference for trees with larger diameters than were available. Den-tree height was similar in both habitats. Animals in tall eucalypt forest denned in trees that were shorter than what was available to them. Rabbit-rats preferred to use eucalypt species as dens. Hollow logs were utilised as den sites in much greater proportion in tall eucalypt forest than in low eucalypt forest. Den-tree characteristics may be a reflection of availability, probably predation, and competition with other tree hollow dwelling animals.

Introduction

The brush-tailed rabbit-rat (*Conilurus penicillatus*) is the only extant member of its genus: its sole congener *Conilurus albipes* became extinct at the end of the 19th century before any but the most superficial of studies could be carried out on its ecology (Taylor and Horner 1971). The brush-tailed rabbit-rat has recently suffered an apparent decline in its range. In the 1890s, it was recorded as common throughout the Kakadu area (Woinarski 2000), however now only one population occurs there (personal observations). In the Northern Territory, it can be found on Bathurst and Melville Islands (Tiwi Islands), and is patchily common on Inglis Island off north-eastern Arnhem Land (Woinarski et al. 1999). The only known remaining mainland populations occur on Cobourg Peninsula (Taylor and Horner 1971; Frith and Calaby 1974), and in a highly restricted area of Kakadu National Park.

There is little known regarding the ecology of the brush-tailed rabbit-rat (Bradley et al. 1987; Friend et al. 1992). It is largely restricted to tall open eucalypt forests and casuarina woodlands close to coastal areas, roosts in tree hollows, and largely forages on the ground (Taylor and Horner 1971; Frith and Calaby 1974; Bradley et al. 1987; Friend et al. 1992). Rabbit-rats are omnivorous and weigh approximately 150 g. Due to the apparent decline of the brush-tailed rabbit-rat and the sparse knowledge on its ecology, I am undertaking an ecological study of the rabbit-rat focusing on habitat use, movements, population dynamics, diet and possible causes of decline. In this paper, I present findings on movements and den-tree characteristics.

Materials and methods

Study site

The study was primarily conducted on the Cobourg Peninsula (Garig Gunak Barlu National Park), approximately 200 km north-east of Darwin in the Northern Territory, Australia (11'18", 132'45"). Animals were radio-tracked on two sites, 10 km apart. Site 1 consisted of tall open eucalypt forest (average tree height, 20 m) adjacent to the coast, dominated by *Eucalyptus miniata*, *E. tetrodonta* and *E. nesophila* with relatively little understorey, though there were small patches of vine thicket and an extensive cover of perennial grasses. Site 2 included coastal dunes with *Casuarina equisetifolia*, open areas of grass, then a relatively low open forest (average height, 14 m) dominated by *E. tetrodonta*, with a denser mid-storey primarily consisting of *Acacia* species, *Planchonia careya* and a ground cover of perennial grasses. This detailed study of the two Cobourg sites is being supplemented by less-intensive trapping studies from a far larger number of quadrats (n = >50) on Cobourg Peninsula.

Forty-one rabbit-rats (26 males and 15 females) were fitted with radio-transmitters and radio-tracked. Telemetry packages were produced by BioTelemetry Tracking Australia (Adelaide, Australia). Each radio-transmitter package weighed approximately 7 g and was fitted around the neck with a collar. Animals were then radio-tracked at night over a period of at least four nights, with a minimum of 12 fixes per animal, during the dry season and wet season of 2000, 2001 and 2002. No more than five fixes were taken throughout the course of a night. Location data was recorded with a global positional system (GPS) and then their activity ranges were analysed and 100% minimum convex polygons were calculated using the Animal movement extension to Arcview (Hooge and Eichenlaub 1997). The number of radio-tracking fixes used to determine home-range size is small, however these activity ranges represent short-term movements and not long-term home-range movements. Animals were also radio-tracked during the day to determine den sites and to describe the characteristics of each den, such as tree or log, species of tree, tree height, diameter at breast height (DBH), and diameter of log. Within a 30 m radius of each den tree, 10 other random tree/log characteristics were also measured to explore possible den selectivity.

Activity ranges were compared between sites and between sexes, using the Mann-Whitney *U* test. The den-tree characteristics of the radio-tracked rabbit-rats were also compared between sites and with the randomly selected trees from corresponding grids, using the Mann-Whitney *U* test. Species of trees used as dens were also compared to species of trees randomly selected, using the Chi-square test.

Results and discussion

Activity range size for the 41 rabbit-rats averaged 0.77 ha and ranged from 0.10 ha to 4.40 ha (Table 1). There was no difference in size of activity range between animals from site 1 and site 2 (U = 148, n = 41, P = 0.138). However, when males (site 1 and site 2) and females (site 1 and site 2) were analysed separately, there was a significant difference in activity range between the sexes (U = 66, n = 41, P = <0.000), with males having significantly larger ranges (Table 1). There was also a significant difference in activity range between males and females from site 2 (U = 22, n = 22, P = 0.003).

In total, 82 dens were used by the radio-tracked animals and 20 of these were fallen hollow logs (Table 2). There was no difference in den-tree height between animals from site 1 and site 2 (U = 368, n = 62, P = 0.539). However, rabbit-rats on site 1 did select trees that were significantly shorter than were available (U = 1683, n = 366, P = 0.046). There was a significant difference between the den-tree DBH of animals from site 1 and site 2 (U = 256, n = 62, P = 0.020), with the DBH of trees from site 1 being larger. The DBHs of just den trees from site 1 were significantly larger than the mean DBH of randomly selected trees (U = 1627, n = 268, P = 0.023) as were the DBHs of den trees from site 2 (U = 4197, n = 369, P = < 0.000) (Table 2).

The radio-tracked rabbit-rats used dens in tree hollows from five eucalypt species, hollows in dead trees (stags), fallen hollow logs and, in one case, in the prickly dense foliage of *Pandanus spiralis* (see Table 3). The radio-tracked rabbit-rats from site 1 used den-tree species disproportionately to availability to them (χ^2 = 1834, df = 19, P = <0.000), as did rabbit-rats from site 2 (χ^2 = 159, df = 19, P = <0.000) (Table 3).

The activity ranges indicate that males move larger distances in the short term than do females—the largest

Table 1. Estimates of activity ranges (ha) for brush-tailed rabbit-rats (*Conilurus penicillatus*) calculated for minimum convex polygons (MCP) determined by radio-telemetry (mean ± 1 sd).

Site	Number of days tracked	Number of fixes	MCP
Site 1			
Female (*n* = 3)	6.3 ± 0.5	15.3 ± 1.1	0.50 ± 0.40
Male (*n* = 14)	8.5 ± 1.9	19.9 ± 3.6	1.07 ± 1.15
Total (*n* = 17)	8.1 ± 1.9	19.1 ± 3.7	0.97 ± 1.07
Site 2			
Female (*n* = 12)	7.8 ± 1.6	19.0 ± 2.0	0.30 ± 0.16
Male (*n* = 12)	7.9 ± 1.5	20.5 ± 4.1	0.94 ± 0.77
Total (*n* = 24)	7.8 ± 1.5	19.8 ± 3.2	0.62 ± 0.63
Grand total (*n* = 41)	7.9 ± 1.6	19.5 ± 3.4	0.77 ± 0.85

Table 2. Number of den trees/logs and their diameter at breast height (DBH) and their heights for 41 radio-tracked brush-tailed rabbit-rats (*Conilurus penicillatus*) (mean ± 1 sd).

Site	Number of den trees	DBH of trees (cm)	Height of trees (m)	Number of logs	Diameter of logs (cm)
Site 1	19	34.4 ± 13.0	11.0 ± 4.5	13	25.0 ± 10.3
Site 1 random trees/logs	249	27.7 ± 12.1	13.2 ± 4.6		
Site 2	43	28.0 ± 7.4	11.6 ± 7.4	7	19.8 ± 7.1
Site 2 random trees/logs	326	21.9 ± 9.9	11.6 ± 3.4		

range for males (4.40 ha) being over four times as large as the largest female activity range (0.97 ha). Perhaps the larger activity range for males is due in part to their search for mates. Rabbit-rats are thought to breed between March and October, when male activity would be expected to be greatest. Changes in activity range due to season need to be tested further. There was no difference in activity range between animals from both sites, suggesting that habitat plays little role in movements of rabbit-rats.

This difference in den DBHs of trees between the grids is a reflection of tree availability with trees at site 1 having larger DBHs than trees from site 2 (Table 2). However, rabbit-rats from both grids preferentially selected trees that were significantly wider than the majority of trees available to them, which suggests that they require trees of particular minimum width for denning. Rabbit-rats from site 1 also used den trees that were significantly shorter than were available to them. Taller trees may require more effort and time for rabbit-rats to climb (personal observations), which could increase their exposure to predators such as owls.

Other factors that might prevent rabbit-rats using other den trees are competition with other denning animals such as black-footed tree-rats (*Mesembriomys gouldii*), which use trees with a DBH of 42.8 cm (B. Rankmore, pers. comm.). Other possible competitors include brush-tailed possums, northern quolls, sugar gliders and various birds that use hollows.

The type of dens used by rabbit-rats at site 1 was not related to availability, with animals using dens particularly in hollow logs disproportionately more than were randomly available to them (Table 3). They also appeared to favour *E. porrecta*, a relatively short eucalypt, which again may be related to climbing effort and exposure to predators. The majority of trees available at site 2 were *E. tetrodonta* (Table 3), which explains why 50% of dens used at site 2 by rabbit-rats were in *E. tetrodonta*. However radio-tracked rabbit-rats from site 2 did use den trees disproportionately more than were randomly available to them. They also used hollow logs in greater proportions than were available to them. Animals from both sites used hollows in trees, particularly in eucalypts, suggesting that these trees may form hollows more readily than other species. However, most of the other trees are smaller and probably possess hollows of insufficient size.

Rabbit-rats appear to be relatively sedentary, at least in the short term, with activity ranges averaging 0.77 ha. Males have larger activity ranges than females, with the maximum range recorded at 4.4 ha. Radio-tracked individuals had activity ranges that did not differ significantly in different habitats. However, there were some differences in use of den sites between the different habitats, possibly related to hollow availability. The rabbit-rats showed some flexibility in denning sites, presumably allowing them to occupy sites with the availability of tree

Table 3. Species of trees used as dens by brush-tailed rabbit-rats (*Conilurus penicillatus*) and relative frequency of tree species present (%).

Species	Site 1 den trees	Site 1 relative frequency	Site 2 den trees	Site 2 relative frequency
Eucalyptus tetrodonta	12.5	27	50	51.3
E. miniata	9.3	25.2	12	5.1
E. porrecta	18.7	5.4	0	0.6
E. bleeseri	0	12.1	10	22
E. nesophila	6.2	7.6	0	0
Pandanus spiralis	0	1.3	2	1.2
Stag (dead tree)	12.5	6.7	12	12.3
Log	40.6	0.4	14	0.9
Acacia leptocarpa	0	1.8	0	0.6
Acacia auriculiformis	0	0.9	0	1.8
Terminalia ferdinandiana	0	1.8	0	0
Brachychiton diversifolius	0	1.8	0	0.3
Erythrophleum chlorostachys	0	2.2	0	0
Planchonia careya	0	1.8	0	2.4
Denhamia obscura	0	2.2	0	0
Gronophyllum ramsayi	0	0.9	0	0
Buchanania obovata	0	0	0	0.6
Gardenia megasperma	0	0	0	0.3
Planchonella pohlmaniana	0	0	0	0.3
Exocarpus latifolius	0	0.4	0	0

hollows limited by natural vegetation factors or intra- or inter-specific competition for hollows.

Conclusion

Given the small activity range reported here for this species, high population densities may place substantial demands on the use of hollows. This study has demonstrated the importance of hollows in trees, particularly eucalypt species, and logs are equally important for providing shelter for brush-tailed rabbit-rats. Therefore, land clearing, even in relatively small patches, and fire, which is an important component of the Northern Territory landscape, could have major implications for this species.

Acknowledgments

I would like to thank the Cobourg Board of Management for allowing me to work in the Park, the Cobourg Rangers from the Parks and Wildlife Commission of the Northern Territory, my supervisors, Dr John Woinarski and Dr Richard Noske, the many volunteers who have helped me with field work, and Australian Geographic for sponsorship.

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Rodent outbreaks in the uplands of Laos: analysis of historical patterns and the identity of *nuu khii*

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Abstract. Rodent outbreaks in the uplands of Lao PDR (Laos) are understood by traditional farmers to be triggered by the episodic and synchronised flowering and seeding of certain bamboo species. Historical data from 24 districts spread across four provinces indicate that these outbreaks have been a feature of the upland agricultural environment for at least 50 years. Although many outbreaks appear to be fairly local in scale, records from Luang Prabang and Oudomxay provinces appear to document at least one widespread and prolonged outbreak, over the period 1988–1993. Somewhat surprisingly, there is no suggestion that rodent 'outbreaks' have become more frequent in recent times, contrary to widespread reports that the level of chronic rodent damage to crops has increased over the last decade. This apparent 'uncoupling' of trends in rodent outbreaks and agricultural crop losses adds weight to the traditional perception that the outbreak events owe their origin to factors outside of the agricultural systems.

A variety of rodent species are probably involved in the outbreak events. The identity of the ethnotaxon *nuu khii*, literally the 'rat of bamboo flowers', remains somewhat enigmatic. In some areas *nuu khii* may refer to one or more species of primarily forest-dwelling rat. However, in other areas, this term appears to describe an ecological phenomenon, namely the eruptive increase of forest rodent populations, with subsequent outpouring into adjacent agricultural landscapes.

The historical records do not help identify the cause of the rodent outbreaks. The pattern of outbreaks shows no clear association with generalised El Niño Southern Oscillation cycles, and with the exception of one geographically widespread outbreak in 1988–1993, there is little to suggest a regional climatic influence of any kind. The traditional belief that rodent outbreaks occur in response to bamboo flowering events is plausible in terms of the general biology of Southeast Asian bamboos, but the historical data do not allow for any direct test of this proposition. Much more information is required on the identity, distribution and phenology of Lao bamboo species, and on the impact of mast-seeding events on small mammal communities in the Lao uplands, before this interesting and economically important ecological phenomenon can be properly assessed.

Introduction

Across much of South and Southeast Asia, episodic rodent outbreaks in upland habitats are understood by traditional farmers to be triggered by the episodic and synchronised flowering and seeding of bamboos (Parry 1931; Janzen 1976; Chauhan and Saxena 1985; Rana 1994; Singleton and Petch 1994; Schiller et al. 1999). This process, otherwise known as bamboo 'masting', involves the production, usually over a period of one or two years, of large quantities of highly nutritious seed, which is believed to trigger explosive increases in rodent populations within the bamboo forest habitat. Following depletion of the bamboo seed-fall, mass emigration of rodents into adjacent agricultural habitats is claimed, leading in some cases to heavy crop losses and even famine (Singleton and Petch 1994; Nag 1999; Schiller et al. 1999).

Although similar connections have been made between bamboo masting and rodent outbreaks in other subtropical regions, including Japan (Numata 1970), South America (reviewed by Jaksic and Lima 2002) and Madagascar (Rakatomanana 1966), to date there has been no detailed study of this important ecological phenomenon. However, at a more a general level, the potential role of mast-fruiting or mast-seeding in driving episodic rodent outbreaks is abundantly demonstrated by examples from deciduous forests in North America (Wolff 1996; McShea 2000) and from cool–temperate forests in New Zealand (King 1983; O'Donnell and Phillipson 1996).

In various parts of Lao PDR (Laos), the rainfed upland ecosystem still plays a predominant role in meeting the food requirements of many ethnic groups. In the 2000 production year, upland rice cultivation accounted for approximately 12% of total production and 21% of the total area under rice cultivation (Lao PDR Ministry of Agriculture and Forestry records). Most upland rice cultivation is still based on the use of ‘slash and burn’, shifting cultivation systems. The productivity of the upland systems of production is generally in decline and problems associated with upland cultivation are on the increase (Schiller et al.1999; Roder 2001). Rodent damage and associated grain loss are cited by upland farmers as being second only to weeds as the most significant production constraints of the uplands. The damage attributed to rodents is a chronic annual problem in most of the Lao uplands. However, the severity of the problem varies from year to year and between localities.

The occurrence of explosive rodent outbreaks in the uplands of Laos was reported by Singleton and Petch (1994) and Schiller et al. (1999), based on information obtained during interviews with farmers and agricultural officers, and on the returns from rat bounty systems. Schiller et al. (1999) noted that rodent outbreaks occur at “irregular intervals” but they did not speculate on the frequency of such events. Nor did they identify the outbreaking rodent species, known locally as *nuu khii* (literally ‘rat of bamboo flower’). Singleton and Petch (1994) suggested that the outbreaks might involve both *Rattus argentiventer* and a species of *Mus*, however this opinion was based on farmers’ descriptions rather than direct observation of specimens.

In this paper, we present the results of historical investigations into rodent outbreaks in four upland provinces of Laos. The study area is characterised by shifting cultivation systems that produce a mosaic landscape of gardens, remnant forest and regrowth habitats (Roder 2001). We also shed new light on the identity of *nuu khii*, based on voucher collections made between 1998–2001.

Although rodent outbreaks have been noted for at least 50 years, the reasons for these outbreaks are not adequately known. To gain a better understanding of the physical and biotic factors that regulate rodent population cycles and their impact on crop production systems, the analysis of historical records of rodent population fluctuations is essential.

Materials and methods

Our main body of historical information comes from five provinces: four of these provinces (Luang Prabang, Oudomxay, Houaphanh and Sayabouly) are in the northern agricultural region, while one (Sekong) is in the south-east of the country (southern agricultural region). Each of the provinces is unique in respect of climatic and/or agronomic factors. Annual rainfall is highest in Sekong (>2000 mm) and lowest in parts of Luang Prabang and Sayabouly (<1440 mm) (Sisophanthong and Taillard 2000). Houaphanh is generally at a higher elevation than the other provinces and is considerably colder in the winter months than the other provinces. The ‘summer’ temperatures in Sekong are several degrees higher than in the more northerly provinces. Among the five provinces, the intensity of upland shifting cultivation is highest in Luang Prabang and Oudomxay (Sisophanthong and Taillard 2000).

In Luang Prabang, Oudomxay, Houaphanh and Sekong, information was obtained from four to eight districts. The sources of information accessed were: (1) documentary records held by the provincial offices of the Ministry of Agriculture and Forestry; (2) interviews with current and former staff of these offices; and (3) interviews with farmers. In Sayabouly, information was gathered exclusively from farmer interviews.

Information was sought on: the year and season of outbreaks; the rodent species involved and their approximate density; the geographical extent of outbreaks within the district; the crops affected and estimates of crop losses; and annual rainfall. Not all classes of information were obtained in all provinces or districts and the time period covered by the records also varies from 15 years (Sekong province) to 50 years (Luang Prabang and Houaphanh provinces).

Estimates of crop losses are based on reported cropping areas and yields from particular districts. Not all of the yield loss is necessarily due to rodent damage, which may be compounded by other factors. On the other hand, yield loss estimates typically will not register ‘foregone’ loss where farmers fail to plant crops in anticipation of their complete destruction by rodent pests. In analysing the historical data, outbreaks that occurred in consecutive years were treated as a single, extended event. Estimates of crop losses during these extended outbreaks support this interpretation (see Results and Discussion).

Rodent specimens were collected between 1998–2002 during the course of regular trapping programs in various agricultural and natural habitats in each of Luang Prabang, Oudomxay, Houaphanh and Sekong provinces. A smaller collection of voucher specimens was made in Sayabouly province in 2002. The trapping results and associated voucher specimens provide a detailed picture of the rodent communities in each province and some information on the pattern of habitat use during ‘non-outbreak’ years (Khamouane et al., this volume). The occurrence of *nuu khii* outbreaks in Viengthong district of Houaphan province during 2001 provided an opportunity to collect voucher specimens directly referrable to this ethnotaxon.

Results and discussion

What constitutes an ‘outbreak’?

The historical data provide a combined total of 155 ‘outbreak’ years across all four provinces. Estimates of crop losses during outbreaks show an exceptionally wide range, from as low as 2% to a maximum of 90% (mean + sd = 55% ± 23.5%). The low crop losses associated with some ‘outbreaks’ are intriguing, but make sense if rodent outbreak events are distinguished from chronic crop losses.

Singleton and Petch (1994) and Schiller et al. (1999) both report that farmers in the upland environment typically sustain annual crop losses to rodent damage in the order of 5–15%. Our discussions with farmers in Luang Prabang, Sekong and Sayabouly provinces suggest that the level of ‘chronic’ damage to upland crops has increased in many areas over the last decade. Interestingly enough, farmers generally attribute this trend to changes in cropping systems, grain storage practices or residency patterns. Furthermore, they consistently distinguish this chronic loss from the ‘outbreak’ phenomenon, which they generally associate either with droughts or with bamboo flowering events (see below).

Crop losses during outbreaks are generally said to exceed the normal chronic levels, sometimes to the point of crop devastation and famine. However, under the scenario where outbreaks are identified on criteria other than the intensity of associated crop losses, it is conceivable that some recognised outbreaks did not cause significant crop losses. For example, this could occur in a situation where rodents disperse out of the forest habitat at a time when few crops are present in the upland fields.

Historical pattern of rodent outbreaks

Luang Prabang

Data were obtained from eight districts, spanning the period 1950–2000. The earliest reported outbreak was in 1958 in Chomamy district. The frequency of outbreaks in any single district has varied from a minimum of one in Chomamy district to a maximum of five in Luang Prabang district (mean + sd = 2.9 ± 1.3 per district, *N* = 23). Individual outbreaks have ranged in duration from 1–5 years (mean + sd = 2.0 ± 1.2 per district), with the period between outbreaks (including the time since the last recorded outbreak) ranging from 1–42 years (mean + sd = 8.5 ± 9.8 per district) with no indication of clustering within this spread. Examination of individual district records suggests possible inter-district variation in the degree of regularity of outbreaks. For example, in Gnoy district, the three outbreak events, with durations of 4, 2 and 5 years, respectively, are each separated by ‘quiet’ periods of 7–8 years (last one ended in 1993). In contrast, in Phonexay district, the four recorded events, each of 1–2 years duration, are separated by less regular periods of 14, 12 and 6 years, while in Luang Prabang district, five outbreaks, each occupying a single year, are separated by periods of 2, 13, 3 and 1 year.

The historical pattern of outbreaks within Luang Prabang province (Figure 1) shows several interesting features. The first is the strong cluster of reported outbreaks over the period 1989–1993, when all but one district experienced a rodent outbreak of between 1–5 years duration. The second is the presence of several extended gaps during which few outbreaks were reported, such as before 1961, between 1971–1989, and since 1993. Various factors may account for these gaps, including uneven reporting or recollection of events, and the general disruption of agriculture across much of Luang Prabang province during the war years. However, the last 20 years of records are almost certainly free of any such uncertainties.

Bamboo flowering is mentioned in connection with 16 of the 23 rodent outbreaks. Drought conditions are also mentioned in relation to 10 outbreaks, either alone (*N* = 3) or in combination with bamboo flowering, while rainy conditions are noted for one outbreak. Unfortunately, no information was available for bamboo flowering events or unusual rainfall during ‘non-outbreak’ years.

All but two of the 23 rodent outbreaks in Luang Prabang province are said to have occurred during the wet season; the exceptions are outbreaks that extended across the wet and dry seasons in Luang Prabang district in 1991 and in Nambark district in 1995. The strong association with the wet season through the greater part of the record may simply reflect the fact that, historically, little crop was grown in upland Laos through the dry season. Over the last decade, the area of valley floor paddy under irrigation has increased, thereby increasing the likelihood of crop damage during the dry season.

Estimates of crop losses during outbreak years range from 2–90% (mean + sd = 48 ± 31%). The low crop losses associated with some ‘outbreaks’ are intriguing, but make sense if outbreak events are being distinguished from chronic losses. Detailed discussions with farmers in Pak Ou district suggest that the level of ‘chronic’ damage to upland crops has increased over the last decade. Interestingly enough, they attribute this trend to changes in cropping systems, grain storage practices and residency.

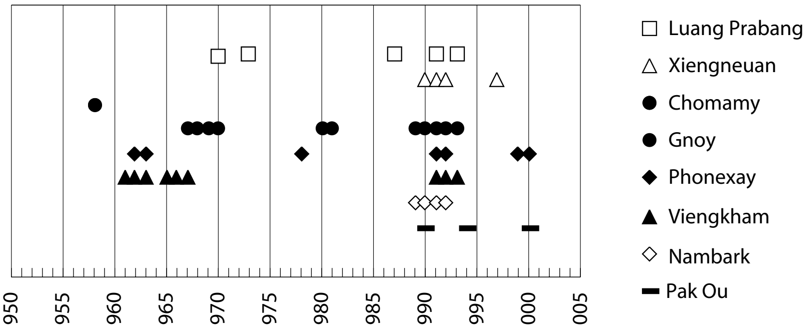

Figure 1. Historical pattern of rodent outbreaks in Luang Prabang province, by district.

Furthermore, they consistently distinguish this chronic damage from damage caused by the ‘outbreak’ phenomenon. Similar comments were obtained from farmers in Sekong and Sayabouly provinces.

Houaphanh

Information was obtained from eight districts. A total of 42 outbreaks were reported, the earliest dating from 1953 in Viengthong and Houameuang districts (Figure 2). The frequency of outbreaks per district ranges from 3–9 (mean + sd = 4.9 ± 1.4 per district). Most outbreaks occupy a single year, however there were three outbreaks of 2 years duration and three of 3 years duration (mean + sd = 1.2 ± 0.6 years). The mean interval between outbreaks, calculated across all districts, is 6.1 ± 4.3 years, with a suggestion of peaks at 4 years and 9–10 years. As in Luang Prabang province, there is considerable variation in the frequency and pattern of outbreaks between individual districts.

When the outbreak events are pooled across the entire province, the Houaphanh data show a weakly cyclic pattern with periods of more frequent and widespread outbreaks (e.g. 1953–1957, 1967–1974, 1981–1987) separated by periods of relative quiet. Other than in Xammneua district, there have been few records of outbreaks in Houaphanh province over the past decade, however this ‘quiet’ phase may have broken recently, with widespread outbreaks reported in late 2001, after this survey was completed.

All historical rodent outbreaks in Houaphan province occurred during the wet season, with the majority specified as occurring in September–October (again coinciding with the major cropping period). Bamboo flowering events are noted in relation to most outbreaks. Drought conditions are indicated for every outbreak in Viengthong district, but are not mentioned for outbreaks in any other districts. The estimates of associated crop damage range from 12% to 90% (mean + sd = 60.8 ± 19.0%).

Oudomxay

We have records covering the period 1975–2000 for each of four districts. For Beng and Xay districts, the information is limited to an estimate of damage where this value exceeds 10%. For La and Houn districts, there is some additional information on the timing of crop damage and bamboo flowering events. Rainfall data are available from a station in La district for the period 1987–2000.

Oudomxay province appears to have experienced a widespread and prolonged rodent outbreak spanning the period 1985–1995 (Figure 3). In all four districts, the highest levels of damage were reported in 1990, with reported crop losses of 40–70% during that year. The local rainfall records show that 1990 was a year of especially severe drought in Oudomxay, with dry conditions also in 1987 and 1992–93. However, higher than average rainfall fell in each of 1991 and 1994, hence any link between rainfall and rodent populations must be complex if indeed

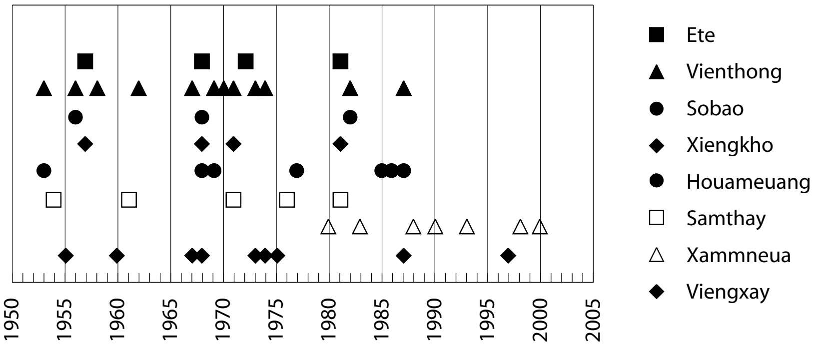

Figure 2. Historical pattern of rodent outbreaks in Houaphanh province, by district.

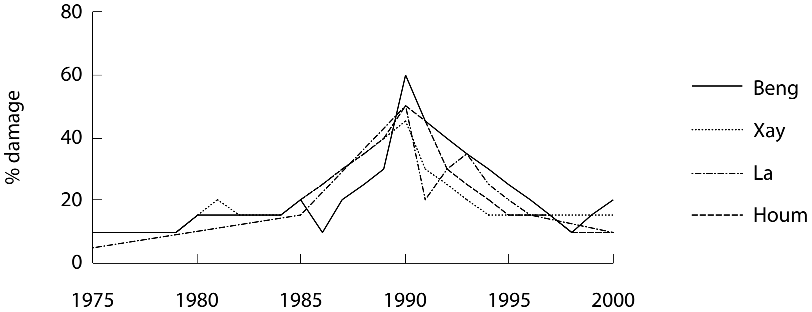

Figure 3. Recent pattern of crop damage attributed to rodent outbreaks in four districts of Oudomxay province.

it exists at all. Bamboo flowering is not mentioned other than for the period 1975–77 in La district and for 1975–78 in Houm district. Interestingly enough, the period of most intense damage in Oudomxay province coincides with the 1989–1993 outbreak identified in nearly all districts of Luang Prabang province to the immediate east.

Sekong

Records are available for the period 1984–2000 from four districts; local rainfall data are available for each district for all or part of this period. The pattern of outbreaks appears to differ markedly between districts. In Duckchiang district, there have been rodent outbreaks almost every year since 1984, with extreme crop losses in the range of 60–75% (Figure 4). In contrast, the other districts appear to experience episodic outbreaks, typically lasting 1–3 years, but separated by 'quiet' periods of 1–2 years. Crop losses of 50–80% are reported during the outbreak periods. The regular cycle of outbreaks is most obvious in the data from Lamam district.

The Sekong rainfall data indicate that Kaleum and Lamam districts are much drier overall than Thateng or Duckchiang (Figure 5). Fluctuations in rainfall since 1984 show no obvious association with reported outbreaks or with the severity of crop damage. For example, in Thatheng district, severe rodent damage occurred in both very wet years (e.g. 1991, 1995) and very dry years (e.g. 1989, 1996).

In all districts, the timing of rodent outbreaks has evidently changed during the period covered by the records, shifting from an exclusively wet-season phenomenon to one that spans both wet and dry seasons. This change evidently occurred at different times in different districts (i.e. 1993 in Lamam, 1995 in Thatheng, 1996 in Duckchiang, 1997 in Kaleum) and it is possible that it reflects the gradual increase in irrigated dry-season paddy over this period. Bamboo flowering events are not mentioned at all in the Sekong data set.

Sayabouly

A detailed historical survey was not undertaken in Sayabouly province. However, interviews with farmers in 2002 suggest that *nuu khii* outbreaks are qualitatively different from normal fluctuations in rodent communities within the village and field habitats. They are said to involve a different species of rodent that emanates from the forest habitat (located approximately 3–5 km away), and to occur episodically—the last one in 1993. A connection with bamboo flowering events in the forest habitat was mentioned, but our informants themselves had not observed an initial eruptive phase in the forest.

The identity of *nuu khii* and other rodents

Six different ethnotaxa are mentioned as being involved in outbreaks (Table 1). As reported by previous authors (Singleton and Petch 1994; Schiller et al. 1999), *nuu khii* is mentioned more often than any other ethnotaxon (53.8% of outbreaks), followed by *nuu ban* (34.4% of outbreaks). The ethnotaxon *nuu mone* (grey colour rat) was mentioned only in Houaphanh province. Many

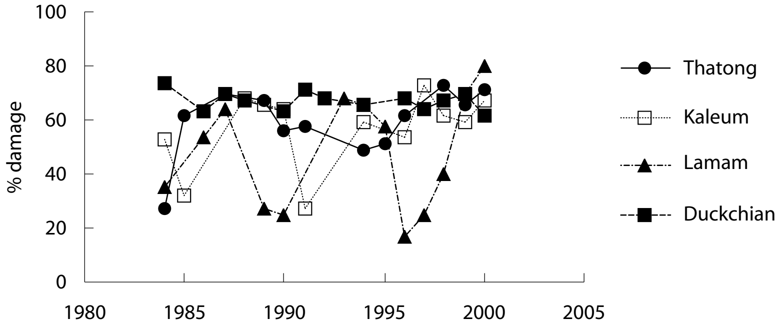

Figure 4. Recent pattern of crop damage attributed to rodent outbreaks in four districts of Sekong province.

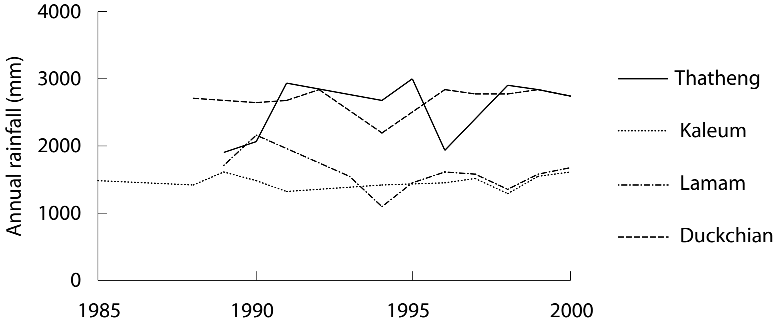

Figure 5. Variation in annual rainfall in four districts of Sekong province.

outbreaks mention both *nuu khii* and *nuu ban* as jointly responsible for the crop damage.

Nuu ban is variously translated as 'house rat', 'field rat' or 'white-bellied rat'. Although Singleton and Petch (1994) tentatively identified this taxon as *Rattus argentiventer*, collections made in six provinces since 1998 suggest that *nuu ban* actually refers to one or more members of the *Rattus rattus* complex, which in Laos comprises the dominant species of village, garden and disturbed forest habitats (Aplin, Chesser and ten Have, this volume). To date, *Rattus argentiventer*, the true 'rice-field rat' of Southeast Asia, is recorded only from lowland habitat in Khammouan province (Francis 1999). The lesser rice-field rat (*Rattus losea*) also is recorded from Khammouan province (Francis 1999) and from one locality in Sekong province (Musser and Newcomb 1995), although it has not been encountered during the course of our fieldwork. Neither of these taxa is likely to be involved in the outbreak events discussed here. An interesting observation on *nuu ban* is that this taxon appears to be more frequently mentioned in 'outbreaks' over the last decade than during earlier times.

Three other ethnotaxa are mentioned either infrequently or on a local basis only. The name *nuu american* (literally 'foreign rat') is applied widely within Laos for *Bandicota indica* (in Sayabouly province this species is also called *nuu ngay*). This taxon was mentioned only twice in relation to outbreaks in Luang Prabang, and farmers in Pak Ou district further claim that this species does little damage compared with *nuu ban* or *nuu khii*. *Nuu mone* is mentioned only for outbreaks in Houaphanh province; this may be a local name for a member of the *R. rattus* complex. In Sayabouly province, a member of this complex was identified as *nuu puk*, further demonstrating the inter-regional diversity within the system of local names.

The identity of *nuu khii* remains enigmatic. In Sekong province, specimens of *Mus cervicolor* and juvenile *Rattus 'rattus'* were both identified as *nuu khii*, in keeping with earlier suggestions that this ethnotaxon might refer to a true mouse. However, farmers in Pak Ou district of Luang Prabang province claim that *nuu khii* is not a species of *Mus*, which they generally identify as *nuu sing*. They also distinguish *nuu khii* from *nuu waay* ('rattan' rat) which, from its description (as a red-backed, white-bellied forest rat), may include *Maxomys surifer*, one or more *Niviventer* species, and possibly also *Chiromyscus chiropus*. In Sayabouly province, farmers were adamant that *nuu khii* is different from *nuu puk* (*R. 'rattus'*). They also claimed that, other than during outbreak events, *nuu khii* is not found in the agricultural landscape. Instead, it is a forest rat that periodically emerges from the forest as a 'rat army' that moves through the agricultural landscape destroying any crops that it encounters. Their detailed description of *nuu khii*—as a short-furred, greyish rat, around 20 cm in body length, with a pure-white belly and a single-coloured tail about equal in length to the body—could fit equally well with several possible candidates, including a species of *Niviventer* or possibly *Berylmys bedmorei*. To date, we have been unable to obtain a voucher specimen of *nuu khii* from Sayabouly for local and scientific identification.

Nuu khii outbreaks in several districts of Houaphan province in 2001 did finally provide an opportunity to obtain voucher specimens for this ethnotaxon. The resultant sample, identified collectively as *nuu khii*, includes a variety of rat species including two different members of the *R. rattus* complex. At least in Houaphanh province, the taxon *nuu khii* thus appears to be an ecological category, perhaps signifying that a particular rodent outbreak is due to conditions or circumstances within the forest habitat rather than the agricultural landscape. However, at a broader scale, these varied results suggest that the term *nuu khii* may be used in different ways across Laos.

Rodent outbreaks and El Niño

The historical information from Laos points to considerable regional heterogeneity in the pattern of rodent outbreaks, even within a single province. However, there is also some evidence for broad-scale synchrony of outbreaks, especially within and between the northern provinces of Luang Prabang and Oudomxay.

The question of what environmental factors might be driving these events is an interesting one from an ecological perspective and a critically important one if resultant crop damage is to be mitigated. The two factors that obviously warrant early consideration are large-scale climatic perturbations and bamboo masting events.

Laos falls within the geographical area influenced by the El Niño Southern Oscillation (ENSO) (Holmgren et al. 2001). El Niño events, caused by anomalously warm sea surface temperatures in the equatorial eastern Pacific, typically occur once every 3–6 years, with widespread and

Table 1. Frequency of mentions of various ethnotaxa in reported outbreaks.

Province	*nuu khii*	*nuu ban*	*nuu american*	*nuu na*	*nuu mone*	*nuu tongkao*	Total
Luang Prabang	36	7	2	1			46
Houaphanh	28	11			8		47
Sekong	20	37		3		3	63
Oudomxay	2			2			4
All combined	86	55	2	6	8	3	160

diverse consequences on both natural and agricultural ecosystems (Meserve et al. 1995; Lima et al. 1999; Zubair 2002). Across Southeast Asia, the impact of El Niño events varies both regionally (Holmgren et al. 2001) and in accordance with the time of onset of the oscillation (Kane 1999). In Laos, the impact appears to be especially variable (Hompangna et al. 2000), although in recent times it has more often led to widespread drought (e.g. El Niño of 1987, 1991–1992, 1997) than to flooding (e.g. El Niño of 1982).

Over the 50-year period covered by the rodent outbreak data, particularly strong El Niño events (as estimated from monthly values of the Southern Oscillation Index) occurred in 1953, 1965, 1972, 1977, 1982–83, 1986, 1991–92, 1994 and 1997–98 (Yue 2001). However, data on the impact of these events across Southeast Asia (Kane 1999) and in Laos specifically (Hompangna et al. 2000) suggest that widespread severe droughts were experienced only in 1965 and 1972, with widespread flooding in 1953 and 1983. The El Niño event of 1991–92 had variable effects in Laos, with drought in the northern provinces but above normal precipitation and some flooding in the south (Hompangna et al. 2000). The 1997–98 El Niño event, rated on some measures as the strongest on record (McPhaden 1999), resulted in widespread drought across Laos in 1998 and a marked increase in forest fires during the dry season of 1998–99 (Hompangna et al. 2000).

The geographically widespread and prolonged nature of the rodent outbreaks in Luang Prabang and Oudomxay provinces in 1989–94 suggests the possibility of some underlying climatic control. These outbreaks followed directly on the El Niño of 1987–88 and overlapped the El Niño of 1991–92. However, as noted earlier, local rainfall data covering this period show complex inter-annual variations, and suggest a need for caution in any interpretation. At a larger scale, the long-term rodent outbreak records from Luang Prabang and Houaphanh provinces do not show any clear pattern of association with El Niño events. While this does not rule out the possibility that climatic factors were behind some or all of the outbreaks, it does suggest that any linkage is likely to be complex. Lima et al. (1999, 2001) found that both a delayed density-dependent response and predator–prey relations mediate the effect of ENSO-related rainfall variations in causing rodent outbreaks in western South America. In the agricultural landscape of the Lao uplands, additional complexity might be anticipated, related to the impact of climatic events on the diverse cropping systems.

Rodent outbreaks and bamboo masting

The wider Asian region supports a high diversity of bamboos, probably around 140 species in all. Mast-seeding is common but not ubiquitous within the group, and it is generally more prevalent in areas with strongly seasonal climates (Janzen 1976; Soderstrom and Calderón 1979). Among bamboos, mast-seeding appears to be controlled by internal, genetically determined factors, such that individuals flower and seed after a certain number of years of growth (Janzen 1976). This is unusual among mast-seeding plants, which more typically do so in response to environmental triggers (Kelly 1994). Bamboos are unusual in two further respects. Most species are semelparous, which means that they usually die after setting seed, and many have a very long period of vegetative growth before seeding, with recorded intermasts of 3–120 years (Janzen 1976). Most Asian mast-seeding bamboos have intermast periods in the order of 15–60 years.

The majority of Southeast Asian bamboos flower at the end of the wet season such that the seeds ripen and fall over the dry season. Many species flower profusely and produce copious quantities of seed. Individual seeds range in size from rice kernel- to pear-sized, with total productivity estimates for two Indian species of around 1 kg of seed/m^2 (*Bambusa arundinacea*; Gadgil and Prasad 1984) and 3.6 kg/m^2 (*Dendrocalamus strictus*; Janzen 1976, p. 355). The seed itself has nutrient qualities slightly greater than rice or wheat, and appears to be unprotected by toxins (Janzen 1976). Apart from rats, many other groups of animals are reported to feed on bamboo seed in the Asian context, including many birds (jungle fowl, pheasants, pigeons, parrots), ungulates (cervids and bovids) and rhinoceros (summarised by Janzen 1976, pp. 354–363). Large congregations of feeding birds are reported, but there are no detailed ecological studies of such events.

Although all mast-seeding bamboos by definition display some degree of synchrony in flowering and seeding, the duration and geographical scale of the ‘events’ vary considerably. In many species, seeding occurs synchronously at the level of an individual clump or closely related group of clumps, but with no overall geographic consistency. Large-scale synchrony is much less common. In India, for example, 70 of 72 bamboo species are mast-seeders but only eight are recorded as flowering synchronously at the district level or wider (Keeley and Bond 1999). However, where widespread synchrony does occur, it can be on a staggering scale. Janzen (1976, p. 361) cites examples from India of mast-seeding across 1200 square miles for *Dendrocalamus strictus*, 6000 square miles for *Melocanna bambusoides* and “hundreds to thousands of square miles” for *Bambusa polymorpha*. Keeley and Bond (1999) suggest a typical scale for synchronous flowering of 102 to 103 hectares. Synchrony is, of course, only a relative concept, and it should be noted that the mast-flowering and mast-seeding process is usually spread over 2–5 years, even within the confines of a single clump (Janzen 1976; Gadgil and Prasad 1984). Fallen bamboo seeds typically germinate after the first rain and they display no special adaptation for dormancy; indeed, they appear to lose their viability (and presumably some of their nutritional value) after one or two months, even if kept dry (Janzen 1976).

Little specific information is available on the bamboos of Laos. Gressit (1970) listed five genera of Bambusacae as occurring in Laos (*Arundinaria*, *Bambusa*, *Cephalostachyum*, *Dendrocalamus* and *Oxytenanthera*).

Bamboos are conspicuous in many upland habitats, with large stands situated along watercourses and in many areas of former slash-and-burn activity. Roder et al. (1995) mentioned two species as important fallow species, *Bambusa tulda* and *Dendrocalamus brandisi*i, while Singleton and Petch (1994, Table 2.10) mentioned two species (*Bambusa tulda* and *Oxytenanthera parvifolia*) as specifically implicated in rodent outbreaks. The intermast period of *B. tulda* is given by Rana (1994; see also Singh et al. 1994 for identity of bamboo species) as 48–50 years and this species is further said to display widespread synchrony of mast-seeding. Species of *Dendrocalamus* typically have long intermast periods in the range 30–50+ years and this genus also includes species with large-scale synchronised masting. Interestingly enough, both of the major fallow bamboos are included by farmers among their suite of ‘good’ fallow plants (Roder et al. 1995, Table 4). Where bamboo is involved in garden fallow systems, short-term regeneration presumably occurs from rhizomes remaining within the ground after land preparation (Christanty et al. 1996). According to Janzen (1976), the cutting, burning or transplanting of a mast-seeding bamboo generally will not impact on its genetically determined flowering calender.

Conclusion

The traditional belief that rodent outbreaks occur in response to bamboo flowering events is clearly plausible in terms of the general biology of Southeast Asian bamboos. Bamboo masts—involving the episodic mass-production of an abundant, highly nutritious food resource—are an example of a ‘pulsed resource’ (*sensu* Ostfeld and Keesing 2000) and as such, may well underpin episodic outbreaks of vertebrate consumers, including rodents, either directly or through intermediate ecological linkages. Jaksic and Lima (2002), after reviewing the historical and ecological evidence of South American ‘ratadas’, also concluded that bamboo masting may be responsible for some of these events, especially in Brazil. However, as in Laos, the South American evidence is largely circumstantial. A detailed ecological study of a Lao *nuu khii* outbreak or a Brazilian ‘ratada’ in progress is sorely needed.

Acknowledgments

We are grateful for the efforts of the provincial staff who collected the historical data used in this paper: Mr Khampheng, Mr Chanhthi, Mr Simone and Mr Banxa. Useful comments on this manuscript were provided by Dr John Schiller, University of Queensland. Research activities in Laos have been carried out with funding support from Australian Centre for International Agricultural Research (ACIAR) Project AS1/98/36.

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How do rodent systematics affect conservation priorities?

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Abstract. The role of sound systematics for setting priorities for biodiversity conservation is receiving increasing recognition. The present work provides some examples about how systematic ambiguities and uncertainties might affect conservation prospects for the most species-rich mammal order. A clear understanding of systematics is fundamental to protect the diversity of rodents, albeit utilising a higher-taxon approach.

Introduction

Rodents have long been considered intriguing subjects for evolutionary studies, yet their commonness, at least of the most studied species, has rarely stimulated interest in their conservation status. This is not surprising, given the emphasis on the serious problems created by the many pest species and the use of a few model species for much biological research. This situation results in little interest in rodent conservation among mammalogists, including taxonomists. Much more conservation interest has been generated by studies dealing with ecological processes in ecosystems, particularly with those concerned with the effects of habitat fragmentation. However, little doubt exists of the importance of correct systematics for evaluating conservation status and priorities. The IUCN/SSC (International Union for Conservation of Nature and Natural Resources (World Conservation Union)/Species Survival Commission) Rodent Specialist Group, from the outset, began to redress this situation of low interest through the compilation of the conservation priority list. In agreement with IUCN/SSC policy, compilations of regional Action Plans have begun and so far are available for North America and Australia, with a few others in an advanced stage of preparation (e.g. Russia, Europe, India, West Asia). Generally, the interest and involvement generated by these initiatives among experts has been limited, contrasting with the size of the task due to the high number of rodent species (c. 2000, comprising more than 40% of mammal species; Wilson and Reeder 1993) and their almost cosmopolitan range. This is similar to patterns seen in the membership of IUCN/SSC Specialist Groups and in papers published in conservation journals; both are heavily biased towards charismatic, large-sized mammal groups such as elephants, carnivores and primates. On the other hand, current rodent taxonomy seems to encourage a low valuation of the group's diversity. For example, rodents were chosen as an example of uneven subtaxa distribution within taxa assemblages (Purvis and Hector 2000), a fact exacerbated by the confusion around the evolutionary systematics within 'Muridae' and a poor knowledge of the taxonomic relationships of some speciose groups. In fact, even definitions of genera such as '*Rattus*', as presently understood, are probably masking a much more complex taxonomic situation. Poor taxonomic knowledge of rodents should be considered when analyses are performed concerning, for example, historic extinction rates among mammals or comprehensive assessment of conservation priorities.

Overview of systematic problems

Higher-level systematics

Much confusion surrounds almost all levels of rodent systematics (Corti 2001). Even monophyly of the order has been questioned on biomolecular grounds, with Hystricomorpha and Sciuromorpha being clearly separate from Myomorpha (Graur et al. 1991) despite a lack of consensus on this issue. The history of higher-level rodent classification is summarised by Carleton (1984). He recognised two suborders: Sciurognathi and Hystricognathi, the first being described sometimes as a 'wastebasket group' for the lack of data supporting this clade. Some African families (Anomaluridae, Pedetidae, Ctenodactylidae) are placed among Sciurognathi but their phylogenetic affinities are uncertain. From a conservation point of view, such ancient and poorly represented lineages (all together, the three families comprise about 14 species) represent obvious priorities. At a lower level, variability in the recognised number of families and subfamilies (around 50–55) is attributable primarily to differences in ranks assigned within the superfamily Muroidea. Molecular studies of 32 species belonging to 14 subfamilies of Muridae reported five major lineages (Michaux et al. 2001). It may be desirable to compare these results with the status of IUCN species to ensure that none of these lineages, particularly the less speciose, such as the Calomyscinae, is threatened. The higher genetic divergence found in small mammal genera, as opposed to those genera usually recognised among larger mammals (Castresana 2001), could imply that, even at this level, rodent diversity has been generally excessively lumped by taxonomists.

Species-level classification

After mammalogists adopted a more ‘lumped attitude’ in the recognition of species in the first half of the 21st century, the number of rodent species dropped to 1719 at the time of publication of the first edition of *Mammal Species of the World* (Honacki et al. 1982). Since then, an increasing trend has occurred in the numbers of recognised species and genera. This is due to application of different species concepts, an increase in museum collections (albeit far from ideal) and the use of karyotypic and molecular investigation techniques, which have led to the discovery of dramatic ‘intraspecific’ variability (even if this has not been easily assigned to taxonomic categories). This trend is expected to continue because many species that are poorly known, have very small hypodigms, and are distributed over large geographical areas (especially in the tropics), are under-surveyed. A crude comparison with primates (Table 1) suggests that 3100 may be a realistic estimate of the number of existing rodent species, with perhaps many more if the phylogenetic species concept is adopted. Regarding conservation activities, accurate species recognition is particularly valuable in the less speciose taxa. Actually, increasing importance is given to protect those taxa which represent a unique part of the evolutionary history of a group (Faith 1992). Therefore, the loss of a species belonging to a monotypic or not a very speciose genus or family may be a greater loss than that of a species of a speciose clade. The species status accorded to the eastern and the southern African springhare, *Pedetes surdaster* and *Pedetes capensis*, respectively, the only members of Pedetidae (Matthee and Robinson 1997), allows more stringent conservation measures for these unique animals, possibly opening the door to more in-depth studies of *Pedetes* phylogeography. In fact, it appears that denying species status to isolated distinctive populations may hamper interest in their conservation, as may be the case with the highly threatened populations of Eurasian beavers in China (*Castor fiber tuvinicus*) and in Mongolia (*Castor fiber birulai*). Effectively, it appears that subspecific status means a fall into oblivion for most taxa, perhaps due to the absence of modern and complete taxonomic revisions for many species, but also because of a general attitude of neglect towards ‘subspecies’, even among conservationists. Perhaps this is the cause of the strong ‘splitting’ attitude adopted, for instance, by the IUCN/SSC Primate Specialist Group. However, a serious limitation of this approach is the risk to the effective use of scarce resources for the conservation of slightly distinctive populations, usually found in developed countries. Species-level recognition of a morphologically distinctive Alpine pine vole population in Germany led to the only recorded European mammal extinction in recent years; that of *Microtus bavaricus*, following the building of a hospital over its restricted range. Fortunately, a new population of *M. bavaricus* has been identified in Austria (Haring et al. 2000), but a broader taxonomic review is needed to establish the true relationships among the different taxa of the *Microtus multiplex* complex.

Intraspecific variability

Geographical variation and subspecies recognition is not an easy task, even in the relatively well-known rodent fauna of Europe, and comparison with well-known groups like primates suggests that the alpha-taxonomy of rodents is still far from a definitive level of knowledge. There is growing interest in the identification of so called ‘evolutionary significant units’ for conservation purposes but such fine-grained levels of rodent diversity are generally not feasible at the moment, except in the most developed countries. In fact, practically no rodent subspecies from outside North America are included in the IUCN Red List, a fact matching the deeper knowledge of rodent diversity in the Nearctic. Under the *Endangered Species Act*, a 16-year-long battle is in place between supporters of the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) and astronomers who want to build several telescopes inside the range of this subspecies. The importance of incorporating the results of molecular phylogeography in conservation planning when these data are available should not be overlooked. In one such study, Taberlet et al. (1998) found that a very distinctive water vole, *Arvicola terrestris*, lineage occured in the Italian Peninsula. Therefore, the introduction of the American

Table 1. A comparison of recognised species number among Rodentia and Primates in the last two decades, giving number and proportional increase of species.

Order	Honacki et al. (1982)	Wilson and Reeder (1993)	% increase since 1982	Groves (2001)	% increase since 1993
Primates	181	233	28.7	356	52.7
Rodentia	1719	2021	17.5	–	–

mink, *Mustela vison*, into Italy—one of the causes of the severe decline in water voles in Great Britain—is particularly risky because of the threat posed to the unique Italian population, which clearly could not be re-stocked with animals from the rest of Europe.

Conclusion

A sound taxonomy is generally regarded as the basis for a meaningful policy on biological conservation and a refined taxonomy allows the unambiguous identification of endemics (restricted-range taxa), often an important part of biodiversity conservation policy. In the case of rodents, we suspect that studies below the species level are rarely of practical use in conservation practice and that higher level taxonomy—at the genus level for instance—is of greater relevance for setting priorities for rodent conservation globally in the foreseeable future (Amori and Gippoliti 2001). Yet taxonomic uncertainties, such as that concerning the endemic mouse on Flores Island in the Lesser Sunda, sometimes referred to the monotypic genus *Paulamys* or alternatively ascribed to the Sulawesi genus *Bunomys* (Kitchener et al. 1991), might affect conservation priorities at this taxonomic level too. Comparative phylogeographic studies have great importance for identifying regions characterised by genetically isolated populations if different taxa are found to follow the same pattern, which is not always the case. This should direct conservation efforts towards areas likely to maintain unique assemblages of populations, not only among rodents, before it is too late. As a final point, it must be stressed here that rodent diversity is still overlooked by the conservation community. The rodents of Madagascar, one of the world's biodiversity 'hotspots', represent a good case in point. If differences in the species richness between Malagasy primates and rodents may be explained both in evolutionary terms and in terms of the history of colonisation of the island, it is not clear why the 32 or so Malagasy primates species are included in five different families while the seven genera of Nesomyinae known in the 1980s (two new genera being described in the 1990s) continue to be included in one subfamily—Nesomyine—even if "...they are so distinct that each could stand as a member of a separate tribe or subfamily..." (Carleton and Musser 1984).

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SYMPOSIUM 3: BEHAVIOUR

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

How does rodent behaviour impact on population dynamics?

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Abstract. Rodent social behaviour has been studied extensively but whether or not social behaviour impacts population dynamics has been questioned. Social behaviour is affected by population density and the question is whether or not this is a circular causal system. Infanticide, dispersal, sexual maturation, and direct aggression are all potential processes that are a part of spacing behaviour in rodents. We need to know both the frequency and strength of these processes in rodents, and how they change with population abundance. Recruitment in rodent populations may be limited by the presence of breeding adults, and the kin structure of populations may affect the potential rate of population growth. Survival of neonates in the nest is poorly studied in rodents and very high losses at this stage may prevent population growth in some populations. We need additional experiments to address and uncouple the potential interaction of social behaviour and extrinsic processes like predation in limiting population abundance in natural populations of rodents.

Introduction

Rodents have been a favourite group for both ecological and behavioural studies, and the background of literature now available in these two scientific disciplines would fill a good library (Stoddart 1979; Watts and Aslin 1981; Elwood 1983; Cockburn 1988; Anderson 1989; Prakash and Ghosh 1992; Singleton et al. 1999). Detailed studies of behaviour are available for some species (e.g. Eisenberg 1962, 1963; Gliwicz 1997) and the broad categories of rodent social organisation are well understood. What is lacking is the bridge between rodent social organisation and rodent population dynamics, and this paper reviews the background of this issue and suggests gaps in need of further studies and experiments.

Avian ecologists had already suggested in the 1920s and 1930s that territorial behaviour could limit population density (Howard 1920; Nice 1937; Hensley and Cope 1951). Mammal ecologists were slower to accept that social behaviour might impact population dynamics, and the first approach was through physiology. Hans Selye in 1936 (Selye 1936) suggested that crowding in rodents could lead to physiological stress mediated through the adrenal gland, and stress could reduce reproductive output as well as increase death rates. David E. Davis and John Christian (Davis and Christian 1956) did the first field experiments to show that aggressive social interactions could reduce Norway rat population size, and since these early experiments, many authors have contributed studies that evaluate the role of social behaviour in affecting population events. In this paper I will examine our current understanding of how social processes might affect rodent population dynamics.

Mechanisms of social limitation

Social behaviour can affect population dynamics via four different mechanisms: control of the timing of sexual maturation, infanticide, control of dispersal, and direct aggression (= interference competition). Wolff (this volume) has reviewed these aspects of the social ecology of rodents and has concluded that social interactions play little role in regulating or stabilising rodent populations. I will not review the detailed aspects of these social interactions, which are covered well in Wolff (this volume) but I wish to concentrate here on his conclusion that social interactions are rarely relevant to population dynamics.

The key behaviours in rodents that might impact on population density can be broadly classed as spacing behaviour. If individual rodents maintain a personal or group space, then clearly the density of that population will reflect this spacing. Spacing is most readily thought of as resulting from direct physical aggression, but this mental image must be broadened to include spacing by avoidance behaviour as well as spacing by direct physical interactions. We first ask if spacing behaviour could limit population density. Watson and Moss (1970) suggested that limitation might occur if three conditions could be satisfied:

1. a substantial part of the population does not breed ('surplus animals');
2. the non-breeding individuals can breed if the social dominants are removed; and
3. the breeding individuals are not using up some other limiting resource.

Populations that satisfy these three conditions can be considered to be limited by 'social space', and the resource being competed for can be considered to be 'competitor-free space'. Let us consider now how we have tested for these three conditions of Watson and Moss (1970).

Surplus individuals

The first problem in testing for possible population limitation by spacing behaviour has been to determine if 'surplus' animals are present. Following the lead of early experiments on songbirds (Hensley and Cope 1951), rodent ecologists used removal experiments to measure the number of surplus rodents. Krebs (1966) reports one early experiment on *Microtus californicus* in California. These and many other removal experiments have shown that when you remove breeding adult rodents from an area, a flood of 'surplus' individuals colonise the removal site, and in many cases bring the population density of the removal site back to the control density (e.g. Krebs et al. 1978). These removal experiments raise many issues that are relevant to rodent pest control: Where do these 'surplus' animals come from? What is their fate if a removal experiment is not taking place? Do the 'surplus' animals differ in age, sex, or size from resident animals? Many of these questions have been discussed by Anderson (1989) and Cockburn (1988). Clearly, if we accept the standard Darwinian principles, each of these individuals is attempting to maximise its own fitness, and our explanations of these results must fit in with contemporary evolutionary theory. Removal experiments to assess 'surplus' individuals have been criticised in some species, since adjacent territory owners may shift their home ranges into the evacuated area (Schieck and Millar 1987). This criticism will affect the quantitative measurement of 'surplus' animals, but it does not eliminate them. Schieck and Millar (1987) and Clinchy et al. (2001) have shown that 'surplus' animals immigrate into unmanipulated areas as well as local residents shifting their home ranges into the evacuated area.

Given that we have 'surplus' individuals, the second question is whether or not these individuals can breed when given the opportunity. Our results with removal experiments on *Microtus* voles have shown that there is no impediment to breeding in 'surplus' voles, once the residents have been artificially removed from the area (Myers and Krebs 1971; Krebs et al. 1978). The impact of adult females on maturation of juvenile females has been studied particularly well in *Clethrionomys* voles (Bujalska 1970; Gilbert et al. 1986; Kawata 1987). The conclusion to date is that if there are surplus individuals in a rodent population, they are capable of breeding if social controls of maturation are relaxed.

Territoriality

If breeding male or female rodents defend a territory, the potential exists for spacing behaviour to limit population density. The larger a territory that is defended, the lower the population density, and the immediate question arises as to what determines territory size. There has been an ongoing argument in the bird literature between those who interpret territory size as a consequence of population density and those who interpret it as a cause:

territory size → population density
population density → territory size

The only way to test these two views is to experimentally manipulate territory size, typically by manipulating aggression (e.g. Watson and Jenkins 1968), but few of these kinds of experiments have been done on wild rodents (Gipps et al. 1981; Taitt and Krebs 1982) because they are technically difficult.

There is an enormous literature on the behavioural aspects of territoriality, and the question we need to ask here is whether we can treat territorial behaviour as a 'black box' and analyse the population consequences via population-level experiments (a top-down approach), or whether we need a bottom-up approach through detailed ethological studies of territoriality. This question is largely unanswered, and I will proceed under the assumption that we can adopt a top-down approach to understanding territoriality.

Recruitment

A key question in rodent population dynamics is what controls recruitment. Rodents are model systems of species with very high reproductive rates coupled with high death rates, and the question we need to answer is what happens to all the young produced in a rodent population. The general finding in rodent trapping studies is that only a low fraction of the young produced ever recruit into the breeding population (Adler et al. 1987). The assumption is usually made that predators, diseases, bad weather and other environmental factors control the survival of juveniles in their first few weeks of life.

Adult rodents can limit the recruitment of juveniles, and this can be another critical bridge between social behaviour and population dynamics. If adults can limit recruitment of juveniles, we must ask if both sexes are involved or only one. We carried out a series of sex-specific removal experiments on voles that showed conclusively that adult females were, for the most part, the key to understanding why recruitment is restricted. We carried out bi-weekly sex-specific removal experiments on *Microtus townsendii* and *M. oregoni* for two years (Redfield et al. 1978) and the results are illustrated in Figure 1. Recruitment was 109% higher in the area with a more male-biased sex ratio, compared with a control area, and 32% lower in the area with a more female-biased sex ratio. The same pattern was found in a more carefully controlled experiment with the same basic design with *Microtus canicaudus* by (Wolff et al. 2002). Boonstra (1978) showed with a juvenile introduction experiment that young juvenile *M. townsendii* would survive well if introduced at 3 weeks of age into a field from which all the adults had been removed, but few survived introduction into a field with only adult females present or both adult sexes present (Figure 2). The implication is that adult females directly kill strange juveniles or drive them out of the area, thereby limiting recruitment locally.

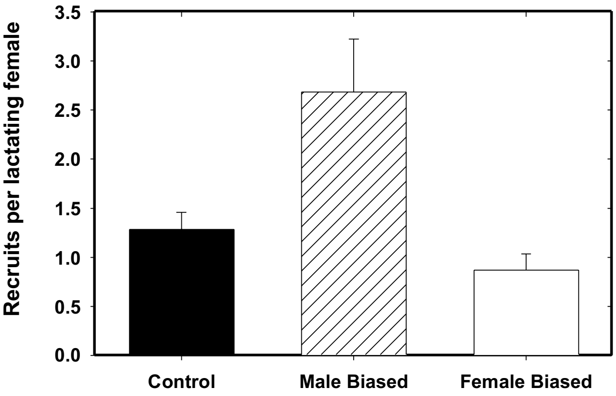

Figure 1. The average recruitment of juvenile *Microtus townsendii* for the summer breeding seasons of 1972 and 1973 on control (unmanipulated), male-biased (80% adult females removed) and female-biased (80% adult males removed) areas. Recruitment was measured as the number of juveniles live-trapped at 2–5 weeks of age per pregnancy. Error bars are 95% confidence limits. (Data from Redfield et al. 1978, Table 6.)

Kinship effects

If spacing behaviour can affect the recruitment rate of young animals, as well as their rate of sexual maturation, we need to find out more information about the rules that govern spacing behaviour in rodents. Darwinian arguments about inclusive fitness would suggest that, for a start, relatives should respond differently to one another than they should to strangers. This simple idea spawns several questions about how relatives might recognise one another, and how familiarity might substitute for genetic relatedness, but the first question we need to answer is whether or not there is a genetic structure of relatives in field populations. Lambin and Krebs (1991) suggested that, since females controlled recruitment in voles, changes in female relatedness might have a significant impact on population dynamics (Figure 3). To test this idea, Lambin and Yoccoz (1998) manipulated the size of matrilineal kinship groups in *M. townsendii* in open populations. Relatives nested closer to one another than did unrelated females, and pup survival in the nest was improved in the first 2 weeks of life when relatives were nearby. In addition, adult female survival at the start of the breeding season was higher for kin group females than for unrelated females. If these kinds of kinship effects are significant, populations with matrilines will grow faster than those with only unrelated females, as illustrated schematically in Figure 3. Lambin and Yoccoz (1998) calculated with a simple Leslie matrix model that the differences in juvenile survival alone would change the monthly growth rate (λ) from 1.28 in low kinship groups to 1.43 in high kinship groups. By contrast, Dalton (2000) analysed kin group effects in *M. canicaudus* and found no effects of kin on population growth rates. These kinds of studies need to be done on other rodent species before we will know if kinship effects are quantitatively significant in affecting rates of population growth in natural populations.

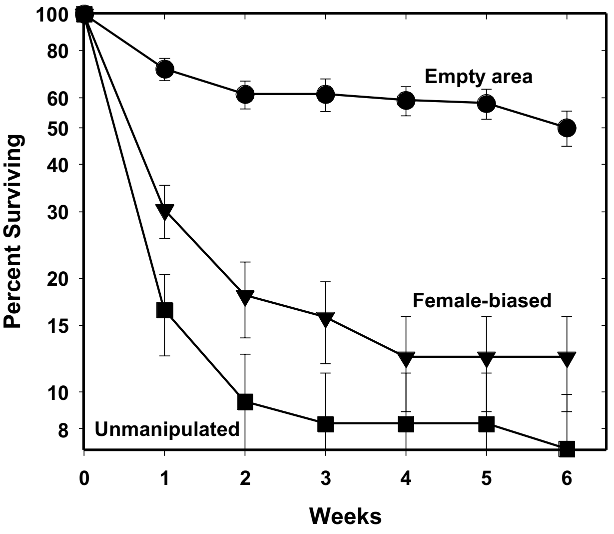

Figure 2. Kaplan-Meier survivorship curves (± 1 se) of juvenile voles (*Microtus townsendii*) introduced in midsummer into three types of areas: an empty grassland from which all adult and sub-adult voles had been removed; an unmanipulated area from which no voles had been removed; and a female-biased area from which all adult male voles had been removed. There is no significant difference between the survivorship curves of the female-biased and unmanipulated treatments. $n = 85$ juveniles in each treatment. (Data from Boonstra 1978.)

Infanticide

Infanticide is without question the most difficult social process to study in natural populations of rodents. If infanticide is the major cause of death of nestlings in rodents, it could be a major driver of population dynamics. I suggest that many rodent pests like the rice-field rat (*Rattus argentiventer*) in Southeast Asia is a pest because it maintains a matrilineal social structure that reduces infanticide to a minor problem.

At the present we do not have a good quantitative analysis of the rate of loss of nestling rodents. I have attempted to do this in a very preliminary way for the house mouse in south-eastern Australia. Figure 4 shows the changes in abundance of house mice in the Murrumbidgee Irrigation Area of New South Wales in recent years. All of the 4 years were similar in having mid- to late-winter declines and summer increases in abundance.

Table 1 attempts to estimate what fraction of neonates reach recruitment age at 2–4 weeks old. Since there are no

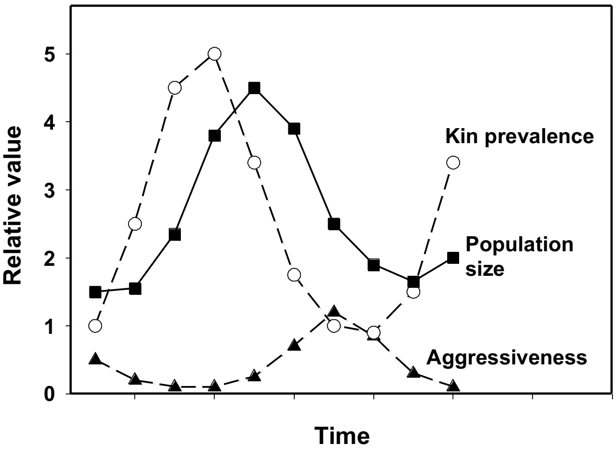

Figure 3. Hypothetical model of the kinship hypothesis of Lambin and Krebs (1991). As the prevalence of kin clusters increases, population density increases with a time lag, with the result of destabilising the dynamics of the population and producing a delayed change in the overall amount of aggression in the population under the general rule that aggression toward kin is low and toward strangers high. This model has been tested by Lambin and Yoccoz (1998) on *Microtus townsendii*.

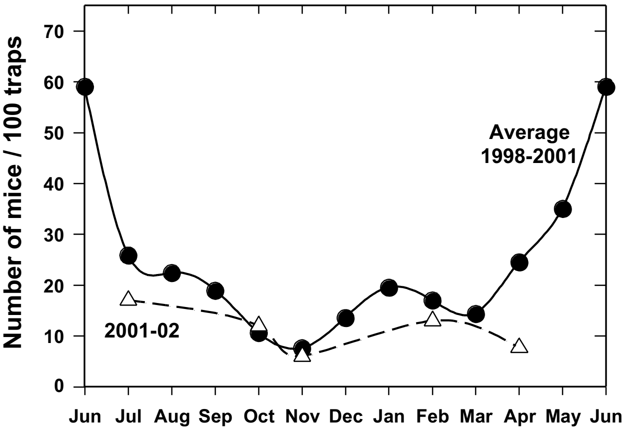

Figure 4. Changes in the abundance of house mice (*Mus domesticus*) in the Murrumbidgee Irrigation Area of New South Wales, Australia, during a series of average years of relatively low abundance. Mice typically decline during the mid- to late-winter months and increase during the summer to reach a peak in the autumn. Two graphs are given for the average density of the years 1998 to 2001 and the 2001–2002 biological year. Cereal and rice-growing areas were the major habitats sampled. (Data courtesy of G.R. Singleton, unpublished.)

direct measures of neonate survival, these can only be approximations but the message is still clear: somewhere between 6% and 20% of neonates survive to recruitment in these house mouse populations. Table 1 suggests a possible improvement of neonate survival as the breeding season progresses but this should be considered only a hypothesis that needs direct testing.

For *Microtus* voles, a few estimates of neonate survival are available for comparison. McShea and Madison (1989) found an average survival to recruitment of 31% in *Microtus pennsylvanicus* from 132 litters of radio-collared females. Boonstra and Hogg (1988) by contrast found an average 57% survival of neonates from 43 litters of the same species in an enclosure study. Lambin and Yoccoz (1998) found even higher neonate survival of 70–75% in *M. townsendii*. It is clear that there can be high variability in rodent neonate survival.

What happens to all these neonates? We do not know whether most of these young die in the nest or just after they leave the nest. It seems unlikely that dispersal is a primary cause of loss in the first 3 weeks of life (since dispersal usually occurs at a later age), and there seem to be only three possible agents of loss: predation in the nest, infanticide, and bad weather (e.g. flooding). There are few data available that allow us to partition these causes of loss in any rodent population with the exception of the work of Wolff and Schauber (1996) on *M. canicaudus* and Lambin and Yoccoz (1998) on *M. townsendii*. Wolff and Schauber (1996) concluded that infanticide was the cause of reduced juvenile recruitment as adult female density increased. It is clear from a demographic perspective that improvement in the nestling survival rate could presage a large increase in rodent abundance.

Dispersal

If resident adults cause new recruits to disperse, and dispersal is costly in terms of survival in unfamiliar habitats, dispersal could be a process that is involved in population regulation. The most striking experimental argument for the role of dispersal in population regulation has been the fence effect (Krebs et al. 1969; Boonstra and Krebs 1977). The fence effect refers to the observation that rodent populations enclosed in a fence which prevents emigration and immigration reach densities inside the fence that are 5–10 times natural densities and then crash from starvation. Ostfeld (1994) suggested that the fence effect was an artifact of predator exclusion, but this conclusion is incorrect, particularly since Boonstra's site was on an island with no mammalian predators that might be restricted by a fence.

Two general problems have plagued efforts to evaluate the role of dispersal in population limitation. First, dispersal is difficult to measure. Removal areas measure some components of dispersal but may bias the quantitative results (Schieck and Millar 1987). Radiotelemetry studies of dispersal are more promising but sample size problems and scale issues complicate interpretations (Beacham 1980; Gillis and Krebs 1999). Second, if dispersal is to assist in population regulation, it must somehow be related to population density. Many early studies have suggested that dispersal rate is maximum in low density, increasing populations and is minimal at high density (Gaines and McClenaghan 1980).

If this generalisation continues to hold, any dispersal impacts on population regulation or limitation will have to be achieved by indirect means. One way to achieve this

Table 1. Estimates of survival rates of house mouse (*Mus domesticus*) nestlings in the first 3 weeks of life for the years illustrated in Figure 4. Murrumbidgee Irrigation Area, New South Wales, Australia. Litter size is the average over 20 years of data (Singleton et al. 2001). Density estimated from Petersen estimates adjusted with the Davis correction (S. Davis, unpublished). Sex ratio assumed to be 50%. Adult survival rate assumed to be 80% per litter period (20 days). Two estimates of nestling survival are given. The pessimistic estimate utilises the observed proportion of juveniles in the catch each month to estimate juvenile recruitment. The optimistic estimate assumes that half of the population is replaced each month with new recruits. These estimates must be considered as crude approximations to the true survival of nestling mice.

Month	Litter size	Average of 1998–2001 years					2001–2002 year				
		Density of females (per ha)	Output of nestlings	No. recruited	Pessimistic nestling survival (%)	Optimistic nestling survival (%)	Density of females (per ha)	Output of nestlings	No. recruited	Pessimistic nestling survival (%)	Optimistic nestling survival (%)
September	8.50	59	401	16	3.9	14.7	40	275	18	6.6	14.7
October	8.26	33	218	9	4.0	15.1	37	247	17	6.7	15.1
November	8.06	24	152	6	4.1	15.5	19	119	8	6.9	15.5
December	6.52	42	220	11	5.0	19.2	25	129	11	8.5	19.2
January	5.96	61	290	16	5.5	21.0	31	148	14	9.4	21.0
February	4.92	53	209	14	6.7	25.4	40	159	18	11.3	25.4
March	5.16	45	185	12	6.4	24.2	31	128	14	10.8	24.2
April	5.50	77	338	20	6.0	22.7	24	105	11	10.1	22.7
May	5.30	110	466	29	6.2	23.6	31	132	14	10.5	23.6
June	5.00	186	745	49	6.6	25.0	–	–	–	–	–
Totals and weighted averages			3224	181	5.6	19.6		1442	124	8.6	16.5

would be for dispersal to be selective for certain phenotypes that have different types of spacing behaviour (Krebs 1985). Whether or not this occurs in rodents is unclear at present.

Dispersal may have evolved as an inbreeding avoidance mechanism, but the demographic consequences of dispersal may play some role in population limitation, if only by increasing the probability that predators or disease or bad weather will kill dispersing individuals.

Conclusion

There are several mechanisms by which social behaviour can affect birth, death, and dispersal rates and thereby population density changes. In any natural population of rodents, social behaviour will operate in a matrix of extrinsic mechanisms like predation, and disentangling the relative contribution of specific factors can be done only with carefully designed experiments. Given this array of potential impacts, I judge it premature to conclude, as Wolff (this volume) and others have, that social behaviour contributes little to stabilising or regulating rodent population densities. Further experiments will help to decide this issue.

Acknowledgments

I thank Grant Singleton, Micah Davies, and Dean Jones for the house mouse data and Alice Kenney and Jerry Wolff for their comments and suggestions on the manuscript.

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Density-dependence and the socioecology of space use in rodents

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Abstract. Social behaviour of rodents involves a complex array of proximate mechanisms associated with competition for breeding space, dispersal, and alternative mating and reproductive strategies. Because rodent population numbers fluctuate dramatically seasonally and multi-annually, these behaviours must be flexible enough to adapt to changing social environments. In this paper, I review several aspects of rodent behavioural strategies that directly or indirectly affect reproduction and population growth. I also propose theoretical and empirical evidence for how these behaviours should vary with density and discuss what role they might play in population regulation. Territoriality, dispersal, reproductive suppression, and infanticide have the potential to limit the rates of population growth, however they appear to play a relatively small role in stabilising or regulating populations. Extrinsic factors such as food limitation, predation, and disease likely play a much larger role in population regulation of rodents than do intrinsic factors.

Introduction

Social behaviour, including territoriality, mating strategies, dispersal, reproductive suppression, and infanticide, has been studied extensively in the laboratory and in the field in many species of rodents. Aspects of these social behaviours potentially affect the rate of population growth and thus have been implicated as mechanisms for self-regulation. In this paper, I briefly review the current theory regarding several aspects of social behaviour and then show how they are altered by changes in density that could affect rates of population growth. I draw heavily on examples from *Microtus* and *Peromyscus* in North America because of the extent of experimental work involving hypothesis testing in field and laboratory studies. I do not review all aspects of social behaviour; rather limit the text to behaviours that show the greatest potential for self-regulation. I do not provide a thorough literature review on this topic or present original data, rather summarise the current state of knowledge in these areas and cite review or recent references on the various topics.

Female territoriality

Social systems of rodents are variable and flexible and appear to depend to a great extent on the distribution of females. In most rodents, individuals or groups of related females defend territorial space against unrelated females. Territories vary considerably in size from as little as 25 m^2 in high-density populations of microtines to several hectares in larger species and/or at lower densities (Wolff 1985). For most grassland rodents that weigh less than 100 g, territories are typically 50 to 150 m^2, whereas forest-dwelling species often occupy territories of several hundred square metres (Wolff 1985, 1989). During the breeding season, territories are relatively exclusive with respect to unrelated females, but often overlap and are shared with daughters or sisters (e.g. *Microtus townsendii*, *M. canicaudus*, *Peromyscus leucopus*). Home range size and daily movements often are related to resource availability, however territoriality in female rodents may not be based on defence of a food resource as proposed by Ostfeld (1985). According to the food-defence hypothesis, the distribution, abundance, renewability, and type of food should determine whether females defend territories or share space with other adult females (Ostfeld 1985). An alternative hypothesis is that females defend territories to protect their offspring against infanticide from conspecific females (Wolff 1993a). Species of rodents that hoard food, such as seeds, in a central larder seem to defend this food source, however green vegetation, perishable or nonstorable and other widely scattered food may not be defensible (Wolff and Peterson 1998), and whether or not they are limiting during the breeding season is equivocal (Taitt and Krebs 1981; Ostfeld 1985; Lambin and Krebs 1993; Wolff 1993a). Infanticide is common among female rodents and is hypothesised to be a form of reproductive competition in which perpetrating females kill offspring to eliminate competitors and gain access to breeding sites (Sherman 1981; Wolff and Peterson 1998). The fact that female aggression that leads to territoriality is associated with lactation and the breeding season (Maestripieri 1992; Wolff 1993a) and does not occur during food shortage or non-breeding seasons supports this latter hypothesis (Wolff and Peterson 1998). The infanticide hypothesis is also applicable to other taxa of mammals and is associated with altricial young that require a burrow, tunnel system, or protected den site for successful rearing of offspring. In that rodents fit these needs, females compete for this limited offspring-rearing space. It is this competition for breeding space that leads to territoriality in female rodents.

Mating strategies

Males

The mating strategies used by males are dependent to a great extent on the spacing and dispersion of females. If optimal breeding space is patchy and defensible, males may employ a resource (or harem) defence polygynous mating strategy such as in prairie dogs, *Cynomys* spp., marmots, *Marmota flaviventris*, California voles, *Microtus californicus*, mice, *Mus musculus,* and Norway rats, *Rattus norvegicus*. In many species of rodents such as most microtines and peromyscines, females are evenly distributed and males have large home ranges that overlap those of several females and several other males (Wolff 1985, 1989). In *Peromyscus* spp., males have territories that overlap at least one female, and often those of one or more neighbouring females, resulting in polygynous mating (Wolff 1989). Although monogamy is uncommon in rodents, males and females share territorial space and parental duties in some species such as the prairie vole, *Microtus ochrogaster*, woodland vole, *M. pinetorum*, California mouse, *Peromyscus californicus*, and oldfield mouse, *P. polionotus.* Monogamous pairings appear to occur in species that are typically at relatively low densities in which females are widely spaced. In the socially monogamous prairie vole, in which densities fluctuate considerably, about half of the males defend a single female whereas the other half exhibit a wandering strategy and attempt to mate with multiple females (Carter and Getz 1993). Whether monogamy is an evolved behaviour in male rodents, or an artifact of distribution of females, is not clear.

Females

In socially monogamous species, females apparently mate with one male, however in most other species of murid rodents in which mating has been observed or paternity examined, females are promiscuous and mate with multiple partners (J. Wolff, unpublished data). During a given oestrous period, females are approached by several males and/or females invoke male–male competition by soliciting copulations from multiple males (e.g. Agrell et al. 1998). Several hypotheses have been proposed for the adaptive significance of multi-male mating (MMM) in mammals (Agrell et al. 1998; J. Wolff, unpublished). In rodents, MMM does not result in increased benefits to the female in the form of provisioning or parental care, most matings do not result in conception or genetic diversity, and guarding against sterility is not well supported. The most parsimonious among the competing hypotheses for MMM, and one that is applicable to all mammals and not just rodents (e.g. primates, van Schaik and Kappeler 1997), is that MMM confuses paternity and reduces the chances that males will commit infanticide (Agrell et al. 1998; J. Wolff, unpublished). Infanticide committed by males is common in rodents and laboratory studies have shown that the act of mating inhibits a male from killing pups for a period long enough for his young to be no longer vulnerable to infanticide. Although infanticide has been difficult to study or observe in the field, MMM may be a mechanism used by females to reduce the chances that neighbouring and intruding males will kill their young.

Dispersal and philopatry

Dispersal has been studied extensively in rodents, primarily from a population regulation point of view and only recently from an evolutionary perspective. Most dispersal involves juveniles or young adults emigrating from the natal site and immigrating to a territory or home range area that will be the adult breeding site. The general dispersal pattern for rodents, as it is in most mammals, is for young males to disperse from their natal site and for daughters to be philopatric and remain on or near their natal site (Wolff 1993b, 1994a). Young males leave the natal site to find vacant space and/or unrelated breeding age females. Dispersal distance in mammals is positively correlated with body mass (Wolff 1999) and averages about 10 home range diameters. However, dispersal distance of young males is highly variable and dependent in part on the degree of habitat saturation (see below) and availability of vacant territories or mating partners (Lambin et al. 2001). In that inbreeding avoidance appears to be an important function of emigration of young males from their natal site, the dispersal distance is probably determined in part by the proximity of related females around the natal area, encounter rates with unrelated females, and competitive interactions of resident males (Wolff 1993b, 1994a; Andreassen and Ims 2001; Lambin et al. 2001).

Young females typically attempt to establish breeding space close to their natal site. At low densities when adjacent space is available, young females establish individual home ranges or territories in close access to the natal site. In some cases, mothers appear to bequeath their natal site to daughters and move a short distance and establish a new territory or nesting site that overlaps the previous natal site (Wolff and Lundy 1985; Lambin and Krebs 1991; Figure 1; however the spatial pattern of mothers and daughters is not well understood for most species, Lambin 1997). At very high densities, mothers and daughters often nest within metres of each other or sometimes communally and cooperatively in the same nest (e.g. Wolff 1994b; Solomon and Getz 1997; Lambin and Yoccoz 1998). The formation of kin groups, cooperation among kin, and having kin for neighbours should be beneficial for group defence and/or to reduce the incidence of infanticide by neighbouring females (Charnov and Finerty 1980; Wolff 1995). Related females nesting close to each other seemed to increase inclusive fitness of the group in Townsend's voles, *Microtus townsendii*, (Lambin and Krebs 1993; Lambin and Yoccoz 1998), bank voles, *Clethrionomys glareolus* (Mappes et al. 1995), and field voles, *M. agrestis*, but not in other species such as gray-tailed voles, *Microtus canicaudus*, meadow voles, *M. pennsylvanicus*, and prairie voles (Dalton 2000). Lambin and Yoccoz (1998) provided a model that predicts higher population growth rates in kin-structured populations, however the only experimental field study to examine differences in growth rate of kin and non-kin populations failed to show that kin groups contributed significantly to the rate of population growth (Dalton 2000) as predicted by Charnov and Finerty (1980).

Young males disperse from the natal site to avoid inbreeding with their mothers, but why do young females not inbreed with their fathers? Inbreeding may occur in some circumstances in experimental or small populations (e.g. Gunderson et al. 2001), but is usually avoided by two mechanisms—high turnover rate of resident males or the immigration of wandering males and incest avoidance (Wolff et al. 1988; Wolff 1994a). Male rodents, as with many other mammals, compete intensively for access to females or territories and thus a male's tenure on a given site is relatively short. Consequently, by the time young females reach the age of sexual maturity, their fathers are usually gone and have been replaced by new, unrelated males. In situations in which fathers are present when their daughters reach the age of reproduction, young females may solicit matings from neighbouring or unrelated males (Wolff et al. 1988). Incest is avoided in that females are not sexually stimulated by their fathers, brothers, or any male nest-mates, whereas exposure to strange males initiates breeding activity (see below). Thus, female philopatry is adaptive for females to form kin groups while avoiding inbreeding; sons, on the other hand, disperse to find unrelated mates and would not benefit by remaining in a kin group.

Social behaviour and population regulation

Many rodent populations fluctuate annually and multi-annually (Batzli 1992). Consequently, we should expect to see considerable variation in the behaviours described above that are adapted or contribute to these fluctuations. In fluctuating or cycling rodent populations, a question often asked is what role social behaviour plays in stopping population growth, which in turn initiates population declines (Krebs 1978, 1996; Heske et al. 1988). The self-regulation hypothesis proposes that individual differences in spacing behaviour, or perhaps a genetic polymorphism in the population or maternal effects, influence reproductive performance and subsequent population trends (Krebs 1978, 1996). In a review of various verbal and mathematical models for social behaviour driving population cycles, Heske et al. (1988) found no support for behavioural polymorphism, social stress, social breakdown, or kin selection hypotheses. In fact, Heske et al. concluded that social behaviour was unlikely to drive population fluctuations in California voles, or perhaps other species of microtines. Wolff (1997) attempted to provide an evolutionary argument for how various aspects of social behaviour could lead to intrinsic population regulation. For social behaviour to limit the growth rate of a population, it must decrease fecundity, or at least juvenile recruitment, and/or decrease survival rates. Decreased juvenile recruitment could result from decreased litter size, decreased number of females breeding, or a delay in time to sexual maturation of young females. There is little or no evidence that litter size is affected by social interactions other than might be affected by decreased nutritional state of females due to limited food resources. However, social stress at high density can delay the onset of sexual maturation which slows population growth. A decrease in the number of females breeding also could be affected by territoriality or some form of reproductive suppression. Below I summarise the results of the conceptual model presented in Wolff (1997; see also Table 1 and Figure 1).

Table 1. Predicted density-dependent effects on various aspects of the social behaviour of rodents.

	Low density	High density
Territoriality	Large territories, widely spaced, mutual avoidance, low aggression, vacant space available	Small territories, considerable overlap, high aggression
Dispersal/ philopatry	All males disperse relatively far, females disperse close to natal site, mothers might bequeath maternal site to daughters	Delayed emigration, sons and daughters remain on natal site, extended families, cooperative and communal breeding of females
Sexual maturation	Sons and daughters mature at young age	Delayed sexual maturation for both sexes, cooperative and communal breeding for some species (see text)
Infanticide	High for males, low for females	Low for males, high for females

Territoriality

If females defend breeding spaces (territories) and these are limited, then potentially territoriality could limit the size of the breeding population. Territory size is not fixed, however—rather it shrinks and expands like an elastic disc with changes in density and intruder pressure (Wolff 1989; Wolff and Schauber 1996). How small can a territory become? Studies with voles in enclosures show that without dispersal, territory size shrinks to only a few square metres with considerable overlap with neighboring females (e.g. Boonstra and Krebs 1977; Wolff and Schauber 1996). The fact that rodent populations in enclosures reach exceedingly high densities suggests that territoriality in itself is insufficient to stop population growth (Boonstra and Krebs 1977; Wolff and Schauber 1996). Little experimental evidence is available to show how territoriality affects the size of the breeding population in species other than *Microtus* and *Peromyscus*, but in these two groups, even at the highest densities, most, if not all, adult females seem to be breeding (Wolff 1985, 1989, 1997). Some delayed sexual maturation and/or suppression of young females may occur at high densities, which may slow the rate of population growth, but whether this is sufficient to stabilise the population growth rate is equivocal (Krebs, this volume). In some species of rodents, males are territorial whereas in others they are not—in neither case, however, does male spacing affect population growth.

Dispersal and philopatry

The characteristic dispersal pattern in rodents is for males to disperse relatively long distances and for females to settle in territories near their natal site (Figure 1). However, in continuous habitats at high densities when all breeding space is occupied by territorial males and/or females, young juveniles are deterred from emigrating from their natal site by a social fence of aggressive territorial owners inhibiting immigration (Wolff 1994b; Lambin et al. 2001). This social fence acts as a negative density-dependent factor reducing the rate of dispersal (Andreassen and Ims 2001). Thus, the rate of dispersal in territorial species is inversely density-dependent (Wolff 1997; Lambin et al. 2001). As density increases, the rate of dispersal decreases, resulting in extended families as sons and daughters remain on their natal sites past the time of normal dispersal and sexual maturation. This delayed emigration from the natal site can inhibit sexual maturation of young females by direct competition with their mothers or as a mechanism to avoid inbreeding with male relatives (Wolff 1997; Lambin et al. 2001). In patchy environments, or those in which individual movements are not deterred by neighbours, dispersal should not be delayed and may, in fact, help to stabilise or regulate density within the patch.

Daughters, sexual maturation and reproductive suppression

The high intrinsic rate of growth of rodent populations is due to a great extent to high fecundity and early breeding of young females. In most species of rodents, young females become sexually mature and can breed shortly after weaning, as young as 20 days of age. Females exhibit post-partum oestrus and breed at regular intervals as short at 21 days. Life expectancy is short, often less than 4 months, however a given female can be expected to produce 20–30 offspring in an average lifetime. In most species of rodents, females rear their young in separate nests, however communal and cooperative

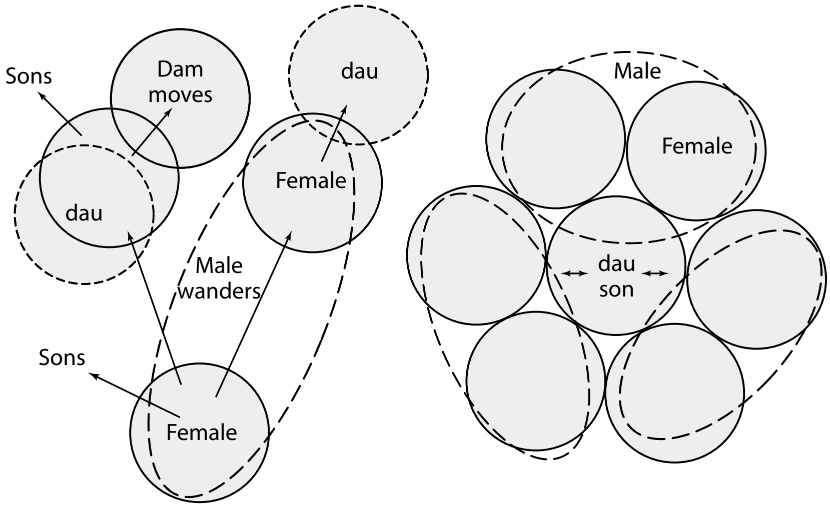

Figure 1. Illustration of spacing and social system of a model rodent, such as many *Peromyscus* and *Microtus* spp. At low density, females (solid circles) are widely spaced and males have large home ranges (dashed ellipses) or wander over large areas to mate with females. Sons disperse relatively far from the natal site and daughters (dau) occupy territories near their natal site or in some cases the mother (dam) bequeaths the natal site to her daughter and moves to an adjacent territory. At high density, females have small, tightly packed territories and males have home ranges that overlap those of several females and other males. Sons and daughters exhibit delayed dispersal and sexual maturation.

breeding is common in many species of *Microtus*, *Peromyscus*, and *Mus* in which related females share breeding space and even the same nests (Wolff 1985, 1989, 1994b; Solomon and Getz 1997). Although laboratory studies frequently have shown reproductive inhibition in young females (e.g. Drickamer 1977), experimental and field observations of numerous species of rodents have failed to support this supposition (e.g. Wolff 1994b; Solomon and Getz 1997; Wolff et al. 2001). In a few species of rodents, however, such as *Clethrionomys* (Gilbert et al. 1986) and perhaps *Microtus oeconomus* (Andreassen and Ims 2001), young females do not breed in their mothers' territories.

Reproductive suppression

A major factor that determines the size of the breeding population is the rate at which young females become sexually mature and experience their first pregnancy. In some species of rodents, such as *Clethrionomys* spp., each female needs its own individual territory to breed; i.e. young females do not breed in their mothers' territories. It is not known how common this pattern is because we have relatively few data on the relatedness of females in wild populations and position of nests within territories for most species of rodents. However, it is well documented for several species of *Microtus* and *Peromyscus* that daughters readily breed on their maternal site, often communally and cooperatively with other female relatives (e.g. Lambin 1994; Wolff 1994b). In *Clethrionomys* spp. and other species in which females require individual territories, territoriality can limit the size of the breeding population and consequent rate of population growth. Females that do remain on their natal site beyond the time of normal reproductive maturity would be reproductively inhibited until they obtain a territory of their own. However, for species in which daughters are not reproductively inhibited by their mothers, rather breed on shared maternal territories or even in the same nest, territoriality appears to have minimal effect on the size of the breeding population.

Resource or reproductive competition within family groups appears to be minimal and plays a small role in self-regulation (but see Lambin and Krebs 1993; Andreassen and Ims 2001). Although little evidence exists to show that mothers suppress reproduction in their daughters (except perhaps for *Clethrionomys* and a few other species), unrelated females are expected to commit infanticide as a form of competition for breeding territories (Wolff 1997; Wolff and Peterson 1998). At high densities, pregnancy rates typically remain high, however juvenile recruitment declines with an increase in density (Wolff et al. 2002; Krebs, this volume). The mechanism for reproductive suppression of young females is difficult to detect in the field, but field observations with other mammals and laboratory experiments with rodents demonstrate that unrelated adult females typically inhibit young females from breeding (Drickamer 1977; and reviewed in Wolff 1997).

The Bruce effect

Another factor that could decrease the rate of population growth is pregnancy disruption, commonly referred to as the Bruce effect. The Bruce effect is a form of pregnancy disruption in mammals in which exposure of a female to an unknown male results in pre- or post-implantation failure. Some form of pregnancy disruption has been reported in the laboratory for at least 12 species of rodents, including seven of the genus *Microtus* (reviewed in Mahady and Wolff 2002). However, two field studies have failed to support this phenomenon. In field experiments with gray-tailed voles (de la Maza et al. 1999) and prairie voles (Mahady and Wolff 2002) 100% turnover of resident males and exposure to strange males every 10 days failed to detect any significant pregnancy disruption. In gray-tailed voles, no differences occurred in pregnancy rates, interbirth intervals, or juvenile recruitment between treatment and control populations. In prairie voles, nulliparous females took slightly longer to initiate first breeding in treatment populations and experienced poorer juvenile recruitment, but this effect was minimal and did not occur in parous females. The decreased juvenile recruitment in prairie voles could have been due to infanticide when young pups were exposed to strange males. In wild populations of voles and other rodents, females are commonly exposed to strange males and it is questionable whether selection would favour any form of pregnancy termination following this exposure. Also, the fact that in most species of rodents, females mate promiscuously and mated males are inhibited from committing infanticide (discussed above), females should not need to sacrifice current pregnancies. The high rates of pregnancy and births at predictable intervals in most rodent populations make it seem unlikely that the Bruce effect has a marked effect on population growth or demography.

Inbreeding avoidance

As mentioned above, young males disperse from the natal site to seek unrelated females as mates and to avoid inbreeding with their mothers and sisters. Daughters can usually breed on or near their natal site with new intruding males that have replaced their fathers (Wolff 1993b, 1994a). In both cases, behavioural mechanisms avoid inbreeding or keep it to a minimum. At high densities, however, delayed emigration results in mothers, fathers, sons, and daughters often remaining on the same breeding territory past the time of normal offspring sexual maturation. If daughters remain in the proximity of male relatives, primarily their fathers, they remain sexually inactive and do not breed (Batzli et al. 1977; Wolff 1992, 1997; Brant et al. 1998). In an experiment with white-footed mice, *Peromyscus leucopus*, I removed mothers or fathers from a high-density population in which extended families formed as a result of delayed emigration (Wolff 1992). When fathers were removed, daughters became sexually mature and bred; when mothers were removed, their sons became sexually mature. Sons and daughters remained sexually inactive as long as they remained in the presence of opposite-sex parents. Laboratory studies also have confirmed that daughters do not breed in the presence of their fathers, but will breed as soon as they are exposed to strange males (e.g., Batzli et al. 1977; Brant et al. 1998).

Infanticide

Infanticide is common among male and female rodents and has been studied extensively in the laboratory and less so in the field (Agrell et al. 1998). Infanticide is committed by females to compete for breeding space and by males to provide a breeding opportunity. Theoretically, the incidence of infanticide should change with density, but differ for the two sexes (Wolff 1995; Table 1). At low densities, males move over large areas and will be more likely to commit infanticide in areas where they have not mated and have low confidence of paternity. At high densities, however, males are confined to smaller areas, have many females with which to mate, and should be less likely to commit infanticide within their resident home ranges or territories. Females, on the other hand, should not commit infanticide at low densities because breeding space would not be limited and thus competition is sufficiently low that all females can acquire breeding space. At high densities, however, breeding space should be limited, competition intense, and the rate of infanticide high as females compete for limited offspring-rearing space. Thus, infanticide is likely to occur at high and low densities, but differ for the two sexes (Wolff 1995), however this has not been tested.

Conclusions

Rodent behavioural systems are complex, variable, and adapted to high reproductive rates and marked changes in density. Social behaviours are shaped by natural selection to maximise individual or inclusive reproductive success. Female territoriality, philopatry, and formation of kin groups improve offspring survival while decreasing competition and infanticide from unrelated females. Competition among females leading to reproductive suppression, infanticide, and reduced juvenile recruitment should be intense at high densities, but appears to be insufficient in stopping population growth. Juvenile males disperse from the natal site and search for unrelated females and attempt to mate polygynously or promiscuously. High rates of dispersal at low densities can reduce the rate of population growth, whereas lower rates of dispersal at high densities can increase the rate of population growth. Sexual maturation often is delayed and juvenile recruitment reduced at the highest densities, however social behaviour does not appear to contribute substantially to stabilising or regulating rodent populations. The fact that populations in enclosures grow to very high densities suggests that social behaviour alone is insufficient to stop population growth. Extrinsic factors such as food limitation, disease, or predation likely play the major role in regulating rodent populations, especially setting the upper limits to stopping population growth. The questions regarding what factors best explain population regulation in rodents will best be answered by experimental studies that incorporate multiple factors, comparative studies with different species under different ecological conditions, and long-term data sets that monitor all pertinent parameters that are known to affect population dynamics.

Acknowledgments

I thank Grant Singleton, Charles Krebs, and the organisers of this conference for inviting me to participate in this symposium. Shawn Thomas, Charles Krebs, and Xavier Lambin provided constructive criticism on an earlier draft of this paper. This project was funded by National Science Foundation and the Biology Department at the University of Memphis.

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Predator odours as reproductive inhibitors for Norway rats

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Abstract. We examined the influence of predator odour on reproductive output of Norway rats (*Rattus norvegicus*). Naïve laboratory rats responded to predator chemical cues with reduced litter size and skewed sex ratio. We found that exposure to predator urine had its greatest effect on implantation and maintenance of implantation when predator urine was applied to the bedding of rats during the first third of gestation. Based on the physical appearance of corpora lutea and uterine implantation scars, we found that the reduction in litter size was due to resorption of the embryos during the early part of gestation. Subsequently, we discovered that the reduction in litter sizes in rats exposed to predator urine could be attributed to suppressed progesterone levels affecting implantation of embryos. Chronically high corticosterone levels did not suppress reproductive output. Suppression of reproduction also occurred when rats were exposed to urine of conspecifics housed under high population densities. The evolutionary adaptive response for reduced litter size is to produce high-quality offspring in an environment where food resources are scarce. The fact that rats respond to certain chemical signals in predator urine in a similar fashion may be fortuitous, and may have more to do with the coincidence that the urine contains similar cues resulting from protein digestion in carnivores and protein catabolism in nutritionally deprived rodents, rather than specific predator–prey adaptations.

Introduction

Reproductive traits in rodents are affected by a number of environmental, social and chemosensory factors, e.g. the nutritional status of females will influence ovulation rate and litter size (Hamilton and Bronson 1985), as will exposure of females to other rodents of various social status (Steiner et al. 1983; Huck et al. 1988). Other well-described influences include synchronisation of ovulation amongst female cohorts (Whitten 1956), acceleration or delay of puberty (Vandenbergh 1969; Lombardi and Vandenberg 1977), pregnancy block owing to stress, and failure to implant blastocysts when female rodents are exposed to the odour or urine of strange males (Bruce 1959). Frequently the magnitude of these effects is species- and strain-specific (MacNiven et al. 1992).

The majority of these studies on reproductive inhibition have focused on intraspecific influences of semiochemicals and how they influence reproductive output and behaviour in females. A few studies have focused on between-strain influences or interspecific influence, although the source odour generally is still confined to rodents.

During our investigations on the effects of predator odour on rodent reproduction and repellency, we found that female rats exposed to cat urine during pregnancy had reduced litter sizes at parturition (Voznessenskaya 2002). Exposure to predator odour also caused disruptions of the oestrous cycle (Voznessenskaya et al. 1992). These effects bear striking similarities to the studies of the effects of rodent urine odour on intraspecific rodent reproduction. If such similarities are broadly based, then similarities in mechanisms of perception, reproductive physiology, and chemical nature of the stimulus might be anticipated.

This study was conducted to address some of these issues of similarity. Specifically, we set out to determine if a sensitive period existed for the effect and, if possible, to narrow the timing of the critical period when the stimulus exerts its reproductive effect.

Materials and methods

Test subjects

We used 3–4 month old Norway rats (Rattus norvegicus) from an outbred laboratory population as a model system. Before the start of the experiments, females were housed in groups of 3–4, and males were housed singly. Experimental rooms were illuminated on 14:10 hours light:dark schedule, and maintained at 20°C. Food and tap water were provided *ad libitum*. Virgin females in pro-oestrus/oestrus, as determined by vaginal cytology, were chosen for the mating experiments. Sexually experienced males that were not mated in the 14 days before the test were used as sires. The morning after pairing, the females were checked for successful mating, as indicated by the presence of a vaginal plug. Successfully mated females were then housed singly.

Reproductive output

For each experimental group, the total number of offspring per female was counted and the sex ratio determined. In addition, we also measured the gestation period.

Determination of implantation sites in utero and post-implantation loss

Female were necropsied 2–3 days after giving birth and the presence and number of implantation scars in their uteri were recorded. Each scar indicates the site of placental/foetal attachment during pregnancy. Scars are roughly 2 mm in diameter and can be counted easily under a microscope (Bacon and McClintock 1994). The numbers of pups carried in utero were compared to the numbers of pups found at birth and thus the amount of post-implantation pup loss could be quantified. The number of implantation scars was compared with number of corpora lutea to detect pre-implantation loss.

Collection of urine

Urine from domestic cats (*Felis catus*) was used as a source of predator chemical cues. These cats normally hunt for mice and have mice as part of their diet. If needed, additional meat was added to their diet. Freshly voided urine was frozen (–22°C). Once defrosted, urine was used only once. Non-predator urine was obtained from guinea pigs and Norway rats. For collection of the urine from Norway rats held in overcrowded conditions, 10–12 animals were placed in a standard size cage for 14 days. Animals received a reduced per capita ration so as to maintain 80% of normal body mass and water ad libitum. Individuals of these species (as appropriate for the type of treatment specified in the experiment) were placed into metabolic stainless-steel cages overnight, and urine was collected and stored using the method described above. Urine was collected and stored at –22°C.

‘Open field’ test with added stress

An ‘open arena’ (1.5 × 1.5 m) with bright lights was used. Pregnant females were placed for 15 minutes in the centre of the arena on the 1st, 4th and 7th day of gestation. During the test, we also used a buzzer, which made a loud noise, every 5 minutes. In addition, rats were handled roughly to physically induce stress. Blood samples were drawn after each test for progesterone and corticosterone assay.

Assay for progesterone and corticosterone

Rats within each treatment were randomly assigned to one of four cohorts. Blood samples (300–400 µL) were obtained from the rear foot pad (Miller et al. 1997) every 3rd day for each cohort for each of the treatments for the first 7 days of gestation. This minimises the handling and sampling of individual rats, while allowing a detailed study of changes in hormonal pattern as a function of time and treatment. Our experience shows that this method of repeated blood sampling has no long-term effect on visible scarring associated with traditional tail sampling technologies (Miller et al. 1997). Samples were centrifuged and the plasma frozen at –20°C until subsequent analysis. Plasma progesterone and corticosterone were assayed (in triplicate) by the coat-a-tube radio immuno assay (RIA) method (Diagnostic Products, Los Angeles, California, ≈50 µL/assay; Miller et al. 1997).

Experimental design and protocol

The experimental method consisted of applying 1 mL of a test solution to the bedding of pregnant rats every other day for different time durations. This application maximised the likelihood of physical and odour exposure of the test stimulus to the female. In the first experiment, six treatment levels were used:

1. tap water (WAT), as a negative control;
2. urine from guinea pigs maintained on a vegetarian diet (vegetables, grains and water ad libitum), as a urine control (GPU);
3. urine from domestic cats maintained on a feral mouse diet (CU), as a model stimulus representing unadulterated predator urine. Cats were maintained on the feral mouse diet for 14 days before urine collection;
4. urine from the same feral cats as CU treated with 4% $HgSO_4$ to yield urine where small peptides, amines, and sulfur compounds were precipitated (CU-$HgSO_4$). The supernatant was used as the test stimulus and did not contain indicators of a carnivorous diet (Nolte et al. 1994);
5. urine from cats on a vegetarian diet (CU-v). After collecting urine from the cats used in the above treatments, we switched the animals to a vegetarian diet (oatmeal, peaches, milk and bread ad libitum) for 14 days before urine collection; and
6. urine from overcrowded rats (OWU), as source of conspecific chemical signals of high population density (intrinsic factor for regulation of population density).

After mating, females were randomly assigned to treatment groups: WAT (n = 20), GPU (n = 20), CU (n = 20), CU-$HgSO_4$ (n = 21), CU-v (n = 26) and OWU (n = 21).

Mean differences among treatment groups were determined in separate analyses for the number of pups and sex ratios using a fixed-effects analysis of variance. Post-hoc differences among treatment groups were determined using a Spjotovoll-Stoline test for unequal sample sizes (Statistica; StatSoft Inc, Tulsa, Oklahoma).

In the second set of experiments, we determined the period during gestation when rats were sensitive to predator urine. The first three treatments focused on exposing pregnant rats to cat urine for varying lengths of time while the blastula was in the oviduct.

1. In the first treatment, cat urine (1 mL) was added to the bedding of female rats (*n* = 22) immediately after mating and left in place for 24 h (E24). During this period of development, the single fertilised cell is found in the oviduct. After 24 h of exposure to the cat urine the treated bedding was replaced with clean bedding.
2. In the second treatment, 1 mL of cat urine was added to the bedding of females (*n* = 20) immediately after mating and left in place for 36 h (E36). During this period, the single cell cleaves into two cells, while still remaining in the oviduct. Following the 36 h exposure period, the bedding was changed as above.
3. In the third treatment, the procedures were repeated as per above (*n* = 21), but the exposure period was 48 h (E48). During this period, the blastula progresses to the four-cell stage within the oviduct.
4. The fourth treatment consisted of applying 1 mL of cat urine to the bedding of female rats (*n* = 20) that had been mated 48 h before application of urine, and the exposure continued for the next 48 h (E48D). During this stage of development, the early blastocyst migrates to the uterus but remains free from attachment to the uterus. Implantation of the blastocyst occurs 6–8 days after fertilisation.
5. A fifth treatment was applied at 12 days post-fertilisation (embryo is well-formed and attached in the uterus) in which cat urine (1 mL) was applied to bedding on 12th day and left in place for 48 h (MGP) (*n* = 20). After this exposure, bedding was replaced with clean material.
6. The sixth treatment (WAT) served as the negative control (*n* = 21). Water (1 mL) was applied to the bedding every other day throughout gestation.
7. The seventh treatment served as positive control (*n* = 20). Cat urine (CU) (1 mL) was applied to bedding every other day throughout gestation. This treatment has been shown to result in 40% reduction in litter sizes relative to water control in previous studies (Voznessenskaya 2002).

The data were statistically analysed as for the previous experiments.

Results and discussion

The number of pups born to female rats varied as a function of treatment ($F = 28.61$, df = 4,102, $P < 0.001$). Post-hoc analysis indicated that diet, specifically urine products derived from meat diets, was important in producing the reproductive inhibitory effect. Females exposed to urine derived from cats maintained on a mouse diet had the smallest litter sizes (Table 1). All other treatments resulted in litter sizes similar to those seen for females exposed to water (i.e. negative control), except for the group treated with urine from overcrowded rats. For this treatment, litter size was significantly reduced relative to both of the controls. Sex ratios also were affected by the treatment ($F = 16.53$, df = 4,102, $P < 0.001$). Fewer female pups were born to rats exposed to urine derived from cats maintained on mouse diets and to rats exposed to urine from overcrowded conspecifics. All other treatments resulted in sex ratios similar to the negative control, which itself was similar to 0.5.

Table 1. The influence of exposure to predator odours and conspecific odours on alternate days during gestation on litter size and sex ratio in Norway rats.

Type of treatment	Litter size	Sex ratio (females/total number of pups)
Exposure to cat urine (CU)	4.8 ± 0.4	0.31 ± 0.07
Exposure to CU treated with $HgSO_4$ to remove indicators of carnivorous diet (CU-$HgSO_4$)	9.3 ± 0.4	0.50 ± 0.11
Exposure to urine from cats on vegetarian diet (CU-v)	8.3 ± 0.4	0.50 ± 0.09
Exposure to tap water (WAT)	8.6 ± 0.2	0.51 ± 0.11
Exposure to guinea pig urine (GPU)	8.6 ± 0.2	0.52 ± 0.12
Exposure to urine of overcrowded conspecifics	6.7 ± 1.2	0.41 ± 0.07

When urine was deficient in compounds characteristic of meat digestion, it had no effect on rat reproduction, irrespective of species, or how the deficiency of these products was obtained, i.e. via diet restriction or chemical removal. Urine derived from rats housed in crowded conditions suppressed the reproductive output of rats at rates comparable to rats that were exposed to predator urine. These data suggest that catabolism of muscle mass due to starvation results in urine that contains reproductively inhibitory materials

Table 2. Effect of timing of predator odour exposure during gestation on litter size in Norway rats.

Type of treatment	Litter size	Sex ratio (females/total number of pups)
Exposure to cat urine (CU) every other day during gestation	6.0 ± 1.3	0.36 ± 0.03
Exposure for 24 h after mating (E24)	8.4 ± 0.5	0.45 ± 0.07
Exposure for 36 h after mating (E36)	6.5 ± 0.3	0.41 ± 0.05
Exposure for 48 h after mating (E48)	6.4 ± 0.3	0.41 ± 0.04
Exposure for 48 h, 2 days after mating (E48D)	6.9 ± 0.3	0.39 ± 0.09
Exposure for 48 h on day 12 (mid-gestation) (MGP)	10.7 ± 0.3	0.49 ± 0.03
Control—exposure to tap water (WAT)	10.7 ± 0.3	0.50 ± 0.10

In the second experiment, litter size varied among treatments (F = 37.65, df = 6,137, $P < 0.001$). Litter size was largest for the negative control (WAT = 10.7 ± 0.3), and smallest for the positive control (CU = 5.9 ± 1.3), representing a 44.9% decrease in litter size. Once the embryo was implanted into the uterus, a 48 h exposure (MGP) to cat urine had no effect on litter size relative to the control (Table 2). Exposure to cat urine while the blastula was in the oviduct resulted in decreased litter sizes relative to the control, with the larger reductions resulting from 48 h exposure. Litter reductions were achieved at the expense of female pups (F = 5.37, df = 6,137, $P < 0.001$). The proportion of females born in the negative control group (WAT) was 0.506 ± 0.011. The proportion of females born in the positive control treatment (CU) was 0.361 ± 0.022: a 28.7% decrease in the expected proportion of females. The change in sex ratio across treatments followed that for overall litter size (Table 2).

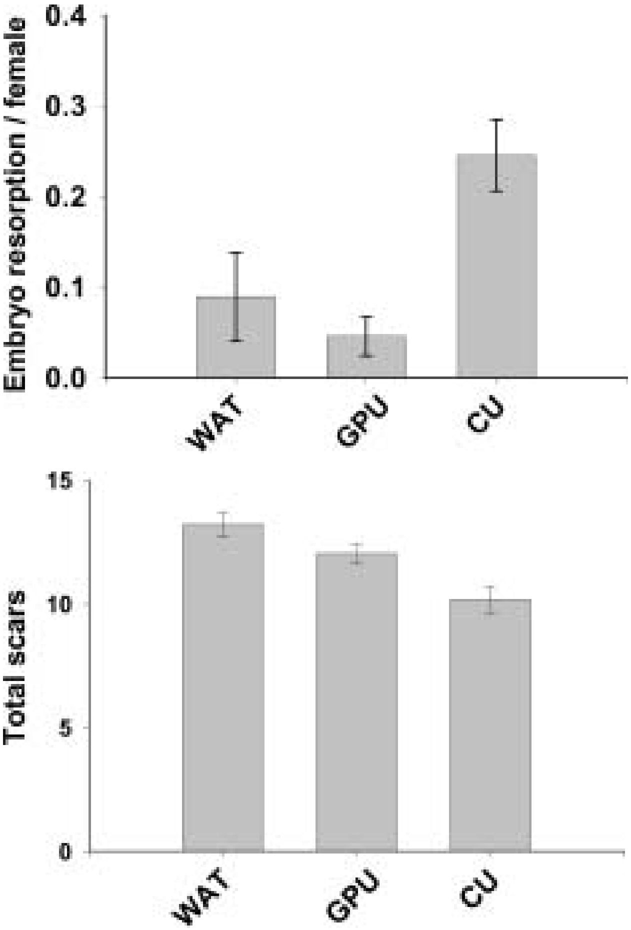

Figure 1. The influence of exposure to urine odours from cats (CU), guinea pigs (GPU) and tap water control (WAT) on (upper) embryo resorption and (lower) implantation in Norway rats. There were no significant differences between the water and guinea pig urine groups.

Although the precise, critically sensitive period during gestation has not been established, we do know that it occurs within the first half of gestation, and that an acute exposure to predator urine of 48 h up to 3 days after mating is sufficient to produce the negative effect on reproduction.

The observed changes to litter size, sex ratio, and gestation period brought about by early exposure to predator urine may involve one or more of the following mechanisms: (1) decreased ovulation; (2) delayed, reduced and/or differential fertilisation of the egg by sperm; (3) reduced implantation; (4) differential resorption of fertilised eggs or blastocoels; and (5) delayed implantation coupled with sex-linked differential survival of the blastocoel.

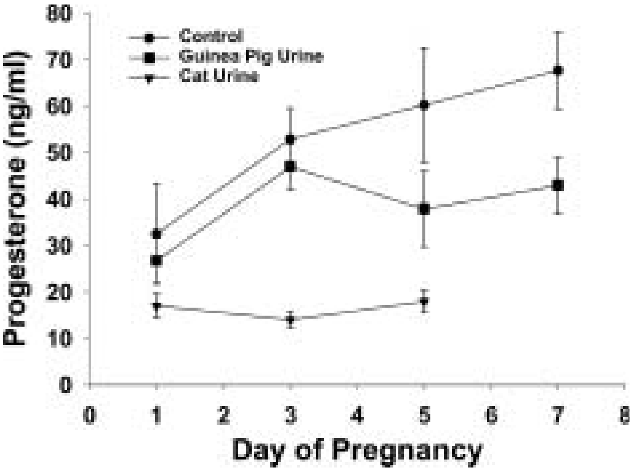

Figure 2. Plasma progesterone levels (mean ± sem) in Norway rats exposed to different urine odours (tap water control, guinea pig urine or cat urine) every other day during gestation.

Progesterone is a key ovarian hormone produced by the corpora lutea, and is responsible for the maintenance of the fertilised egg, preparation of the endometrium, and maintenance of pregnancy. Factors that disrupt progesterone production could lead to the altered reproductive success observed for rats exposed to predator urine. In follow-up experiments, we monitored plasma progesterone and corticosterone (a hormone released in response to stress) in female Norway rats during early gestation. In addition to groups exposed to urine odours, and control treatment, there was another group in which rats were handled roughly to physically induce stress ('open field' test with added stress). As we observed in our previous studies, female rats exposed to cat urine had smaller litter sizes. Based on the number of corpora lutea and implantation scars, it appeared that reduction in litter size was due to reduced implantation and resorption of embryos during the early part of gestation (Figure 1). Both of the control groups had similar embryo resorption rates, while the cat urine group experienced a higher embryo resorption rate per female (Figure 1a). These effects were also observed between treatments for the number of implantation scars (Figure 1b). Consistent with the morphological evidence was the observation that plasma progesterone levels were dramatically suppressed in rats exposed to cat urine relative to levels observed in the water control group and for rats exposed to guinea pig urine (Figure 2). We did not observe statistically significant differences in plasma corticosterone levels for rats exposed to predator and non-predator urine, while rough handling of animals caused a clear elevation of corticosterone (Figure 3). Plasma corticosterone levels were unrelated to the two measures of reproductive output, i.e. number of live births and resorption of embryos, with stress per se not influencing reproductive output (Figure 4).

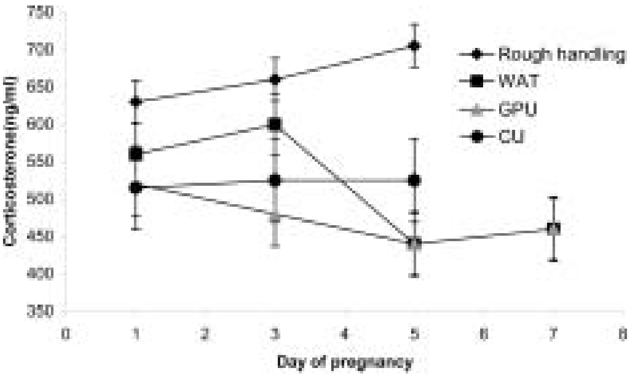

Figure 3. Plasma corticosterone levels (mean ± sem) in Norway rats exposed to urine odours (cat urine, CU; guinea pig urine, GPU; or control tap water, WAT) every other day during gestation or to rough handling in an 'open field' test with added stress.

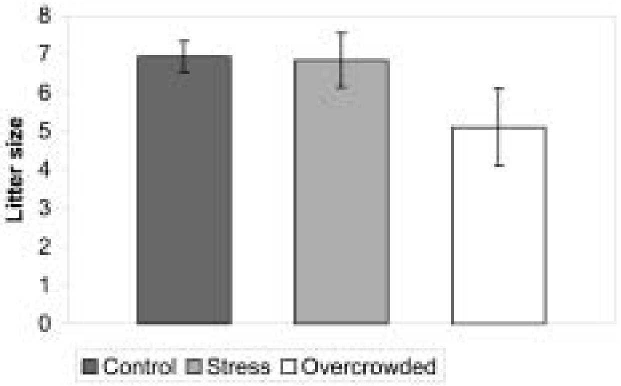

Figure 4. The influence of stress or exposure to urine derived from overcrowded conspecifics on litter size in Norway rats where: control = exposure to tap water every other day during gestation; stress = 'open field' test with added stress; overcrowded = exposure to urine from overcrowded conspecifics every other day during gestation.

Conclusion

We do not believe that reduction in litter size is attributable to an adaptive response by rodents to predator odours. Rather, we propose the following interpretation. Urine contains information about the identity of individuals, reproductive status, and dominance status. We postulate that urine also contains information about environmental quality as reflected by nutritional status. Investigation of urine from a variety of sources would serve as an efficient way to integrate environmental information. During times of food depletion, an individual could assess the nutritional status of the population. If food becomes limiting, rodents will begin to catabolise their own muscle protein and the urine will contain larger amounts of protein degradation products. These signals could serve to trigger mechanisms that would affect reproduction. Given that the generation time of rodents is short, complete reproductive inhibition may not be adaptive. However, reduced reproduction may be beneficial. Reduced reproduction would relieve energetic constraints on lactating females that might otherwise jeopardize survival if a full litter size were attempted.

Litters are biased toward producing males when predator or rat catabolic urine is used as a stimulus. This is consistent with theory on reproductive value. Even with reduced litter size, females may still experience lower survival probabilities during reproduction and lactation in food limiting environments because of energetic constraints. However, males would be less constrained by such energetic considerations. Thus, their survivorship probabilities may be higher than females, and by implication their value in contributing to fitness would also be higher. So then, why should rodents reduce reproduction when presented with predator urine? Predators on rodent diets would produce urine with many of the same rodent-derived metabolic products. It is only coincident that the two urines produce the same effect: an artifact of the experiments.

Rodents cause considerable economic damage to field and fruit crops on an annual basis. The magnitude of the problem is exemplified for a single commodity, apples. In the United States of America (USA) alone, rodents cause US$90 million of damage each year. Efforts to control rodents responsible for apple crop damage in the USA include the application of 321,000 pounds of herbicides for habitat management and 1000 pounds of acute rodenticides, including strychnine, zinc phosphide and chlorophacinone (National Agricultural Statistical Service, 1996). The most extensive damage occurs at the apex of rodent population cycles. It is our goal to develop a product that will dampen the amplitude of these rodent population cycles, thus resulting in less rodent pressure on crops and, by implication, result in less economic damage. We envision encapsulating active ingredients from urine and auto-catabolism of rodent muscle protein into bait that a rodent will take back to its burrow. Once in the burrow, female rodents would be exposed to the active ingredients on a schedule that would result in reduced reproductive output. This method utilises naturally derived compounds that pose no environmental hazard. Thus, this method should prove useful in reducing our reliance on pesticides with less favorable environmental properties while achieving the goal of reducing rodent populations.

Acknowledgments

This research was supported by grants from Russian Foundation for Basic Research No 98-04-48865, 01-04-48411, the Civilian Research and Development Foundation No RB1-2036, the Foreign Agricultural Service grant No RS72, Government of Moscow grant 1.1.205 and the Russian Academy of Sciences (Program 'Regulatory systems').

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Boreal vole cycles and vole life histories

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Abstract. The multi-annual vole cycle of boreal northern Fennoscandia is a population ecological play that has fascinated researchers already for 100 years. The final consensus of the causes of this phenomenon is still to be reached. However, individual short-lived iteroparous voles live for only a short part of the density cycle. This cyclically fluctuating environment forms the biotic and social environment into which individual voles adapt their life-history strategies. During the increase phase, there are only a few factors constraining optimal reproduction. During population peaks, however, complicated density-dependent processes including social stress, but also interspecific competition and increasing predation pressure, slow the population growth rate. A dramatic impact of predation by small mustelids results in a deep decline of the population. The following low population densities over large areas need a year or more to recover. We review mostly our own experiments on the life histories of common boreal voles, the bank vole, *Clethrionomys glareolus,* and the field vole, *Microtus agrestis,* in environments mimicking especially the peak phase and the decline of the cycle. There are considerable similarities as well as basic differences between the boreal cycle and Southern Hemisphere rodent outbreaks. The recent accumulation of data on life histories and behaviour of boreal rodents may well be beneficial in future studies on less well-studied Southern Hemisphere rodent species.

Introduction

Eighty years have passed since Charles Elton, after an expedition to northern Norway, used his last coins in a small bookshop in Tromso to buy a book by Robert Collett: *Norges Pattedyr,* Norwegian mammals. After arriving in Oxford, Elton had the book translated into English. Probably strongly influenced by Collett's book, he published some years later the first English description of the northern Fennoscandian phenomenon that has become famous among population ecologists as the vole and lemming cycle (Elton 1924; c.f. Stenseth 1995). For enthusiastic natural historians, like priests and schoolteachers in poorly populated Lapland, lemming (*Lemmus lemmus*) outbreaks and migrations were known already at the end of 19th century.

Since Elton's days the Fennoscandian vole cycle has become one of the major examples given in population ecology textbooks. A number of hypotheses have been proposed and tested with long-term data, experiments and modelling to explain the causality of population fluctuations in Fennoscandian rodents (Stenseth et al. 1996). The present paper does not deal with causality of vole cycles, but rather uses the multi-annual fluctuation, with its biotic and social processes, as background for experimentation on individual vole life histories (Figure 1). It might well be that few common factors explain the observed pattern (Hanski and Henttonen 1996; Stenseth et al. 1996), although a holistic explanation and consensus between researchers has still to be reached (c.f. Lambin et al. 2000). However, the strength of different factors certainly change along the density cycle and these changes impact on individual life-history strategies.

Our aim is to review mostly our own comparative and especially experimental studies on social and external factors possibly affecting population dynamics. These factors should also strongly affect individual reproductive and survival strategies along the density cycle. Our main study objects are two common rodents in the boreal habitats, the forest-dwelling, granivorous–omnivorous bank vole and the green biomass-exploiting herbivorous field vole. Both fluctuate in synchrony during the multi-annual cycle (Henttonen et al. 1987). During low and moderate density years they exploit different habitats but during a common population high they coexist in marginal habitats (Ylönen 1989a; Eccard and Ylönen 2002). During population declines, predation by small mustelids, the least weasel, *Mustela nivalis nivalis*, and the stoat, *Mustela erminea*, is the major mortality agent for voles (Norrdahl and Korpimäki 1995). We have conducted a number of experimental studies in the last 10 years in the laboratory, large outdoor enclosures, and open study areas to mimic variable environmental conditions and monitor their effects on individual behaviour, reproduction and survival. These studies form the source of our evaluation and speculation on the validity of using short-term experimental approaches to explain complicated long-term behavioural processes in the field. We believe strongly in this approach, but for explaining boreal cycles we need the whole range of different approaches of researchers to the vole cycle and vole reproduction.

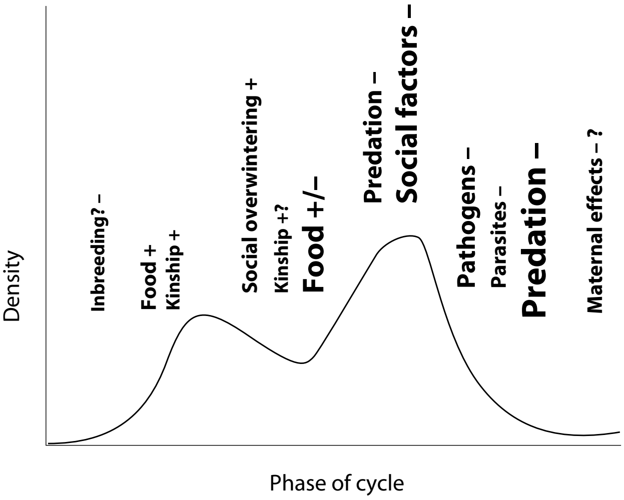

Figure 1. Schematic picture of possible factors having positive effects (+) on population growth rate during different phases of a multi-annual density cycle of voles, or having negative effects (–) on either individual performance or population growth rate during the cycle (after Ylönen 1999). The size of the font indicates the suggested strength of the factor.

Fascinating multi-annual cycles

We can observe multi-annual vole cycles over large areas in northern and central Fennoscandia. The cycle length is 4–5 years in the north and decreases to 3 years towards the south. In central Sweden, the cycles disappear and the population fluctuation becomes more irregular. This change correlates with factors like the duration of permanent snow cover and number of resident predators (Hansson and Henttonen 1988). Typically, several species fluctuate in synchrony. In the north, up to six species of microtines may fluctuate in synchrony (Henttonen et al. 1987). In the southern part where cycles occur, the two most common voles, bank vole and field vole, exhibit the same phenomenon. However, across the geographical range of occurrence of cycles, species like the yellow-necked mouse, *Apodemus flavicollis*, the smallest rodent in the boreal areas, the harvest mouse, *Micromys minutus*, and the largest vole—the water vole—*Arvicola terrestis*, do not join in the fluctuation patterns of bank voles and field voles.

Many of the population ecological studies on vole cyclicity derive from data from northern Fennoscandia (e.g. Henttonen et al. 1987). However, the first experimental evidence for the impact of small mustelids on the decline of vole populations came from western Finland (e.g. Norrdahl and Korpimäki 1995). Studies on population decline have been overwhelmingly numerous compared to other phases of the cycle. From the point of view of individual life history, however, the increase phase should form the basis of comparison with the high-density, decline and low-density phases. In the increase phase, environmental factors (food, predation, disease) and inter- and intra-specific social factors have only a minimal effect on the individual strategies and the population growth rate.

Synchronous peak density phases of several vole species are the subject of intense debate, but they are particularly complex and difficult to simulate under experimental conditions. Therefore, a great number of hypotheses have been proposed to explain the interactions between several factors causing the population growth rate to slow or become negative, such that predation catches the prey populations and they start to decline (Stenseth et al. 1996; Hansson 1998).

After the decline: the landscape is empty of voles

In many population ecological studies, the unit of capture success of voles is the number of individuals per 100 trap-nights. For example, setting 200 traps for three nights yields 600 trap-nights. If trapping success is ≥30%, we regard the density to be very high. However, during population lows, a researcher having set the same 200 traps for three nights might well have some shrews, and possibly 1–2 voles. This extremely low trapping success of ≤1% demonstrates how difficult it is to obtain information on population structure, or simply to determine where the few survivors are located during the population lows.

If the size of a breeding territory affects the breeding success of females, then during and just after the population lows, there should be no constraints to the size of territories. Klemola et al. (2000) showed also experimentally, that possible overgrazing of food resources during high density of voles does not affect vole performance during subsequent breeding seasons. In an experiment using litter size manipulations in the bank vole, Koskela et al. (1999) showed that females with larger territories were better able to raise experimentally enlarged litters successfully than were females with smaller territories. Also in comparative data over 6 years in an enclosed population, Ylönen (1990) reported a trend in home-range size of females; these were largest during years of low densities and smallest during years of peak densities. Further, under experimental conditions where food was supplemented, the first litters during spring seemed to be larger than in control areas with no food supplement (H. Ylönen and J. Eccard, unpublished data). All these small pieces of information suggest that the breeding performance of individual voles is density-dependent and recruitment of young individuals into the breeding population is most effective during low and moderate densities of conspecifics. Furthermore, in an extensive field transplant experiment, Ergon et al. (2001) demonstrated how rapidly voles respond in their growth and reproduction to immediate environmental conditions. This observation should apply also for life histories of voles when resources are rich and density of conspecifics low during the increase phase of the cycle.

Harsh and long winter, but the snow protects

Thick and stable snow cover is characteristic of boreal northern European winters. All diurnal raptors migrate to milder over-wintering habitats because they are not able to hunt through the thick snow. The only owl, the diurnal pygmy owl, *Claucidium passerinum*, caches food in nest holes before the onset of 'real winter'. Avian predation pressure during winter is low and caused by a few nocturnal large owls. The thick snow probably protects voles living in the sub-nivean space relatively well from mammalian predation by larger carnivores as well. The role of generalist predators probably is much stronger in shaping vole population fluctuations already in southern Fennoscandia (Hansson and Henttonen 1985; Bjørnstad et al. 1995) and in northern Britain (Lambin et al. 2000). In northern Fennoscandia, only the stoat and particularly the least weasel are able to enter the same habitat where voles are living under the snow.

However, during the winter after population lows and the increase year of the voles, weasels and stoats still are rare. The over-wintering success of voles depends on factors other than predation, like temperature, food and stability of the winter conditions. After the onset of permanent snow cover, the survival of voles under the snow is relative high until the onset of the spring thaw (Ylönen and Viitala 1985). Over-wintering in social aggregations is common in boreal rodents (Ylönen and Viitala 1985). This saves energy and heat (Vickery and Millar 1984), because during foraging trips, some conspecifics remain in the nest and consequently the nest temperature does not drop. Heating an empty nest would be energetically costly for a vole living alone.

Because experimental studies over winter are scarce, there are few data on the determinants of the onset of breeding at the end of winter. Eccard and Ylönen (2001) conducted supplemental food experiments to determine the influence of food and density on the onset of spring reproduction in bank voles. In enclosures with a large quantity of food, reproduction started earlier than in the surrounding forests with low food supply. However, local density affected the onset of reproduction in food treatments. In nature, the suitability of a habitat for over-wintering can create local density variations, which may be the reason for an asynchronous onset of reproduction after winter, regardless of the food situation. The low density of females after a population decline would thus offer favourable conditions for an early start to the breeding season.

Complicated density-dependent processes during population peaks

When several vole species reach peak abundance at the same time, the factors affecting their population dynamics become difficult to untangle (c.f. Stenseth et al. 1996), and at present we can only speculate about the strength of different factors rather than conduct rigorous experiments. However, as a general premise we can suggest that density-dependent processes, like social processes, competition, possible food constraints and spreading of pathogens and parasites, become very important. From the individual life-history point of view, intensified intra- and inter-specific competition and food depletion might be the most crucial factors determining breeding strategies. Rising predation pressure as weasel and stoat populations increase causes increasing mortality, and possibly affects individual behaviour as well. Individual voles are short-lived animals and thus live through only a short time window of the cycle. Voles are iteroparous, breeding several times normally during a single breeding season. But since a proportion of individuals can breed in two successive breeding seasons (Prevot-Julliard et al. 1999), individual voles have phenotypic flexibility in their breeding and survival strategies.

The strength of different density-dependent factors during population highs can only be speculated about. However, without these processes the population growth rate would not decline enough to allow the predation impact to overwhelm the growth rate and turn it into a population decline. On the role of pathogens during the high vole densities, we have our own observations from the winter of 1988/89 after very high field vole densities the previous autumn. Field voles entering the trap chimneys were too weak to enter the traps, and we collected dead voles in front of the traps. In pathological examinations we found the lung-fever bacteria, *Bordetella bronchiceptica* (T. Soveri et al., unpublished data), in the voles. Disease caused by this organism occurs commonly at all population densities, but probably interacts with other processes during high population density and may become an effective pathogen.

During the last 5 years, we have conducted several sets of enclosure experiments on the impact of interspecific competition on breeding and survival of voles of different ages and sexes. In our experiments (Eccard 2002; Eccard et al. 2002; Eccard and Ylönen 2002) we have used the field vole as a socially dominant competitor and followed its impact on the fitness of subordinate bank voles. The presence of field voles reduced survival of bank voles. Different age classes were affected differently—survival was not reduced in breeding voles that had over-wintered, but was reduced in the newborn voles. This suggests that the combined effects of inter- and intra-specific competition caused an increased mortality in bank voles. Immature young-of-the-year bank voles, however, were not affected by the presence of field voles. Behavioural aspects may thus play a role in the impact of competition.

Territory holders have to interact more with other individuals than with immatures, and high aggressive contact rates can contribute to mortality (Bujalska and Grüm 1989).

Our results thus demonstrate a different impact of field vole competition on different age categories of bank voles. Since population growth is determined both by the numbers and the age structure of the population, the demonstrated impact of competitors altering the age structure of vole populations may contribute to cyclic fluctuation patterns.

The beast during the decline: the least weasel

There is a quite unambiguous body of evidence on the strong impact of small mustelids, the least weasel and the stoat, in shaping the decline phase of the vole cycle in central and northern parts of Fennoscandia (e.g. Henttonen et al. 1987; Hanski and Henttonen 1996). Small mustelid populations follow the vole cycle with a time lag of a half to one year; in theory, a necessary condition to create predator–prey cycles (e.g. May 1973). Weasels and stoats become more abundant during the second year after vole populations have started to increase, and small mustelid populations crash about half a year after the decline of vole populations due to food deprivation and intraguild predation. During the late summer of the crash year, the researchers trying to capture a few remaining voles are commonly greeted by a high weasel screech from the live-trap.

Despite a large number of publications suggesting the crucial role of small mustelids during the decline, Norrdahl and Korpimäki (1995) were the first ones to verify experimentally the strong mortality effect of weasels during the vole decline. They followed intensively over 3 weeks the fate of radio-collared voles in a vole crash year and during an increase year of the vole populations when the small mustelids were suggested to be rare or absent. There was a crucial difference in mortality rate of voles between the study years, and during the decline 85% of the voles were killed by least weasels. They concluded also from the predation rate and the litter sizes of voles that female voles would have to produce twice as large a litter as they do on average to be able to compensate for the mortality caused by weasels and to slow the population decline.

Our own work dealing with the role of predation in the cyclic decline of rodent populations has been experimental studies in the laboratory on weasel hunting preferences in relation to olfactory cues of the prey (Ylönen et al. 2002) and enclosure experiments on the functional response of weasels in single-species vole populations and mixed communities (Sundell et al. 2002). In addition, many experiments have investigated the anti-predatory adaptations of voles (Ylönen 1989; Ylönen and Ronkainen 1994; Koskela and Ylönen 1995).

Least weasels are regarded as specialised hunters of small mammals and they especially prefer field voles (Erlinge 1975; Henttonen 1987). This preference might be due to easier hunting habitats, simply due to higher reward in hunting denser field vole populations, or due to odour cues or behaviour of individual voles. In our experiments following radio-collared prey voles and prey selection of weasels, we have observed, in contrast, that weasels do not show any preference for field voles (Sundell et al. 2002; Ylönen et al. 2002). Instead, they either prefer bank vole or hunt opportunistically according to availability of prey. These results suggest that predation by weasels may contribute to the coexistence of these two vole species in the same habitats and explain the synchronised population fluctuations of sympatric vole species.

There exists a quite good consensus from studies across various taxa that, in addition to their direct mortality effects, predators have strong indirect effects through increased risk of predation on prey behaviour (Lima and Dill 1990). Because of the dramatic mortality effect of least weasels during the population decline, we predicted that indirect cues of weasels would also have an impact in changing the behaviour of prey voles. We have been able to verify responses in activity, feeding and reproduction in the laboratory trials to odour-mediated increased predation risk by weasels (see Ylönen 2001 for review). Verifying the effects under field conditions, especially regarding delay or suppression of breeding in females as an anti-predatory strategy against small mustelids that hunt by olfaction, has not, however, been successful. But it remains a fact that least weasel is the only predator which can hunt in almost the smallest cavities where voles live (Sundell and Norrdahl 2002) and under the snow. Due to the extremely strong mortality impact of least weasels, their habit of killing more prey than needed (surplus killing), the hunting behaviour of weasels including a Type II functional response typical of a specialist predator (Sundell et al. 2000), and the high reproductive capacity of this mammalian predator (Sundell and Norrdahl 2002), the coevolutionary relationship between weasels and voles may be an important case of predator–prey coevolution.

Conclusions

Most of the studies devoted to the cyclicity phenomenon are long-term population studies or modelling exercises. In Fennoscandia, there has been quite good agreement on the role of specialist predation by small mustelids, coupled with social factors during population peaks (Stenseth et al. 1996) and with permanent, long-lasting snow cover (Hansson and Henttonen 1985) causing the rapid population decline and extremely low population densities during the low phase of the cycle (Henttonen et al. 1987; Hanski and Henttonen 1996; Korpimäki and Norrdahl 1998). This view has been questioned recently, based on long-term data over large areas in northern Britain, where field voles also exhibit cyclical population fluctuations, without the strong impact of specialist predation (Lambin et al. 2000; Mackinnon et al. 2001; Sherrat et al. 2002). The study populations of Fennoscandia and Britain exhibit strong similarities but also some important differences in their fluctuation patterns, e.g. the much higher densities of voles during the population lows in northern Britain. Besides Fennoscandia and Britain, long-term studies from Hokkaido, Japan (Saitoh et al. 1998) and from Central Europe (Tkadlec and Stenseth 2001), demonstrate that there might be relatively similar cyclic population fluctuations of voles in different environments, but with different causes producing the cyclicity.

However, from the point of view of the life history of an individual vole, there are great similarities in environmental conditions for breeding voles in different phases of the cycle. In the last two decades, many studies have focused on breeding behaviour or life histories in general, and the behaviour of cyclically fluctuating vole species, starting long ago with Kalela (1957). Many of the species that have been studied have broad geographical ranges across the Holarctic region or have sibling species in the Old and New World. This has allowed comparative studies of the same species in areas where the populations fluctuate either cyclically or annually, or between similar species in Europe and North America. There is a broad research approach with population ecologists and theoreticians trying to clarify the causality in large-scale patterns, and life historians and behavioural ecologists focusing on small-scale and temporally short-time processes, as we do. However, these research approaches must be strongly linked. From our point of view, the link is from the large external timers, ‘Zeitgebers’, affecting large-scale patterns to effects on the ‘world view’ of short-lived individual voles, or rodents in general, adjusting their life histories accordingly. The large-scale fluctuations, even in the form of regular cycles, are too slow to permit genetic adaptations for individual voles. Rather, they act through constraints formed by changes in the social and resource environments.

Recently, there has developed a strong interest in understanding a variety of population patterns in rodents on different continents. Many of the data sets from Southern Hemisphere rodent population dynamics are collected from the management point of view, and under strong pressure to control high economic losses from pest rodents (Singleton et al. 1999). Probably, in the near future, together with accumulation of population data on the diverse rodent assemblage in the south, there will also be a more pronounced accumulation of data on reproduction, behaviour and life histories. We believe that, in analysing these data, the already existing experimental data on behaviour and reproductive strategies of boreal rodents can be of great mutual inspiration. Small-scale processes determining reproductive output and survival of individuals should be the same regardless of the regularity or irregularity of the large-scale population patterns. However, we should be obliged to agree on the causes of regular population patterns of rodents, like the vole cycles, to be able to approach the much more complicated systems of irregular outbreaks of rodents, like those observed in the southern hemisphere (e.g. Leirs et al. 1996; Singleton et al. 2001) as well as in Europe (Frank 1957).

Acknowledgments

We thank Charles J. Krebs, Dave Spratt and one anonymous reviewer for valuable comments on our manuscript. Our research has been financially supported by the Academy of Finland.

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Scent marking in rodents: a reappraisal, problems, and future directions

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Abstract. Experimental studies on scent marking in rodents have centred on how the frequency and placement of initial, secondary, and overmarks are used in reproductive competition, sexual attraction, and self-advertisement. We review the literature on these primary functions of scent marking, drawing examples primarily from mice, voles, and hamsters. Although the frequency and placement of scent marks may function in competition and sexual attraction for some species such as mice and gerbils, little evidence exists to show how these contribute directly to reproductive success. Most studies are designed to support a given hypothesis rather than reject alternatives. For voles, scent marking is more consistent with the self-advertisement hypothesis. Scent quality, which has received little attention, might convey more information and be used more in rodent communication than scent quantity. Overmarking has been proposed as a form of reproductive competition, however studies with prairie voles and meadow voles concluded that overmarking was a chance occurrence and not an adaptive reproductive strategy. Scent marking behaviour lacks a central focus or paradigm so we provide five theoretical and empirical directions for future research on scent marking in rodents.

Introduction

Individuals attempt to provide information about themselves to facilitate and enhance interactions with each other and their environment. One way to convey this information is through chemical signalling in the form of scent marking. Scent marking has several non-mutually exclusive functions but appears to be used primarily in reproductive competition and sexual attraction (reviewed in Gosling 1982; Johnston 1983; Halpin 1986). Scent marking is used by rodents to discriminate the identity, sex, age, competitive ability, and reproductive status of conspecifics (Johnston 1983). Although the ability to discriminate among individuals by olfactory cues is based on variation in the components within the scent (Halpin 1986), the majority of studies on scent marking have focused on the frequency and placement of these scent marks, rather than the properties of scent itself. Once an individual has scent-marked an area, conspecifics often deposit secondary marks in response to initial marks. Some of these secondary marks are placed adjacent to previous marks, whereas others may overlap initial marks and are referred to as overmarks. Supposedly, overmarks are used to express dominance of one individual over another and females are supposed to prefer to mate with males that can overmark their opponents. The frequency and placement of these initial and secondary marks are used in communicating information about individuals to conspecifics.

In this paper we review the two main functions that have been proposed for scent marking, reproductive competition and sexual attraction, with special reference to the frequency and placement of initial and secondary scent marks. In reviewing the literature for this paper, we found that several experimental studies on scent marking failed to support the reproductive competition or sexual attraction hypothesis (Table 1), rather concluded that the frequency and placement of scent deposition was used primarily for self-advertisement. We also found considerable controversy regarding the interpretation of overmarking as a competitive behaviour. Therefore, we compare scent marking in several species of rodents to assess its role in reproductive competition, sexual attraction, and self-advertisement. We draw largely from experimental studies with house mice, *Mus domesticus*, and voles, *Microtus* spp., and provide additional examples where data are available.

Reproductive competition

For scent to be effective in intrasexual competition, it must benefit the donor by conveying fighting ability or status to competitors. The quality of scent might convey some direct information about an individual, but scent most likely serves as a reminder of an individual's identity following an initial agonistic encounter. Because of this association, scent can be used in defending territorial boundaries or in reducing agonism in maintaining a hierarchical relationship among known neighbours or individuals in a group (Gosling 1982). If one of the functions of scent marking is reproductive competition then (1) individuals should deposit scent marks within their space to indicate presence and ownership, (2) the frequency of scent marking should be associated with social rank or territorial ownership, (3) dominant individuals should increase the frequency of marks (countermark) or overmark the scent of subordinates, and (4) when encountering the marks of a dominant individual, subordinates should behave so as to avoid encounters with the higher-ranking individual (modified from Gosling 1982). Alternatively, the self-advertisement hypothesis predicts that an individual might mark to provide information about its identity and presence in an area. In this case, the frequency and placement of marks should be similar in response to the previous marks of any age, sex, or status conspecific as it would on a clean substrate (Thomas and Wolff 2002). The lack of countermarking or overmarking would support the self-advertisement hypothesis more so than reproductive competition or sexual attraction (Table 1).

Among males

Scent marking appears to function in male–male competition in species such as house mice (Hurst 1990), Mongolian gerbils, *Meriones unguiculatus* (reviewed in Halpin 1986), golden hamsters, (Johnston 1983), and bank voles, *Clethrionomys glareolus* (Rozenfeld et al. 1987). Males of these species of rodents place marks on clean substrate to indicate their presence or ownership and dominant males place a higher frequency of marks than subordinates. Subordinate males reduce the frequency or avoid marking in areas containing previous marks of conspecifics that have defeated them in prior encounters (Halpin 1986). Male Mongolian gerbils that defeat a previously dominant conspecific increase their frequency of marking (Halpin 1986). In house mice, dominant males countermark the initial scent marks of subordinate males (Hurst 1990 and references therein). Further support that male house mice use the frequency of scent marking in competition is that dominant males become more aggressive toward subadult males as they mature and increase their frequency of marking within the territory (Hurst 1990). These findings suggest that scent marking by subordinates may have a cost of eliciting aggression from higher-ranking individuals. Male

Table 1. Three alternative functions for the frequency and placement of initial and secondary scent marks, supportive evidence associated with each function for males and females, and suggested research needed to demonstrate the function(s) of scent marking in the study species.

Proposed function	Supportive evidence		Research needed
	Males	Females	
Reproductive competition: individuals scent mark to indicate social status and competitive ability	• Dominate > subordinate • Territory owners > intruders/ dispersers	• Same as for males	• Determine if differences in scent marking occur based on social status and territory ownership • Demonstrate the ability of a receiver to associate a scent donor and its specific marks • Manipulations of scent quality
Sexual attraction: individuals scent mark to advertise their current reproductive condition or to attract mates	• Frequency is correlated with age and reproductive condition • Countermark or overmark the previous marks of oestrous females more than anoestrous or pregnant and/or lactating females • Countermark or overmark the previous marks of other males in the presence of marks from oestrous females	• Increase the frequency of marks as oestrus approaches • Alternatively, post-partum oestrous females might decrease marking to avoid detection by infanticidal conspecifics and predators • The scent of oestrous females is more attractive than anoestrous and pregnant and/ or lactating females	• Correlate scent marking with age and reproductive condition • Determine scent-marking effect on mate choice • Compare scent-marking response to the previous marks of same and opposite-sex conspecifics • Determine the cost and benefits associated with advertising reproductive condition
Individual identity: individuals place marks to advertise their recent presence in the area	• Similar number of marks in response to previous marks of other conspecifics and clean substrate • Avoid overmarking other marks	• Same as for males	• Compare frequency of overmarking to a calculated expected value based on total marks and the available area to mark

voles, *Microtus* spp., have been proposed to use scent to indicate their status or fighting ability (e.g. Ferkin 1999; Woodward et al. 2000). However, laboratory studies designed to discern among alternative hypotheses have failed to support the predictions of this hypothesis. The frequency and placement of scent marks by male prairie voles and meadow voles are most consistent with the predictions of the self-advertisement hypothesis (Thomas and Wolff 2002). Male prairie voles and meadow voles placed a similar number of marks in response to the previous scent of another male conspecific, their own marks, and on clean substrate, and overmarking was uncommon. Additionally, males did not avoid areas previously marked by another male. We do not doubt that differences exist in the quality of marks among male prairie voles and meadow voles, however it does not appear that the frequency and placement of marks and responses of conspecifics meet the predictions of the reproductive competition hypothesis.

Among females

Few studies have investigated scent marking among females. However, golden hamsters (Johnston 1983) and house mice (Hurst 1990) appear to use the frequency and placement of scent marks in competition with female conspecifics. Female golden hamsters increase their frequency of flank-gland marking, an aggressive behaviour, in response to the previous marks of other females compared to those of male conspecifics (Johnston 1983). Resident breeding female house mice investigate and countermark the previous marks of other breeding females more so than the marks of other conspecifics. Additionally, non-breeding, subadult, and juvenile female house mice place significantly fewer marks than breeding females (Hurst 1990). Further support for the use of scent marking for communication among female house mice is that not all breeding females defend a territory, however these females still countermark in response to other breeding females (Hurst 1990). These findings suggest that the scent of female house mice and golden hamsters contains information about the competitive ability of the donor and might be used to defend breeding space or, in the case of golden hamsters, food caches.

As with male prairie voles, scent marks by females appear to be deposited so as to advertise the donor's presence in a particular area rather than for competition. In a recent study with anoestrous, oestrous, and lactating prairie voles, similar numbers of marks were placed by females in various reproductive condition in response to those of another female and on clean substrate, and overmarking was uncommon (Wolff et al. 2002). Females investigated all substrate and were not deterred from entering previously marked areas. We do not doubt that scent marking by female prairie voles may have a competitive function, however results from laboratory studies were not able to demonstrate that responses from secondary individuals to initial scent marks supported any of the predictions of reproductive competition. In that female voles maintain exclusive territories in the wild (Getz et al. 1993), it is likely that scent marking functions in part to maintain these boundaries.

Mate attraction

Numerous studies with rodents have concluded that individuals can determine the sex and reproductive status of conspecifics based on odour cues. Individuals encountering previous marks respond differently to the scents of same- and opposite-sex donors, indicating that scent could be used in reproduction (Johnston 1983; Halpin 1986). Furthermore, females of many species of rodents spend the majority of their reproductive lifespan pregnant or lactating. Therefore, it might be necessary for a female to signal her approaching oestrus to potential mates. The predictions for the frequency and placement of marks for the mate attraction hypothesis are as follow. (1) Females will increase scent marking just before or during oestrus and more in the presence of males than females. Alternatively, females in behavioural or post-partum oestrus might reduce their frequency of marking if it increases the possibility of detection by predators or conspecifics that might harm them or their offspring. (2) Males will be attracted to the scent marks of oestrous females more so than non-reproductive females and will respond by overmarking or countermarking the marks of oestrous females. By overmarking the scent of an oestrous female, a male might mask her presence in the area or make her odour less attractive to other males, thereby reducing possible competition to mate with the female. Countermarking could signal interest and possibly indicate a willingness to compete for the female donor to other competitors encountering her marks.

Laboratory studies indicate that females of several species of rodents such as Mongolian gerbils, golden hamsters, and Norway rats, *Rattus norvegicus*, increase their frequency of marking as oestrus approaches and males are more attracted to these marks than those of anoestrous, pregnant, or lactating females (Johnston 1983). Additionally, female golden hamsters reduce the frequency of flank-gland marking and increase their frequency of vaginal marking in the presence of scent from males, indicating that vaginal marking is sexually motivated (Johnston 1983). Some evidence exists that male house mice are attracted to and countermark the urine of breeding females more so than that of other females. However, studies conducted in enclosures failed to support this conclusion in that breeding males countermarked similarly in response to all marks encountered within their territory (Hurst 1990). Although male prairie voles discriminate between and prefer the scents of oestrous to anoestrous females (Halpin 1986), experimental laboratory studies failed to show that males countermarked or overmarked oestrous females more than anoestrous females (Wolff et al. 2002). Prairie voles in post-partum oestrus, male-induced oestrus, and anoestrous placed similar numbers of initial marks and secondary marks, however the tendency was for post-partum oestrous females to place the fewest marks (Wolff et al. 2002). Wolff et al. concluded that the cost of attracting predators or conspecific competitors to the nesting area might have outweighed the benefits of mate attraction. The quality of scent of oestrous females differs from that of non-receptive females (Johnston 1983), however this difference does not appear to be reflected in the frequency of scent marking.

Several studies suggest that the scent of males provides information to females that facilitates mate choice and mating. For example, males of two species of Saharan gerbils, *Meriones libicus* and *Psammomys obesus*, scent mark the home ranges of females to promote their presence to the females. Female Mongolian gerbils apparently associate prior exposure to scent with the donor and are less aggressive toward males after continued exposure to their scent than to novel males (reviewed in Johnston 1983). Additional support comes from studies with house mice that have shown oestrous females are more attracted to the odours of males that defend exclusive space and exhibit more sexual behaviour when encountering these males than those unable to exclude intruders (Rich and Hurst 1998). Several studies have suggested that the frequency and placement of scent marks by male prairie voles and meadow voles provide information about social rank and females use this information in mate choice (Woodward et al. 2000 and references cited therein). However, experimental studies directly testing the effects of prior exposure to male scent and mate choice found no correlation between the frequency and placement of marks and social rank of males or mate choice by females (Thomas 2002). Although little, or no, relationship occurs between the frequency and placement of marks and mate attraction in prairie voles, the quality of scent might be a better indicator of mate quality and reproductive condition and thus used in mate choice (Thomas 2002).

Overmarking

Overmarking has been studied extensively in golden hamsters (Johnston et al. 1994), meadow voles (Ferkin 1999) and prairie voles (Woodward et al. 2000). These studies found that females could discriminate between the top and bottom scent donor of an experimentally created overmark and ‘prefer’ the top scent. This conclusion is based on the fact that females spent more time sniffing the top than bottom scent when presented with the two scents separately after exposure to the overmark. Based on these studies, overmarking has been considered a tactic for reproductive competition. However, in two experimental studies in which male prairie voles and meadow voles were allowed to secondarily mark initial marks of potential male competitors, they overmarked less often than expected by chance based on the space available (Thomas and Kaczmarek 2002; Thomas and Wolff 2002). Thus, Thomas and Wolff concluded that overmarking was avoided, rather than an adaptive reproductive strategy. The frequency of overmarking is typically less than 10% of the original marks, which begs the question of why >90% of scent marks are not overmarks. When rodents do overmark, the top scent typically covers only a small portion of the bottom scent and does not negate or mask it entirely (Johnston et al. 1994; S.A. Thomas and J.O. Wolff, personal observations). The facts that the majority of secondary marks are not overmarks, overmarks typically cover only a small portion of the initial mark, and females do not appear to use scent in mate choice support the supposition that overmarking might be an artifact of space available for marking and not an evolved reproductive tactic. We concluded that if individuals scent marked to retain their individual identity, then they should not blend their scent with other individuals, rather mark in clean, unmarked areas to maximise the exposure of their scent. The role of overmarking and its interpretation as a reproductive strategy requires further theoretical and empirical development.

Conclusions and future directions

For rodents, it appears that individuals attempt to provide information about themselves by depositing scent marks within their environment. Conspecifics have evolved the ability to identify others based on the donor’s odour; which provides the opportunity for individuals encountering these marks to exploit the information to their benefit. Although methodology for experimental studies on the function of scent marking has focused on the frequency and placement of scent marks, quality of scent might convey much more information and be a fruitful area of future research. The current literature on scent marking has been difficult to synthesise because of a lack of consensus on methodology, research approach, or discerning among alternative hypotheses. Therefore, the use of scent communication by rodents is poorly understood from a theoretical or empirical point of view. To advance the understanding of scent communication as has been noted by Gosling and Roberts (2001), we propose the following directions for future research:

1. a clearly-stated paradigm with a list of alternative hypotheses and predictions for testing and rejecting each hypothesis independently (Table 1);
2. a standard methodology that uses similar experimental approaches and protocols, which allows for cross-species comparisons;
3. incorporation of variation in scent quality with frequency and placement of scent;
4. field validation that scent marking in the laboratory represents that in natural environments; and
5. an application of the paradigm to evolutionary theory.

Future research that incorporates these five directions should aid considerably in developing a comprehensive paradigm for scent marking and other aspects of olfactory communication in rodents and other mammals (see also Gosling and Roberts 2001).

Acknowledgments

We thank Grant Singleton, Charles Krebs, and Lyn Hinds for inviting us to participate in this symposium. Two reviewers provided constructive criticism on an earlier draft of this paper. This project was funded by the Departments of Biology at the University of Memphis and Delta State University.

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Predator presence affects the reproductive success of prey in outdoor conditions

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Abstract. The reproductive outcomes of laboratory rats (*Rattus norvegicus*) housed at different distances (2, 20 and 80 m) from a predator (*Lynx lynx*) were investigated. Virgin female (n = 120) and male (n = 40) rats of an outbred laboratory population were used for the experiments. Groups of rats (one male and three females) were housed in standard cages in close proximity to the predator. Litter size, sex ratio, number of live pups, number of placental scars and corpora lutea were counted; and pre- and post-implantation losses were calculated for each female. The reproductive success of females, estimated as the number of live pups per female, was significantly higher in both control groups (20 and 80 m) than in both experimental groups (2 and 2 m). Equal numbers of corpora lutea in all groups but different numbers of placental scars between control and experimental groups indicated higher pre-implantation losses in the experimental groups. Post-implantation losses were also higher in both experimental groups. Total losses (calculated as a difference between the number of corpora lutea and live pups) were twice as high in experimental groups. Reproductive success of rats depended on concentration/intensity of predator scents: when concentration/intensity was higher, the number of live pups was less and the total loss was higher.

Introduction

Many mammals utilise olfactory cues to detect potential danger from predators. Avoidance of the predator odours and suppressed feeding behaviour have been described for potential prey species of three main mammalian taxonomic groups: rodents, lagomorphs and ungulates (Muller-Schwarze 1973; Sullivan et al. 1988; Boag and Mlotkiewicz 1994). Other behaviours of prey may also be affected by the presence of a predator or its odours. For example, predator odours derived from predator faeces, urine and gland secretions, and compounds isolated from these sources, suppress feeding behaviour in rodents (Sullivan et al. 1988). On the bases of these studies, predator scents as natural repellents have been used to develop pest management products to protect plants from herbivores. However, behavioural responses of prey species are not restricted to avoidance and changes in feeding behaviour. Prey species under high predation risk may change their activity rhythms to minimise risk. High predation risk may decrease the locomotor activities of prey, change their activity level and spatial distribution or alter their natural rhythm of activity (for example, from nocturnal to diurnal) (Fenn and MacDonald 1995).

Predator odours may also directly affect the reproductive physiology and behaviour of rodents. In nature, predators are one of the most powerful extrinsic factors affecting prey population cycles (Hentonnen et al. 1987; Klemola et al. 1997). We previously showed that oestrous cycles were extended in Norway rats that were exposed to mink (*Mustela vison*) anal sac secretions (Voznessenskaya et al. 1992). Similarly, the duration of oestrous cycles was extended in bank voles (*Clethrionomys glareolus*) exposed to weasel (*Mustela nivalis*) odours (Koskela et al. 1996). Fewer bank voles bred when exposed to weasel odours relative to control voles not exposed to weasel odours (Ylonen 1989; Mappes and Ylonen 1997). In our earlier laboratory studies, we observed reductions in the litter size of Norway rats when they were exposed to predator chemical cues. Reductions in litter size are correlated with resorption of embryos and declines in plasma progesterone (Voznessenskaya et al. 1999, 2000).

The aim of this study was to determine the relationship between reproductive responses of the prey and the proximity and intensity of predator signals.

Materials and methods

The study was performed at the biological station ‘Tchernogolovka’, 50 km north of Moscow in 1998–1999. Eurasian lynx were kept in large enclosures and fed a diet of chicken meat, rats and voles. Four shelters for rats were constructed at different distances (2 m (n = 2), 25 m and

80 m) from the lynx enclosures. Rats from a laboratory outbred population (120 virgin females, 40 males) were used for the experiments. Animals were kept in groups of one male and three females. There were 11 groups of 4 animals at 2 m; 9 groups of 4 animals at 2 m, where the lynx urine was placed on the bedding; and 10 groups of 4 animals at each of 25 m and 80 m. Rats received rat chow and water *ab libitum.*

Each group of rats could not see any lynx but they could smell and detect their auditory signals. In addition, lynx urine was placed directly on the bedding of the rats' cages for one of the groups held 2 m from the lynx. We recorded the duration between pairing of animals and parturition, total number of pups for each litter, number of live pups for each litter, number of corpora lutea and number of placental scars for each female. Pre-implantation loss was recorded as number of corpora lutea versus number of placental scars. Post-implantation loss was counted as number of placental scars versus number of newborn live pups. We included stillborn pups and pups that died within a few hours of birth because of the mothers' mistakes or their birth injuries.

For the statistical analysis, the data for both experimental groups at a distance of 2 m were pooled and compared with the pooled data of the groups held at 25 and 80 m. Student's *t*-test was used to analyse the data with normal distribution and Fisher's test was used for analysis of percentages of pre- and post-natal losses. All indices were calculated for each group.

Results and discussion

Predator presence did not affect the percentage of females breeding (86.7–97%) in the two groups held within 2 m of a lynx. The addition of the lynx urine on the bedding of the rat cage did not decrease the reproductive success of females in comparison to the other group situated within 2 m of the enclosure. No significant differences in numbers of females giving birth were found for the experimental groups within 2 m of the lynx in comparison to the control groups (25 and 80 m). However, the average litter size was slightly less (about 7.4%) and the average number of live pups was significantly less in both experimental groups than in the control groups (Table 1). Estimated post-implantation losses (Fisher test, $T = 6.26$, $p < 0.001$) and pre-implantation losses (percent of non-implanted eggs) (Fisher test, $T = 2.44$, $p < 0.05$) were higher in the experimental groups than in the control groups. The average number of corpora lutea per female was similar for the experimental and control groups (Student *t*-test, $T = 1,10$, not significant). Analysis of the number of successfully implanted eggs (placental scars) showed that control females had significantly more scars than other females (*t*-test, $T = 11.43$, $p < 0.001$; 9.1% less in experimental groups). Total losses (calculated as number of live pups versus number of ovulated eggs) were almost twice as high in the experimental groups where almost two thirds of the ovulated eggs died at different stages of preg-

Table 1. Influence of distance from predator presence on reproduction of rats (mean ± standard deviation; numbers given in brackets = number of animals; * = $p < 0.05$, *** = $p < 0.001$)

Reproductive parameter	Distance from predator odour and sound			
	Experimental groups		Control groups	
	2 m	2 m + urine on bedding	25 m	80 m
Pregnant females (%)	97.0 (33)	96.3 (27)	93.3 (30)	86.7 (30)
Time interval (pairing–parturition) (days)	25.5 ± 2.9 (28)*	25.5 ± 2.4 (23)	25.0 ± 4.2 (27)	24.9 ± 4.5 (25)
Litter size (*n*)	8.9 ± 3.1 (29)*	8.5 ± 2.7 (24)***	9.4 ± 3.1 (28)	9.4 ± 2.8 (25)
	8.7 ± 2.9 (53)***		9.4 ± 3.0 (53)	
Live pups (*n*)	5.4 ± 4.0 (29)***	6.9 ± 3.8 (24)***	8.4 ± 3.7 (28)	8.7 ± 3.3 (25)
	6.1 ± 4.0 (53)***		8.5 ± 3.5 (53)	
Placental scars (*n*)	9.9 ± 3.7 (31)***	10.1 ± 2.9 (25)***	10.8 ± 3.6 (28)	11.2 ± 2.4 (26)
	10.0 ± 3.3 (56)***		11.0 ± 3.1 (54)	
Number of corpora lutea	12.9 ± 2.2 (15)	13.6 ± 4.4 (12)	12.5 ± 2.8 (8)	13.2 ± 2.2 (10)
	13.2 ± 3.3 (27)		12.9 ± 2.4 (18)	
Estimated pre-implantation losses (%)	23.8 (193)	29.4 (163)*	19.0 (100)	16.7 (132)
	26.4 (356)*		17.7 (232)	
Estimated post-implantation losses (%)	47.6 (288)***	33.8 (237)*	22.4 (303)	25.2 (290)
	41.3 (525)***		23.8 (593)	
Estimated total losses (%)	69.0 (171)***	51.3 (158)**	33.0 (100)	34.2 (117)
	60.5 (329)***		33.6 (217)	

nancy (eggs did not implant, embryos resorbed at different stages, pups died during or after parturition). Among the control females, significantly fewer ovulated eggs (less than one-third) were lost (Fisher's test, $T = 6.15$; $p < 0.001$).

Thus, pre- and post-implantation losses were higher for the experimental groups. It is possible that losses during both of these stages of pregnancy may be an important reproductive strategy for the prey in the presence of predator.

Litter size decreased significantly in rats exposed to domestic cat odours in the laboratory with a high percentage of embryos resorbed after implantation (Voznessenskaya and Naidenko 1999; Voznessenskaya et al. 1999). The resorption rate was probably due to a low level of progesterone in the blood plasma of rats exposed to cat urine (Voznessenskaya et al. 1999, 2000). This study in outdoor conditions with natural light and temperature provides an opportunity to estimate prey reproductive success with respect to intensity and proximity of predator signals. Some of the pups that died soon after birth had morphological deformities, which could have been due to partial resorption at the late stages of pregnancy.

In this study, female rats in close proximity to lynx had higher pre-implantation losses than control groups held at greater distances. Total losses in experimental groups were twice as high as in control groups. The presence of the predator affected pre-implantation losses, though not as much as the effects on post-implantation losses. Although the predator odour decreased reproductive success of Norway rat females (Voznessenskaya et al. 1999; Voznessenskaya and Naidenko 1999) the addition of lynx urine on the bedding of rats' cages did not increase the effect. Possibly the optimal reproductive strategy for rats under high predation risk might be to decrease reproductive output but not to stop reproduction.

The reproductive output of female rats measured as the number of live pups depended on intensity of lynx signals. Close proximity to the predator affected significantly the reproductive success of each female prey but it did not change the percentage of females reproducing as was described for voles (Ylonen 1989).

Conclusion

The concentration of lynx olfactory signals and/or the intensity of auditory signals significantly influenced the reproductive success of rats. Average litter size and number of live pups were lower in experimental groups. Prenatal mortality before and after implantation was lower in both control groups. Approximately two of three ovulated eggs failed during the pregnancy in experimental females, twice as high as in control females. The decrease in litter size and number of live pups in the presence of the predator might represent an adaptive response of female rats to the high intensities of predator signals.

Acknowledgments

This study was supported by the grants RB1 N 2036 of Civilian Research and Development Foundation, RFBR N 98-04-48865 and N 01-04-48411, RFBR-mas 02-04-06367, Russian Academy of Sciences (grant N 236 from Youth Committee), The Programme of Presidium of Russian Academy of Sciences 'Regulatory Systems' and Moscow Government grant N 1.1.205.

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Exploratory behaviour and response to olfactory cues by the *Mus musculus* species group: implications for the origins of Transcaucasian forms of *Mus*

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Abstract. A comparative experimental analysis of exploratory behaviour in different commensal taxa of the *Mus musculus* species group was conducted in a 4 × 4 × 1.5 m enclosure. The interior of the enclosure imitated a room with a table, a chair, plants, shoes and some other objects. The exploratory behaviour of the commensal Transcaucasian house mouse (a genetically intermediate form between *M. musculus* and *M. domesticus*) in a new territory was similar to that of other, closely-related commensal taxa. These results support the idea that Transcaucasian house mice are well adapted to a commensal lifestyle. In addition, these results are in correspondence with our previous hypothesis that populations of Transcaucasia have an ancestral genotype derived from an ancient form of *M. musculus*. There was no evidence that Transcaucasian house mice and other commensal taxa examined in two-choice odour tests could discriminate between conspecific and heterospecific urine. This suggests that their olfactory communicative systems are similar.

Introduction

The nature of species, the process of speciation and the efficiency of isolating mechanisms for speciation are important problems in evolutionary theory. The *Mus musculus* sensu lato species group includes closely-related taxa in different stages of divergence: sympatric species (*Mus musculus – M. spicilegus*, *M. domesticus – M. macedonicus*, *M. domesticus – M. spretus*); parapatric taxa which hybridise at their zones of contact *(M. musculus – M. domesticus – M. castaneus*); and allopatric species *(M. spicilegus – M. macedonicus*, *M. spicilegus – M. sprertus*). As a result, the *Mus musculus* species group has served as an excellent model group in studies of microevolution (Sage et al. 1993). In addition, this species group has been valuable in studies concerning pre-copulatory isolating mechanisms and their formation in phylogenesis and ontogenesis (Kotenkova and Naidenko 1999).

Electrophoretic analysis has shown that Transcaucasian populations of the house mouse have a mosaic distribution of *M. musculus* and *M. domesticus* genes (Milishnikov et al. 1990; Mezhzherin et al. 1998). Either the region is a zone of secondary contact between *M. musculus* and *M. domesticus*, with very wide introgression of *M. domesticus* genes into genome of *M. musculus* (Mezhzherin et al. 1998), or the populations are descendants of non-differentiated forms with a specific ancestral polymorphism (Milishnikov et al. 1990). There is an unusually large distribution of *M. domesticus* genes throughout the entire Transcaucasia (about 300 km^2). The origin of the Transcaucasian population is not clear and we discuss this problem elsewhere (Kotenkova, this volume).

The aims of this investigation were to: (i) compare the exploratory behaviour of Transcaucasian house mice, *M. musculus*, and *M. domesticus*, in connection with the orgins of Transcaucasian mice and their adaptation to the commensal lifestyle; and (ii) examine the ability of the Transcaucasian house mice to differentiate between the odours of conspecific and heterospecific urine of differentiated commensal taxa of the *Mus musculus* species group.

Materials and methods

Experimental animals

The comparative study of exploratory behaviour used 50 laboratory-reared individuals (F_1–F_5 generations) from five electrophoretically marked populations of mice. Among them were seven males and seven females from Transcaucasia, Botanical Garden of Batumi (Adjaria); six male *Mus domesticus domesticus* from Havana (Cuba); four male and six female *Mus domesticus praetextus* from Syria; five male and five female *Mus musculus musculus* from Moscow (Russia); and five male and five female *M. m. musculus* from the Kerch Peninsula (Ukraine).

In the two-choice olfactory discrimination experiments using urine odours, the adult mice used as test subjects included seven males and six females of a Transcaucasian population collected in Tbilisi, Georgia; eight male and eight female *M. m. musculus* collected in Moscow; 12 male C57Bl × CBA (laboratory strains, considered to be *M. domesticus);* and five male and seven female *M. d. praetextus* from Syria.

Species identification of experimental individuals was conducted according to morphological features and the area of their collection.

Design of experiments

Experimental analysis of exploratory behaviour was conducted in a 4 × 4 × 1.5 m enclosure. The interior of the enclosure was made more complex by imitating a typical room with a table, a chair, plants, shoes, glass on a table, different boxes, a bed, a besom, a bottle on the floor, a suitcase (in total, 24 objects) (Kotenkova et al. 1994; Meshkova et al. 1994). Mice were placed in the enclosure in pairs (male and female) except for the experiments with *M. d. domesticus* from Havana, in which only single males were used. They were initially placed into a shelter (small metal box from their home cage) during the evening period of maximal activity. Eight patterns of exploratory behaviour were recorded by the observer via direct narration into a tape recorder (Kotenkova et al. 1994; Meshkova et al. 1994; Table 1). This approach differs from the standard open field technique (Meshkova et al. 1994) and was designed to increase the ecological validity of the technique and the resulting data by decreasing subject stress during experiments. We used a free exploration situation in which subjects could enter the enclosure from the shelter when and if they chose to do so, using an increased test duration (2 hours after leaving the shelter) and providing time for a subject to express its full repertoire of behaviours.

For examination of olfactory preferences, two-choice odour tests were used. Animals were housed individually for 2 weeks before tests commenced and were unfamiliar with their test subject. Individuals were tested in their home cages using two plastic Petri dishes (35 mm in diameter). Two cellophane squares treated with the urine of conspecific and heterospecific strangers were placed in the dishes. The dishes were covered from above with mesh to prevent direct contact of mice with the source of the odour. A stopwatch, with accuracy to 0.1 s, was used to record the time mice spent investigating the odours in the first one to two activity periods after emergence of the test individual from its nest. After this time, mice, as a rule, did not investigate the odour sources. Individuals were tested 6–10 times with 2–3 days between tests. Each urine source was presented more than once, but was interspersed with others (Sokolov et al. 1984).

Urine collection

As animals were handled approximately 0.5–1 h before the beginning of a test, urine from each adult individual was collected in Petri dishes.

Statistics

Nonparametrical statistical tests (Mann–Whitney test for analysis of exploratory behaviour and Wilcoxon matched pairs test for two-choice odour experiments) were applied because data were characterised by a high level of variability. In previous studies, we have demonstrated that responses to conspecific and heterospecific urine odours in male and female mice were similar (Sokolov et al. 1984). As a result, we combined data for males and females in some two-choice experiments.

Results and discussion

In our previous comparative studies of exploratory behaviour in large enclosures with different interiors (including enclosures having many features in common with a human dwelling), commensal and outdoor populations of species of *Mus* had different strategies for exploring their environment (Kotenkova et al. 1994; Meshkova et al. 1994). Although commensal populations investigated the floor and practically all objects in the enclosure, outdoor

Table 1. Comparisons of patterns of exploratory behaviour of Transcaucasian house mice and commensal differentiated species and subspecies of *Mus musculus* species group.

Patterns of behaviour	*Mus domesticus domesticus*	*Mus musculus musculus* (Moscow)	*Mus musculus musculus* (Kerch)	*Mus domesticus praetextus*	Transcaucasian house mice
Latency of leaving shelter (min)	0.7 ± 0.2	11.2 ± 3.5	5.0 ± 1.3	0.5 ± 0.2	6.1 ± 1.1
Distance covered (m)	517.0 ± 53.0	428.5 ± 44.8	579.6 ± 100.3	338.4 ± 42.9	409.6 ± 79.2
Duration of activity (min)	134.7 ± 13.2	126.2 ± 9.3	131.3 ± 10.3	86.9 ± 13.0	101.1 ± 12.6
Number of contacts with objects	335.6 ± 35.6	143.6 ± 15.8	148.7 ± 25.8	146.4 ± 21.5	149.9 ± 27.6
Number of uprights	47.0 ± 15.0	8.6 ± 1.2	18.4 ± 3.2	13.0 ± 2.0	14.1 ± 3.8
Number of uprights with foreleg(s) on an object	184.7 ± 17.8	74.6 ± 12.8	84.3 ± 14.8	75.6 ± 12.3	39.1 ± 7.4
Number of climbs on objects	41.3 ± 6.6	9.1 ± 2.0	26.4 ± 6.9	12.1 ± 4.1	25.9. ± 6.8
Latency from leaving the shelter to first instance of climbing on object (min)	10.0 ± 4.1	37.5 ± 11.3	37.5 ± 11.3	22.3 ± 8.4	24.1 ± 0.9

populations investigated the floor and only some of the available objects. There were many other qualitative and quantitative differences between commensal and outdoor populations. These differences and adaptive character of exploratory behaviour in genus *Mus* was reviewed by Meshkova et al. (1994). From our previous results, we conclude that strategy and some features of exploratory behaviour (number and character of upright postures, the pace, number and features of climbing, the number and type of contacts with different objects) were adaptations to commensal or outdoor living conditions.

In the current experiments, all the house mice taxa examined demonstrated exploratory behaviour typical of commensal species (Table 1). They left the shelter quickly, ran to the wall and around the enclosure. In 15–30 minutes they had begun to investigate and climb on the various objects in the enclosure. Their locomotory activity was generally high but, overall, all *M. d. praetextus* spent a high proportion of their time in the shelter.

Pairwise comparisons of the behavioural patterns between all taxa (Table 2) revealed that the Transcaucasian house mice and *M. d. domesticus* differed significantly in four patterns. Transcaucasian house mice were less active when investigating new objects, were slower to leave the shelter, and demonstrated less uprights than did *M. d. domesticus*. The exploratory behaviour of the Transcaucasian house mice was more similar to that of *M. musculus*, there being only two significant differences with *M. musculus* from Moscow and only one difference with *M. musculus* from the Kerch Peninsula. They differed from *M. d. praetextus* in two behavioural patterns. As mentioned above, analysis of exploratory behaviour of commensal and free-living mice has demonstrated some differences in patterns of exploratory behaviour that closely correlate with ecology and lifestyle of species. If exploratory behaviour in commensal and outdoor mice is an adaptation to their living conditions, and the Transcaucasian populations show similar patterns and strategy to differentiated commensal species, we can suppose that these results support the idea that Transcaucasian house mice are well adapted to commensal living conditions. Previous studies of sexual behaviour and reproduction of Transcaucasian house mice in the field and in laboratory did not reveal lower fitness of males in comparison with *M. musculus* (Potanskyi and Kotenkova 1992). Indeed, all patterns of exploratory behaviour of Transcaucasian mice were similar to patterns in *M. musculus*. These results do not contradict our hypothesis that populations of Transcaucasian house mice have ancestral genotypes and could be one of the ancient forms of *M. musculus* (Kotenkova, this volume).

In all but one experiment, the individuals of parapatric commensal taxa spent the same amount of time sniffing at the two odour sources for all pair combinations. Hence, no preference was demonstrated for odours of one commensal species or the other. Mice from Transcaucasia also did not demonstrate a preference for either odour.

In previous studies, we demonstrated that individuals of sympatric (*M. musculus – M. spicilegus*) and allopatric (*M. spicilegus – M. macedonicus*, *M. musculus – M. spicilegus*) taxa could discriminate the urine odours of conspecifics and heterospecifics and preferred the odours of conspecifics (Kotenkova and Naidenko 1999). We supposed that the odours of these sympatric and allopatric species combinations differed strongly and proposed that responses to olfactory cues could be a pre-copulatory

Table 2. Significance of differences of patterns of exploratory behaviour in different taxa of house mice (Mann–Whitney test) (M.mus. = *Mus musculus*; M.dom. = *Mus domesticus domesticus*; M.pr. = *Mus domesticus praetextus*; Trans = Transcausasian house mice, + = $P < 0.05$, ++ = $P < 0.001$, NS = not signficant).

Patterns of behaviour	M.mus. (Moscow) – M.dom.	M.mus. (Kerch) – M.dom.	M.dom. – M.pr.	M.pr. – M.mus. (Moscow)	M.pr. – M.mus (Kerch)	M.dom. – Trans	M.mus. (Moscow) – Trans	M.mus. (Kerch) – Trans	M.pr. – Trans
Latent time to leaving the shelter (min)	++	++	NS	++	++	++	NS	NS	++
Distance covered (m)	NS	NS	NS	+	+	NS	NS	NS	+
Duration of activity (min)	NS	NS	+	NS	NS	NS	NS	NS	NS
Number of contacts with objects	++	+	++	NS	NS	++	NS	NS	NS
Number of uprights	++	NS	+	NS	NS	+	NS	NS	NS
Number of uprights with foreleg(s) on object	++	++	++	NS	NS	++	+	+	NS
Number of instances of climbing on objects	++	+	++	NS	NS	NS	+	NS	NS
Latency from leaving the shelter to first instance of climbing on object (min)	+	+	+	NS	NS	NS	NS	NS	NS

isolating mechanism in the *M. musculus* species group. Similar results were obtained for *M. musculus* from Bogemia and *M. domesticus* from Turkey (Munclinger and Frynta 1997). These findings suggest that because olfactory cues of these taxa are similar, they can hybridise in nature.

There is a narrow, 16–50 km wide, zone of introgressive hybridisation between *M. musculus* and *M. domesticus* in Central Europe and a well-studied zone of secondary contact (Sage et al. 1993) traversing different habitats through the Alpine and Balkan mountains and across the plains of Central Europe. It has been shown by electrophoretic analysis that Transcaucasian populations of house mice are genetically intermediate between *M. musculus* and *M. domesticus* (Mezhzherin et al. 1998). We analysed this problem (Kotenkova 2003; Kotenkova, this volume) and consider that Transcaucasian populations are the remains of an early-differentiated form of *M. musculus* that preserved its ancestral gene pool and in Adjaria has made secondary contact with already-differentiated *M. domesticus* from Turkey. House mice from Transcaucasia (Tbilisi, Georgia) did not demonstrate differences in the duration of investigation of urine odours of *M. musculus*, *M. domesticus* and other specimens from Transcaucasia in different pair combinations. In two-choice tests using odours deposited on bedding material from male and female *M. domesticus* (16th–17th generations from wild-caught animals trapped in Denmark), mice showed no preference either for their own species' odours or those of the other taxa. In contrast, *M. musculus* (7th–9th generations from the same locality) individuals and three types of hybrids (all female hybrids and males from crosses between *M. musculus* female and *M. domesticus* male) sniffed for the odours of *M. musculus* longer than those of *M. domesticus* (Christophe and Baudoin 1998). This difference could be explained by differences in the European and Transcaucasian hybrid zones (Mezhzherin et al. 1998).

Conclusions

Our experiments support two conclusions. First, the strategy used to explore new territory in the Transcaucasian house mice is similar to that of other commensal taxa. Second, there were no olfactory preferences shown by the Transcaucasian house mice and other taxa to each other's urine, suggesting similarity in olfactory communicative systems. These results support the idea that Transcaucasian house mice are well adapted to a commensal lifestyle.

Acknowledgments

This research was supported in part by grants 01-04-48283 from the Russian Foundation of Basic Research and Ja 0047 from the Center 'Integracia'. We thank the Organising Committee of the 2nd International Conference on Rodent Biology and Management for supporting our participation in this conference.

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Studies on neophobic behaviour in Norway rats (*Rattus norvegicus* Berkenhout, 1769) from farms in Germany

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Abstract. Results of field trials had shown differences in the amount of bait uptake among farm rat populations of the Münsterland area (Westphalia, Germany). This was assumed to be the result of differences in neophobic behaviour of the rats. Laboratory experiments were designed to determine whether differences in neophobic behaviour could be measured in rats originating from different farm populations. Wild rats live-trapped at the farms were adapted to an experimental room, where feed was offered inside two boxes. After the adaptation period, a new object (a device producing light and noise which switches on and off regularly) was placed in the preferred box. Consumption of food and time spent inside both boxes were recorded. The experiments were conducted both at the group and individual level.

The highest level of neophobic behaviour was found in rats stemming from very quiet locations without disturbance. The lower the level of neophobic behaviour, the more easily rats accepted several kinds of food. However, neophobic behaviour was much reduced if rats had to make a choice between a food source of low palatability and tolerating a new object. Our results suggest that behavioural characteristics of rat populations are long-lasting features that can be detected in the laboratory even after the rats have been kept in captivity for some time. The differences in behaviour observed in the laboratory using rats from these farms mostly reflected those observed previously in rats on the farms during field trials.

Introduction

During field trials in Münsterland, Germany, striking differences between a number of farm rat populations in response to rodenticides used during control operations became obvious (Pelz 1999). There are three main causes of failure in rat chemical control: physiological resistance to the poisons used, low palatability of the bait offered, and behavioural resistance or neophobic reactions. Various types of changes in their surroundings disturb the behaviour of rats, and this will lower the efficiency of control measures. Norway rats have a great suspicion of and alertness to change and unfamiliar objects in their environment (Shorten 1954).

Neophobic behaviour in rodents and birds was reviewed by Brigham and Sibly (1999). Based on this knowledge, an experimental study to observe the behaviour of Norway rats towards a device producing a combination of light and noise treatments was conducted. We examined differences in neophobic behaviour of Norway rats taken from several farms in the Münsterland area and acclimatised to the laboratory for up to a year. Rats were assessed either in groups or individually using the same (rolled oats) and different (rolled oats and plain oats) foods. In addition, tests were also conducted with individuals caught recently from two farms and not acclimatised to the laboratory.

Materials and methods

Conditions on farms where rats were removed

Conditions on each farm were recorded to determine the relationship between the results obtained in the experiments and the background experience of rats on the farms. The general conditions on each farm where the rats were caught are described in Table 1.

Experiment 1: testing for neophobic behaviour in groups of rats

Groups of 3–4 female rats were placed inside an experimental room of 12 m^2. All rats were individually marked by hair clipping on the back. The experimental room was provided with three wooden boxes with hay inside and a layer of straw along one side of the room to provide shelter. At the opposite side of the room, bait containers were placed on the left and right side and a water container in the middle. Feed and water containers were covered by opaque boxes (50 × 30 cm), leaving a 10 × 5 cm entrance facing the shelter-boxes (Figure 1). Rats were adapted inside this room by offering rolled oats *ad libitum*, in both bait containers for 3–7 days, until they showed a constant pattern of feeding behaviour based on the total amount of food consumed. This was reflected in a preference for either the left or right container.

In the next step, a new object was introduced into the preferred feeding box in the form of a device producing light (10 watt lamp) and noise which switched on and off regularly. Consumption of food from both experimental boxes was recorded. The trial was stopped when the total consumption in the treatment was equal to that before the device had been put inside the box. Each trial was run for 1–2 weeks.

Behaviour of the rats throughout the trial was recorded on videotape using infrared-sensitive video cameras. Adaptation time was determined as the interval between the first time the rats observed the device and the time they entered the box with the device. The lamp inside the experimental room was set up for 12 hours daylight and 12 hours red-light, automatically. The rats used in the trials were kept in the laboratory singly caged for up to one year after being trapped on particular farms. In contrast, rats in group 23B came from the same farm as those in 23A but were used shortly after they had been caught and without adaptation to the laboratory.

Experiment 2: testing for neophobic behaviour in individual rats

The same rats and method as in experiment 1 were used to test for neophobic behaviour in individual rats (experiments 2A and 2B). However, in experiment 2B, different food was offered *ad libitum* in the two bait containers, i.e. rolled oats, known to be highly palatable and plain oats, known to be of low palatability. Both foods were familiar to the rats because both were available to rats on the farms. A final test (experiment 2C) was conducted with 10 individual rats caught recently (not acclimatised to the laboratory) from the two farms from which rats had shown the most pronounced differences in neophobic behaviour in the previous tests.

Data analysis

Food consumption data were expressed as g of feed consumed/100 g of body weight (Marsh 1986). Statistical analysis of variance was done using SAS System for Windows v 6.12, followed by paired *t*-test and Tukey's test at $\alpha = 0.05$ to test the differences in food consumption, total and mean time spent in both experimental boxes, and adaptation time to the device among rats from different farms.

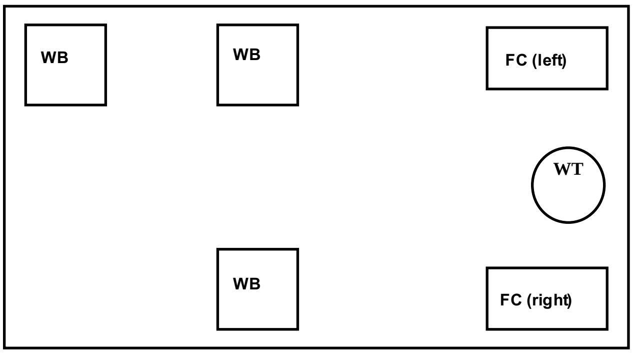

Figure 1. Layout of the experimental room (WB = wooden box, FC = box with feed container inside, WT = water container).

Results

In experiment 1, the rats from farm 4 showed the lowest level of neophobic behaviour, only in terms of consumption, but not in terms of total time spent in the box, or the adaptation time (Table 2). However, the rats from farm 23A spent the longest mean time in the box with the device, although it was not significantly different from the time spent by rats from farm 4. The rats from farm 3 showed the highest level of neophobic behaviour in all variables recorded. Rats adapted in the laboratory for a long time (farm 23A) did not show a different response in comparison with rats caught recently (farm 23B) in terms of food consumption, mean time in the experimental box, or adaptation time to the device.

In the individual test (experiment 2A), the rats from farm 4 again showed the lowest level of neophobic behaviour. The highest level of neophobia was observed in the rats from farms 3 and 5. In the adaptation time to the device, the same tendency as in the other variables was found, although there was a large variation. The same rats

Table 1. General conditions at the farms from where rats were taken for laboratory trials.

Type of farm	Disturbance	Effectiveness of rat control	Feed available	Farm numbers
I	High	High to moderate	Maize silage, pig feed, and cereal	3, 17, 23
II	Medium	High	Maize silage and cereal	9
III	Medium	Low	Maize silage, pig feed, and cereal	4
			Maize silage	14
IV	Low	Low	Maize silage and pig feed	5

used in both experiments (experiments 1 and 2A) showed no learned response to the experimental protocol. The suspiciousness and alertness of rats towards the device in the group experiment was similar to that shown in the individual experiment.

When food of different palatability was provided in the two boxes (experiment 2B), almost all of the rats consumed more food and spent more time in the box with the device where the highly palatable food was offered, than in the box without the device where the unpalatable food was offered. There was a large, although non-significant, difference between rats from farms 4 and 5. The rats from farm 4 immediately entered the box with the device, whereas those from farm 5 entered after 567 minutes. The same tendency was recorded with regard to the mean time spent in the box. The total time spent in the box by rats from farm 17 was the highest, however the mean time spent in the box was less than that of rats from farm 4. This discrepancy was caused by the frequent movement into and out of the box by rats from farm 17, indicating that those rats had a higher level of neophobia than rats from farm 4.

In experiment 2C, the newly caught rats from farm 4 again showed a lower level of neophobic behaviour compared with rats from farm 3. The differences were significant for consumption, and total and mean time spent in the box. Among the recently caught rats from farm 4, only two out of ten did not show a pronounced avoidance towards the device, whereas all rats from farm 3 showed strong avoidance.

Discussion

The rats showing the highest level of neophobia (experiment 2A) came from farm 5 which was quiet, dark and had an abundant food supply. Rats at that farm were reported to be very cautious and were quite suspicious in their approach to exploit new resources (Macdonald et al. 1999). This view was supported by the low level of effectiveness of rat control at that farm. The neophobic behaviour of rats from this farm observed in our laboratory experiments may explain the difficulties in achieving satisfactory control using compounds like difenacoum or brodifacoum. The low efficacy in rat control on that farm could not be explained by resistance problems (Quy et al. 1992).

As already discussed by Macdonald et al. (1999), an abundant supply of alternative food and a stable environment are probable explanations for the reluctance of rats to consume new food, thus demonstrating a higher level of neophobia. In contrast, rats from farm 4 showed the lowest level of neophobic behaviour, both in the group

Table 2. Consumption of feed, total and mean time spent in the feeding box with the device and adaptation time in tests with groups of rats and individuals. Means in the same column in the same experiment followed by the same letter were not significantly different according to Tukey's test (experiments 1, 2A and 2B) or paired *t*-test (experiment 2C), $\alpha = 0.05$.

Farm number (no. of rats)	Consumption (g/100 g of body weight)	Total time (minutes)	Mean time (minutes)	Adaptation time (minutes)
Experiment 1				
3 (4)	0.05 ± 0.08 c	1.11 ± 0.83 b	0.26 ± 0.18 b	444.13 ± 432.44 a
4 (3)	3.69 ± 0.07 a	97.19 ± 9.56 a	1.94 ± 0.08 ab	8.00 ± 6.00 b
5 (6)	0.57 ± 0.36 c	20.45 ± 18.30 b	0.61 ± 0.16 b	190.38 ± 230.14 ab
9 (3)	0.34 ± 0.67 c	14.70 ± 20.39 b	0.50 ± 0.17 b	111.83 ± 128.32 b
17 (3)	0.28 ± 0.28 c	12.57 ± 7.81 b	2.45 ± 1.45 ab	69.00 ± 111.20 b
23A (3)	1.50 ± 0.45 b	93.46 ± 48.57 a	3.87 ± 4.38 a	115.00 ± 110.82 b
23B (4)	0.84 ± 0.38 bc	33.55 ± 16.40 b	1.77 ± 0.68 ab	28.25 ± 39.49 b
Experiment 2A				
3 (3)	0.57 ± 1.18 a	11.23 ± 15.19 b	0.51 ± 0.80 d	403.26 ± 580.79 ab
4 (3)	2.31 ± 1.43 a	59.92 ± 41.14 a	10.74 ± 10.19 ab	1.40 ± 1.67 b
5 (3)	0.38 ± 0.72 a	1.68 ± 3.43 b	1.31 ± 3.50 cd	719.91 ± 708.78 a
9 (4)	2.08 ± 1.74 a	34.55 ± 26.08 ab	5.52 ± 3.56 abcd	293.80 ± 604.34 ab
17 (3)	2.07 ± 1.88 a	38.69 ± 40.07 ab	6.90 ± 5.63 abc	149.15 ± 398.68 ab
23B (3)	1.22 ± 1.44 a	15.41 ± 19.04 b	1.22 ± 1.70 cd	540.13 ± 719.90 ab
Experiment 2B				
3 (3)	4.54 ± 0.58 a	32.88 ± 68 b	1.50 ± 1.08 a	170.75 ± 135.33 a
4 (3)	5.23 ± 1.29 a	94.54 ± 15.86 ab	12.45 ± 11.85 a	0.00 ± 0.00 a
5 (3)	2.67 ± 2.84 a	27.65 ± 26.34 b	7.77 ± 6.96 a	567.67 ± 677.31 a
9 (4)	1.60 ± 2.38 a	25.06 ± 21.62 b	7.82 ± 8.96 a	41.5 ± 75.21 a
17 (3)	4.30 ± 2.93 a	113.65 ± 48.54 a	7.52 ± 2.86 a	59.67 ± 103.35 a
23B (3)	5.82 ± 0.35 a	42.61 ± 21.20 ab	3.23 ± 3.09 a	46.67 ± 80.83 a
Experiment 2C				
3 (10)	0.06 ± 0.11 b	0.43 ± 0.69 b	0.07 ± 0.10 b	951.47 ± 662.73 a
4 (10)	0.92 ± 2.30 a	5.49 ± 12.86 a	0.38 ± 0.95 a	884.08 ± 668.88 a

and individual experiments (1 and 2A). Rat control at this farm was very efficient and could be achieved within a very short time. The high level of neophobia in rats from farm 9, particularly in using food of different palatability (experiment 2B), was reflected in the difficult control situation at that farm. It took 27 weeks to control rats with poisoned bait, while only 2–14 weeks were required at other farms. Mitchell et al. (1977) reported that rats in frequently controlled areas generally showed a higher level of neophobia.

At farms with rats of a higher level of neophobia, there were only two kinds of food available compared with at least three kinds of food at farms with a lower level of neophobia. The combination of the variability of food supply and environmental changes may be important in the determination of neophobia in animals. Rats were found to be trapped easily on landfill refuse areas, where the frequently changing environment renders a neophobic strategy impossible (Boice 1971).

Rats reacted sensitively to bait quality in our experiments. Using food of different palatability, rats preferred to consume the most palatable food (rolled oats), despite the presence of the sound and light device around the feed and in contrast to the experiments using an identical food supply in both bait containers. However, differences related to the origin of the rats remained but were not significant. These results are in accordance with findings by (Mitchell et al. 1973).

The results of our experiments with wild-caught rats kept in the laboratory for 12 months suggest that behavioural characteristics of rat populations are long-lasting features that can be detected in tests with individuals in the laboratory. Rats from farm 23 (23A and 23B) showed similar reactions to the new object, irrespective of the time since capture.

Experiments with individual rats offered a good indication of the level of neophobia prevailing in the rat population from which they were derived. Experiments with individuals are thus preferable to experiments with groups, where social interaction may influence and probably change the behaviour of the rats. Three important factors that may govern the neophobic behaviour are: genetically enhanced neophobia, experience, and the stability of the environment (Macdonald et al. 1999). The differences in the level of neophobia in rats in this study were very likely caused by the experiences of the test animals on the farms.

Our final trial (experiment 2C) was designed to check the validity of the results from the previous experiments, where the sample size had been low and rats had been used repeatedly. The results of this experiment with ten recently caught individuals concurred with the results of our previous experiments (experiments 1, 2A and 2B).

Conclusions

Three factors at the farms could have affected the levels of neophobia observed in rats in the laboratory, i.e. disturbance, effectiveness in rat control, and feed availability. The lower the level of the neophobic behaviour in rats, the more easily rats accepted several kinds of food. The rats with a high level of neophobia came from quiet locations, without disturbance, and where rodent control was practised frequently. The differences in the behaviour of rats observed in the laboratory reflected the differences observed in rats on farms during field trials (Pelz 1999).

Acknowledgments

We thank J. Klatte and E. Kampling for technical help with the trials and for keeping the test rats and N. Klemann for valuable information and discussions. The studies of S. Priyambodo were supported by a grant from Bogor Agricultural University, Bogor, Indonesia in cooperation with the Centre of Tropical and Subtropical Agriculture and Forestry, University of Göttingen, Germany.

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Monitoring activity patterns and social interactions of small mammals with an automated event-recording system: wild house mice (*Mus domesticus)* as a case study

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Abstract. We have developed an automated event-recording system based on passive integrated transponder (PIT) technology and have used it to monitor the passage of small mammals in and out of burrows. Rod-shaped antennae were inserted into burrow entrances of wild house mice, *Mus domesticus*, so that an event was recorded when a mouse carrying a PIT tag was active at one of these burrow entrances. Sixteen antennae were used at one time, each linked to a reader unit and data-logger station. The unique identity code of the PIT tag as well as the date, time and duration of each event were recorded. To illustrate the potential uses of this system, we compared the daily timing of mouse activity for males and females and described the use of burrows by individuals over a nine-month period. The system has great potential to be adapted for use with other species and to record events at various focal points of activity. The strengths and weaknesses of the system are reviewed.

Introduction

The ability to follow movements of small mammals and monitor social interactions between individuals can be vital for understanding the mechanisms underlying dynamics of populations and behaviour of animals. Free-ranging populations present particular challenges due to their relatively unrestricted movements and the potentially high abundance and turnover of individuals within the study area. This study aimed to investigate the spatial dynamics of wild house mice, *Mus domesticus,* and hence needed a system that could satisfy five criteria. These were the ability to: (1) mark a large number of individuals with a unique and permanent tag; (2) recognise each tag with minimal interference to the behaviour of an animal; (3) pinpoint when and where a tag was detected; (4) record all of this information and have it easily accessible; and (5) be used at remote locations regardless of weather conditions. A system based on passive integrated transponder (PIT) technology satisfied these criteria.

PIT tags consist of a microchip encapsulated in small, bio-compatible glass tubes that can be implanted into individual animals under the skin. PIT tags employ radio frequency identification (RF-ID) technology (see Prentice et al. 1990 for a detailed explanation). These passive tags have no internal power supply; they are energised when they come in close proximity of an electromagnetic field generated by an antenna. The tag modulates this frequency signal in a precise way so that when the reader detects this reply signal, the tag's unique identification number is decoded. The use of PIT tags for identifying individuals has been compared with other forms of marking in many rodent species. PIT tags have been recommended as safer and more humane than other available techniques (Rao and Edmondson 1990; Ball et al. 1991) and recommended as a more reliable marker because of lower rates of loss or misinterpretation (Schooley et al. 1993; Harper and Batzli 1996). PIT tags have the additional benefit that, unlike external markers, they do not modify the appearance of the animal.

A further advantage of PIT tags is the ability to monitor free-living animals passing near a stationary reader antenna. Such systems have been used to monitor rodents, though predominantly in captive populations. The difficulty with monitoring individuals from free-living populations is the short detection range of the readers; which is approximately 50 mm, depending on tag orientation to the antenna (Elbin and Burger 1994). Hence, to ensure tags come into close proximity with the antennae, studies on wild populations of rodents have provided artificial feeder stations as a focal point of activity (Quy and Cowan 1996; Dell'Omo et al. 1998) or have taken advantage of existing runways (Harper and Batzli 1996).

This paper describes a custom designed and built system based on PIT technology that can monitor patterns of activity of small mammals at entrances to burrows. The system was designed for small mammals with a minimum body mass of 4.4 g—the first reported use of a PIT system for monitoring the field activity of animals weighing less than 25 g. Burrows were selected, as they are thought to be a key limiting resource for populations of house mice, *Mus domesticus*, in Australia (Newsome 1969) as well as important points for social interactions (Crowcroft and Rowe 1963). Also, this approach would provide a seasonal index of circadian activity of mice to assist planning and interpretation of studies that use radio-tracking for measuring patterns of movement at a landscape level. We present results on activity patterns and social interactions of house mice to illustrate the potential of this system.

Materials and methods

System description

The automated event-recording system (Francis Scientific Instruments, Cambridge, United Kingdom) was a stand-alone system, capable of functioning in remote locations and after modification was capable of withstanding extremes of weather. It consisted of five main components: a PIT tag, a sensor or antenna unit, a decoding unit, a multi-channel data-logger unit and a power source (Figure 1). The system was designed for Identichip brand PIT tags by 4D Technologies (0.07 g, 11.4 mm long by 2.1 mm diameter, supplied by Veterinary Marketing Network, Wahroonga, New South Wales, Australia). Identichips use Zoodiac H4005 microchips by Sokymat that are energised at the standard International Standards Organisation (ISO) frequency of 134.2 kHz.

For ease of insertion into burrows, rod-shaped antennae measuring 50 mm long and 11 mm diameter were designed and constructed for this study. Each rod-antenna coupled to a decoding electronics box that served as a reader. Antennae and electronics boxes were constructed incorporating weatherproof casings. Four readers were connected to a four-channel data logger via 25 m long cables (cables may be up to 100 m in length without loss of signal). The data-logger and four readers were powered by one 75 Ah 12 V deep-cycle battery that lasted up to 8 days of continual use between recharges. Both battery and data-logger were housed in a ventilated shelter that could be moved between sites. Records stored on each data-logger were downloaded onto a portable IBM compatible computer and records could then be interrogated using commonly available spreadsheet or database software. Four such units were used, bringing the total number of readers to sixteen.

For the system to record the activity of a mouse, the PIT tag must be within the generated electromagnetic field (approximately 50 mm from the antenna) for at least 25 ms (Prentice et al. 1990). If two or more tags are within the field, only the strongest reply signal will be detected with RF-ID technology. The interval between records of detected PIT tags with this system is less than 2 s and records are timed in increments of 1/16th second (62.5 ms). One ‘event’ was considered to encompass the period from when a mouse entered the detected range of the antenna to when it left. In other words, records with the same PIT tag code were considered part of the same ‘event’ if an interval between any two successive records was no greater than 2 s. The duration of each event was determined as the interval from the beginning of the first record to the end of the last record.

Field study

The monitoring study was conducted in the agricultural landscape surrounding the Mallee Research Station, Walpeup, in north-western Victoria, Australia (35°07.5'S, 142°00.5'E). This region has a Mediterranean-type climate with typically cold, wet winters and hot, dry summers. Mice were live-trapped using Longworth traps at the interface between a wheat crop, its boundary stock fence, and an adjacent pasture field. This was conducted at 6 sites, each 100 m long, for 4 consecutive nights on 12 occasions from October 2000, early in the breeding season, to peak population abundance in June 2001. PIT tags were injected subcutaneously by lifting a scruff of skin between the shoulder blades, inserting the 12-gauge needle (3 mm diameter) behind the ears pointed slightly downwards and towards the posterior of the animal. The trigger of the inserter tool was then squeezed, forcing the PIT tag into the space between the skin and the body wall. PIT tags and needles were sterilised in 70% ethanol and dried before use. No anaesthetic or suture was required and animals regained normal activity immediately. A hand-held reader was used to verify that PIT tags functioned after implantation and to record the PIT tag number

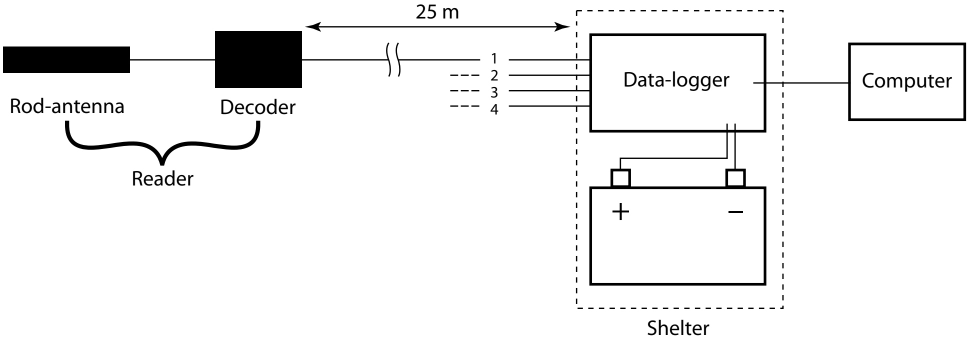

Figure 1. Schematic layout of the automated event-recording system.

of newly captured and recaptured animals. Early in the study, animals with new PIT tags were held for several minutes to ensure the tags were not lost. However, because tags were always retained within this time period, animals were subsequently released at the point of capture without being detained. Tagged animals ranged in body mass from 4.4 g to 35.0 g.

Burrows were monitored with the event-recording system for four consecutive nights immediately after each trapping period at each site. Trapping was never conducted while burrows were monitored. Open burrows with signs of activity were selected for monitoring. The entire antenna was positioned inside each burrow entrance (entrance diameters were approximately 50 mm) then pressed into the base and covered with soil. Therefore, only mice passing into, out of, or deeply investigating a burrow would be recorded. If there were more active burrows than readers at a site, readers were relocated so that as many burrow entrances were monitored within a 4-day period as possible. Each burrow entrance was monitored for at least 24 consecutive hours.

The effectiveness of the system for detecting tags that passed within range of the antennae was assessed by video observations between January and April 2001. A Sony TRV99E video camera with inbuilt infrared light source and time stamp was set on a tripod with a view of the burrow entrance and antenna approximately 30 mins before official sunset. The camera was left to continuously record for 3 hours when mice became active. Events viewed on video were compared to events recorded by the system at the same time and location.

Statistical methods

A two-tailed Kolmogorov–Smirnov goodness-of-fit test was used to determine if distributions of times of activity for each sex belonged to populations with the same distribution.

Results and discussion

PIT tags proved to be an effective marking and identifying technique for mice and are seen to be especially beneficial for long-term studies. Of 1452 PIT tags implanted into mice, 740 were recovered by trapping marked mice. Of the mice recaptured, 13 were missing their PIT tag (1.8%) and 1 animal had a replacement PIT tag missing. There were no observed tag failures. This loss rate is lower than that reported for laboratory mice (5%, Rao and Edmondson 1990), free-ranging *Spermophilus townsendii* (5%, Schooley et al. 1993) or free-ranging voles, *Microtus ochrogaster* and *M. pennsylvanicus* (5%, Harper and Batzli 1996). In the current study, a higher proportion of PIT tags were retained as the handler gained experience in the implanting technique. Of the 14 tags found missing, 8 were inserted by a handler who had inserted less than 200 PIT tags.

The temporal and spatial activity of mice was successfully recorded at multiple burrows. The automated event-recording system detected the activities of 1123 mice on a total of 37,199 occasions ($\overline{X}$ = 33.1 events per animal) over 8 months. Mice were predominantly nocturnal, exhibiting activity throughout the night with the greatest proportion of their activity in the first 2 h after sunset (Figure 2). Event times have been presented relative to sunset because the length of each night varies across the year. Males and females were active in a significantly different distribution of times ($D_{\max}$ = 0.069, D_{crit} = 0.014, $p < 0.05$). 26% of male activity versus 20% of female activity was concentrated in the first 2 h after sunset.

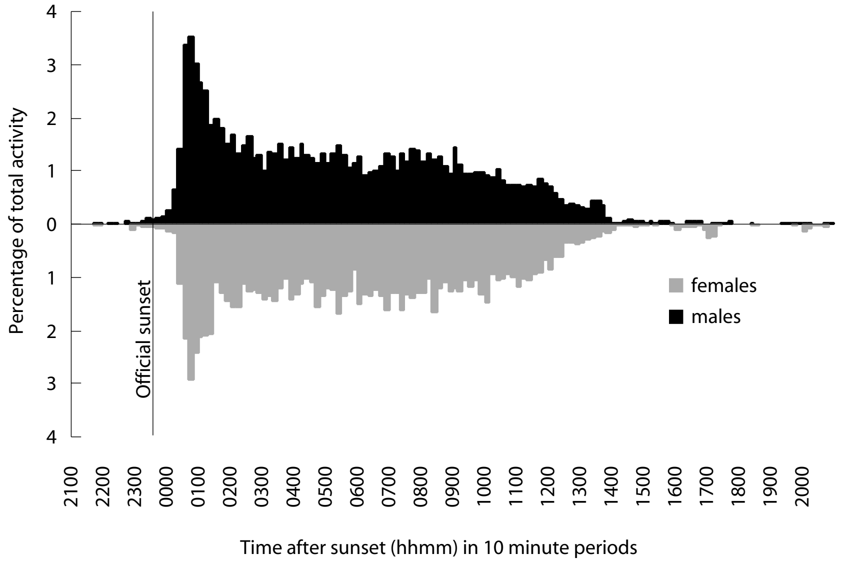

Figure 2. Percentage of the total activity across 24 h that occurred in each 10 minute interval after official sunset for male (black bars) and female (grey bars) mice (*Mus domesticus)* between October 2000 and June 2001. The total number of events recorded was 19,257 for males and 17,942 for females.

Potential interactions between mice may also be observed with this system. Burrow activity was monitored for 1148 reader-nights and activity was recorded at 295 burrows. These data will be analysed in a companion paper in relation to temporal changes in the demography of the population. We found that the number of different individual mice that entered, exited or investigated the same burrow within 24 h ranged from 1 to 44 (median = 3.5, $\overline{X}$ = 4.8; Figure 3). Furthermore, individual mice were detected visiting between 1 and 19 different burrows within a distance of 100 m over a 96 h period (median = 3, $\overline{X}$ = 3.8; Figure 4). We detected a large number of social interactions using this system. This daily activity profile reflects those of previous studies of confined mice. In captivity, many nest boxes are visited by several individual mice per night, either as a territorial patrol or for seeking potential mates (Crowcroft and Rowe 1963). This may have a profound influence on gene flow through the population (Singleton and Hay 1983).

Automated event-recording systems based on PIT technology provide detailed information on the temporal and spatial activity patterns of marked individuals. Such information may be obtained by radio-tracking, however at a far coarser level and not to the same degree of accuracy as PIT technology (activity at one particular burrow entrance to the nearest 1/16th second) nor for the same study duration (PIT tags are not limited by battery life). Importantly, studies using automated PIT technology can monitor the activity of a much larger proportion of the population than radio tracking due to the lighter weight of PIT tags, the lower cost of each tag and the relatively less amount of effort required to collect data. Moreover, any animal greater than 4.4 g can be monitored with these systems, whereas there is a weight limitation of 13 g for

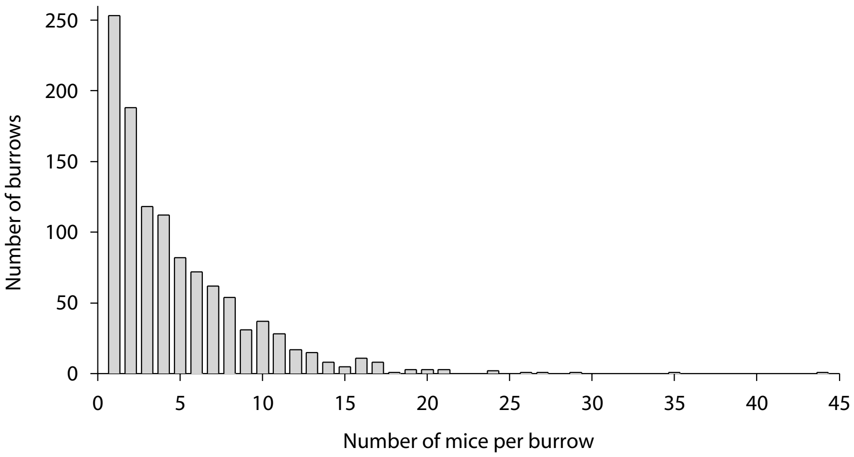

Figure 3. Number of different mice (*Mus domesticus)* tagged with a passive integrated transponder (PIT) tag that visited the same burrow entrance during a 24 h period. The total number of 24 h periods was 1114. Only visits by individuals tagged with a PIT tag were monitored. Mouse density was approximately 100 to 500 mice per hectare during the study

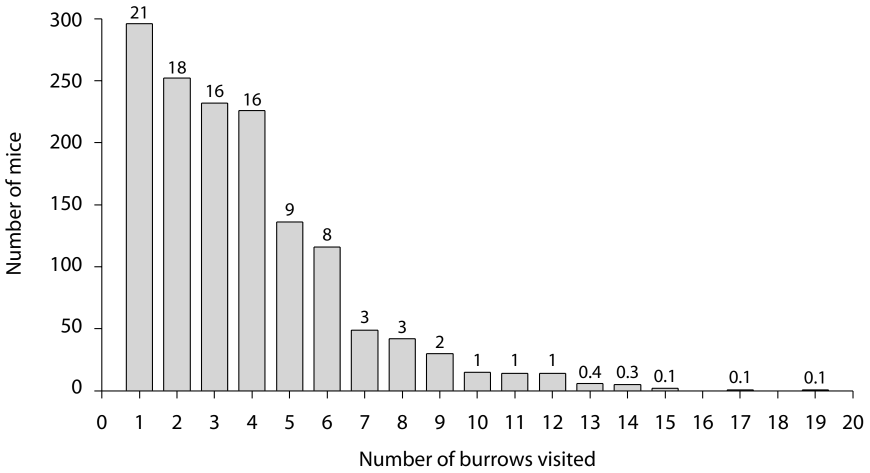

Figure 4. Number of burrows visited by one individual over a 96 h period. The percentage of total monitored mice visiting multiple burrows is indicated above each column. The total number of 96 h periods was 66; the total number of mice monitored was 1437.

mice with current radio-tracking technology (Chambers et al. 2000). Consequently, PIT technology presents the opportunity to monitor important population events such as juvenile dispersal in mice. PIT technology may also enhance a trapping study because it is not necessary to recapture animals to monitor their activity. Individuals within a population that have a low probability of recapture may continue to be monitored for their presence and movements within the study area. In this case study, we were able to monitor the activity of an additional 396 mice that were never recaptured but were detected with the event-recording system. We were also able to repeatedly detect the same individual mice on up to 22 different nights over a period, in one case, of almost seven months. Hence, PIT technology will enable further assessment of mouse activity and of any differences in the trappability of mice both between seasons and between habitats.

In addition, an alternative arrangement of this system can permit the direction of movement to be determined by placing two antennae in series along the path of movement (for examples, see Brannas et al. 1994; Burns et al. 1997). Assuming an animal does not return by some other route, the sequence of successive events will reveal the direction of an animal's movement. The system was sensitive enough to detect an interval between events of 62.5 ms or greater, however to prevent the two antennae from interfering with the electromagnetic field generated by each, they must be placed at least 200 mm apart. We did not use two antennae in series to determine the direction of movement in this study for two reasons. Firstly, antennae could not be forced 200 mm into mouse burrows due to frequent bends in the tunnels, and secondly, two antennae in series effectively halved the number of burrows that could be monitored at one time. Hence, PIT technology is capable of monitoring similar, yet at the same time quite distinct, information when compared to radio-tracking. When choosing between these technologies, though, it is worth considering that although PIT tags are far less expensive than radio transmitters, the high initial cost of the PIT reader system makes this system comparatively inexpensive only when large numbers of animals will be monitored.

The most significant drawback of the event-recording system is that animals not marked or that have lost their PIT tags are not recorded. The extent of this error will be a function of the trappability, and/or the intensity of trapping effort, of the study population because the rate of tag loss was relatively low. This error was estimated for the period between January and April 2001 by observing activity at 15 monitored burrows for 43 h with a video recorder. The assumption was made that the animals visiting burrows represent a random sample of the population. Video observations revealed that the system was reliably detecting individuals marked with PIT tags, including those moving at great speed and when multiple individuals passed in rapid succession. The activities of mice were recorded 398 times on video within range of the antenna, however only 31% of those events were of mice marked with a PIT tag. It appears that although the system was accurately recording the activities of marked individuals, during the video observation periods a significant proportion of the population was being missed.

Some technical problems were experienced with this automated event-recording system. Firstly, some reader errors were detected, though most were easily accounted for. Most were events containing identification codes with non-numeric characters or zero values. Occasionally, legitimate codes were recorded that did not correspond to PIT tags used to mark mice in the study. The causes of these errors were unknown. Secondly, metal objects interfered with the electromagnetic field generated by the antennae reducing the range of detection. This problem was isolated to large metal objects like fence posts that were within approximately 50 mm of an antenna. Lastly, the data-loggers provided with this system were not waterproof and were sensitive to extremes in temperature and humidity. Therefore, ventilated shelters were necessary to keep the data-loggers and batteries dry and cool. With these modifications, the system continued to function well in ambient temperatures ranging from –1.2 to 43.7°C as well as a maximum 24 h precipitation of 18.4 mm.

Conclusion

The event-recording system with PIT technology as described can monitor the identity, timing and location of activity for a large proportion of a population at fine temporal and spatial scales. Automated systems allow researchers to collect data over extended periods with relatively little effort. Although this system was designed to monitor activity patterns and potential interactions between individuals at burrow entrances, many additional applications exist for this technology. For example, marked individuals can be detected at various focal points of activity such as nests, resting locations, regular paths for movement, latrines, food sources or perhaps bait locations. Any location of interest to the researcher may be used. The direction of movement to or from these points of interest can also be determined, allowing the researcher to determine the location of the individual relative to the antennae. Interactions at these points may be detected both within and between target species. Furthermore, PIT technology is still developing. The reader range is increasing with either larger tags or battery-assisted tags (for examples, see Hutching and Harris 1996; Boarman et al. 1998). The technology may also be integrated with other technologies such as automatic scales (Boisvert and Sherry 2000), temperature probes or infrared motion detectors. The applications found for this technology and the insights gained with its use will only increase.

Acknowledgments

We wish to thank Ivan Mock and the staff at the Mallee Research Station, Graeme Wakefield, Neil Corbett, Roy Wakefield, and Bob Latta for all their support and for allowing us to conduct this study on their properties. For their assistance in the field, we particularly thank Vanessa Guthrie, Jason Cody, and Jacqui Richardson. Invaluable advice was given by Mike Francis and Roger Quy pertaining to the design of the system. Helpful comments were made on earlier drafts by Gordon Sanson, Charley Krebs and Laurie Twigg. This research was funded by the Pest Animal Control Cooperative Research Centre and the CSIRO/University Collaborative Grant Scheme.

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Predation risk and behaviour during dispersal: implications for population dynamics of rodents

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Abstract. Models of predation risk assume that animals that are more exposed to predators are at a higher risk of mortality. Young animals may behave in a more 'risky' way than older animals, thereby exposing themselves to a greater degree of risk. But do such behaviours have implications for the population dynamics of a prey species? I explored this idea for juvenile arctic ground squirrels in the boreal forest at Kluane, north-western Canada, from 1992 to 1995. First, I tested whether radio-collared juvenile squirrels that moved further, on average, between regular radio-telemetry fixes during dispersal had higher mortality from predation than those with shorter inter-fix distances. Results supported this hypothesis: (1) movement rates of squirrels that survived to hibernation were significantly lower than movement rates of squirrels that died from predation and (2) juvenile males, which had faster movement rates, were more likely to die from predation than juvenile females. Second, I did a sensitivity analysis using a stage-based simulation model of the population dynamics of ground squirrels to determine which of eight demographic parameters had the strongest effect on the instantaneous rate of population increase (r). Survival of adult and juvenile females had the strongest influence on r in the model, which concurred with a strong relationship between observed survival of juvenile female squirrels and rates of population increase at Kluane from 1992 to 1995. Individuals with behaviours that expose them to predators (such as greater movement rates) increase their chances of mortality. Furthermore, such behaviours can have a strong effect on a prey species' population dynamics, a result that explains the observed multi-annual fluctuation in arctic ground squirrel populations at Kluane, synchronous with the 10-year snowshoe hare cycle.

Introduction

Models of predation risk assume that animals that spend more time exposed to encounters with predators have a higher risk of mortality (Sinclair and Arcese 1995). Animals are assumed to be able to assess the potential risk of being killed by a predator, and alter their behaviour to reduce this risk (Hik 1995). However, behavioural responses to predation risk may change with sex, age, and reproductive condition. For example, young animals may be especially vulnerable to predation because they may not have learned appropriate strategies to avoid predators. Can these observed differences in behaviour be linked to mortality from predation, and subsequently to population dynamics?

Arctic ground squirrels (*Spermophilus parryii plesius*) are a burrowing, ground-dwelling, polygynous sciurid rodent inhabiting much of northern Canada, Alaska, and Siberia. They are found primarily in open meadows and tundra, but part of their range includes boreal forest at Kluane in the south-western Yukon Territory (61°N, 138°W), where the population dynamics of this species are closely linked to the 10-year snowshoe hare (*Lepus americanus*) cycle (Krebs et al. 2001). In terms of biomass, arctic ground squirrels are the second most common herbivore at Kluane, providing an extremely important food source for predators during the summer months (May through to August or September). The main predators of squirrels are lynx (*Lynx canadensis*), coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), and great horned owls (*Bubo virginianus*). Squirrels hibernate for about 7 or 8 months during winter (October through April), so during the short active season, squirrels are primarily concerned with reproduction and fat storage for the coming winter. Juvenile squirrels born in the active season remain in a natal burrow for about 28 days before emerging, and have only a few months to disperse from their natal area, establish a new territory, and gain enough weight to survive to spring.

I measured movement rates and behaviour of dispersing juvenile squirrels in order to quantify the level of risk (exposure to predators) for each individual squirrel during dispersal. Exploratory movements made during dispersal differed between male and female squirrels (Byrom and Krebs 1999). Juvenile males moved in longer increments, whereas females made shorter movements. Here I examine the consequences of these two general types of dispersal behaviour by relating them to a known risk of predation. I also examine the consequences for the population dynamics of the species as a whole, and link this to observed changes in squirrel numbers at Kluane during a snowshoe hare cycle.

Methods

Study sites and field methods

Dispersal movements of 172 juvenile arctic ground squirrels were studied on three 9 ha sites (see Byrom and Krebs 1999 for a description of study sites at Kluane) from 1993 to 1995, and one site from 1992 to 1995. Squirrels were radio-collared on experimental and control sites, but there were no differences in movement rates between treatments or years (A. Byrom, unpublished data) so data were pooled for this paper. Expandable radio-collars were fitted to juvenile squirrels after emergence from the natal burrow at 35–40 days of age and squirrels were radio-tracked through to hibernation (from mid-June to mid-August each year). Each squirrel was radio-tracked by an observer on foot with a hand-held yagi antenna every 2 days. Predation was deemed a relevant cause of death because 97% of radio-collared squirrels died from predation (Byrom and Krebs 1999).

Statistical analyses

For each squirrel, the distance between each radio-telemetry fix and the subsequent fix was recorded using a Trimble Basic global positioning system (GPS) (fix locations were differentially corrected using a base station at Kluane Lake Research Station). Movement rates were estimated by calculating the average distance between fixes for each squirrel. Movement rate data were examined for normality and homoscedasticity and transformed where appropriate. Data that satisfied these assumptions were analysed using conventional parametric tests. Data that violated assumptions of normality even after transformation were analysed using nonparametric tests (Sokal and Rohlf 1995). Movement rates of squirrels that were lost (presumably because they moved far off the study area and the transmitter signal could not be heard) were treated separately.

Simulation model: sensitivity of *r* to demographic parameters

A stage-based simulation model of arctic ground squirrel populations at Kluane (created in Microsoft Excel 5.0) was used to determine the sensitivity of the instantaneous rate of population change (r) to eight demographic parameters (litter size, survival of juveniles below ground, survival of juveniles and adults during hibernation [over winter], survival of adult males and females during the active season [summer], and survival of juvenile males and females during the active season). The annual cycle of activity and hibernation was compartmentalised into 12 one-month periods, with the population densities of adults and juveniles calculated monthly and multiplied by a survival parameter. Juveniles that survived over winter were recruited into the adult population at the beginning of the active season each year. Squirrel population density was calculated in spring each year by adding the separate population densities of adult males and females. The instantaneous rate of population change was calculated as $r = \ln[N(t+1)/N(t)]$. To measure sensitivity of r, each parameter was varied individually while all others were held constant. Parameter values were increased or decreased, for example by ±10%, ±20%, and ±30%. In some cases, it was necessary to change parameter values by 1% increments. Each simulation was run for 20 years or until r reached an asymptote.

Results and discussion

Movement rates of juvenile arctic ground squirrels

All movement rates presented refer to the distance moved by squirrels every 2 days. Juvenile arctic ground squirrels that survived to hibernation moved shorter distances between fixes than squirrels that were killed by predators or were lost during dispersal (Figure 1). The average distance between fixes for surviving juveniles was 51.8 ± 4.6 m ($n = 97$) (mean ± se) whereas for juveniles that died the average distance between fixes was nearly twice as great, 86.2 ± 11.4m ($n = 43$). This difference was significant ($t = -3.36$, df = 138, $p < 0.0001$).

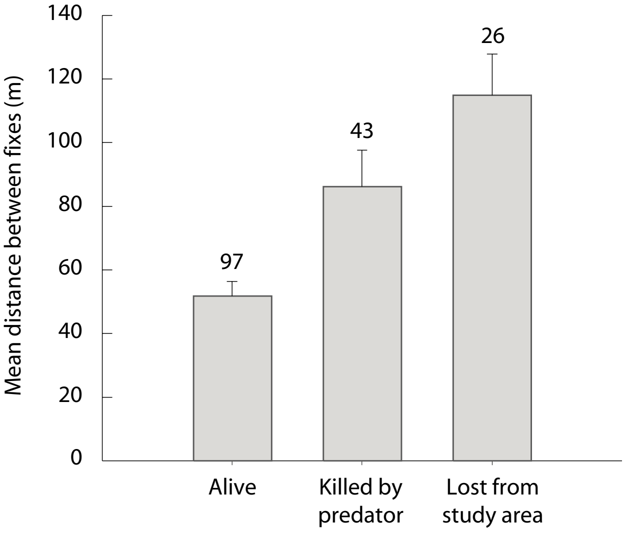

Figure 1. Movement rates (measured as the mean distance between radio-telemetry fixes taken every 2 days, ± se) of juvenile arctic ground squirrels that survived to hibernation in their first active season, squirrels that were killed by predators, and squirrels that were lost (radio-transmitter could no longer be heard and presumably squirrels moved far off the study area). Numbers show sample sizes in each category.

Juvenile males (whether they survived or were killed by predators) had faster movement rates than juvenile females (males: 100.7 ± 9.0 m [$n = 69$]; females: 47.5 ± 3.9 m [$n = 96$]). This difference was significant ($t = 1.97$, df = 162, $p = 0.000$). Overall, juvenile males that survived moved an average of 93.9 ± 15.5 m ($n = 22$) between fixes, while juvenile females that survived moved an average of 39.4 ± 2.5 m ($n = 75$). Juvenile males that were killed by predators moved an average of 105.8 ± 10.9 m ($n = 47$), while juvenile females that were killed by predators moved an average of 76.5 ± 13.8 m ($n = 21$). Differences between males and females were significant (surviving squirrels: Welch's $t = 3.75$, df = 24, $p = 0.001$; squirrels killed by predators: $t = 2.35$, df = 66, $p = 0.022$). Movement rates of juvenile males that survived did not differ significantly from those of males that died (Welch's $t = -1.14$, df = 32, $p = 0.26$), but movement rates of juvenile females that survived were significantly lower than those of females that died (Welch's $t = -3.22$, df = 29, $p = 0.003$).

The results reported here support the hypothesis that faster movement rates result in increased exposure to predators. Models of predation risk assume that animals that spend a greater proportion of time at risk are more likely to die from predation, but an empirical link between risky behaviour and mortality has rarely been reported. Fitzgibbon (1994) described aspects of Thompson's gazelle (*Gazella thomsoni*) behaviour that increase their susceptibility to predation, such as being more solitary, less vigilant, and more likely to be found at the edge of a group. Sommer (2000) reported lower survival in male rats (*Hypogeomys antimena*) as a result of males moving greater distances and encountering predators more frequently. Holekamp (1984) suggested that frequent exploratory excursions by juvenile Belding's ground squirrels (*Spermophilus beldingi*) might enable individuals to familiarise themselves with an area before settling permanently (although she did not provide an empirical link between survival and movements). Results of this study focus on specific aspects of rodent behaviour during dispersal that predispose individuals to higher rates of predation, and provide a plausible mechanism linking the behaviour of individuals to population-level consequences.

Sensitivity of *r* to demographic parameters: implications for population dynamics

In the model, r was highly sensitive to survival of female squirrels (both adults and juveniles) during summer. For example, a 10% increase in summer survival of juvenile female squirrels resulted in a 13% increase in r. Comparable changes in r with a 10% increase in parameter values were: adult female survival, 37%; survival of adults over winter, 5%; litter size, 4%; survival of juveniles pre emergence in summer, 4%; survival of juveniles over winter, 4%; survival of adult males in summer, 1%; and survival of juvenile males in summer, 0%. This result makes intuitive sense. Female squirrels influence population trends in two ways: directly (higher survival means greater population density) and indirectly (through recruitment). Coupled with the polygynous social structure of arctic ground squirrels, the observed high mortality of female squirrels with the fastest movement rates would create strong selection pressure on females to remain close to their birthplace whenever possible. Conversely, male survival had less overall effect on r. This suggests that the potential fitness benefits for males that successfully establish new territories must be relatively high in order to outweigh the chance of predation as a result of faster movement rates.

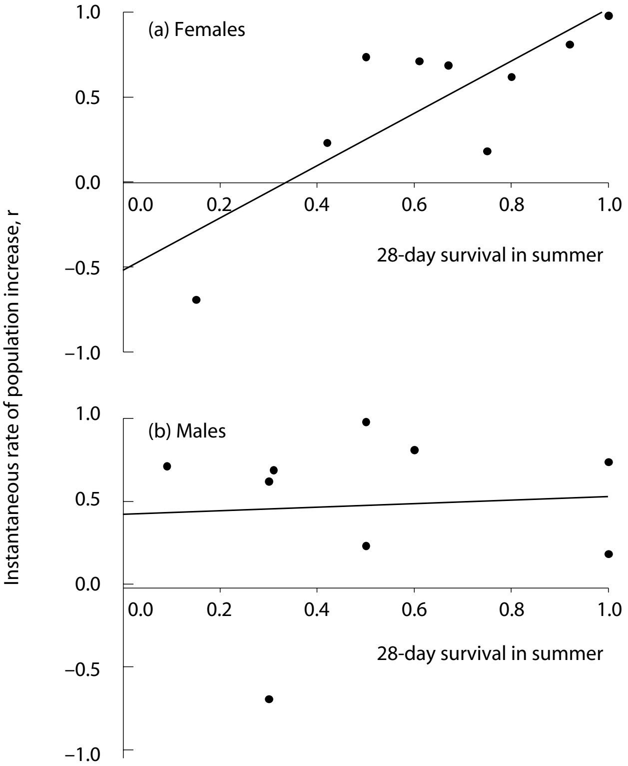

Figure 2. Instantaneous rates of population increase (r; measured annually in spring each year) for (a) juvenile female ground squirrels and (b) juvenile males as a function of survival per 28 days in summer. Rates of increase were measured in each of 3 years at one site (1992/93, 93/94, and 94/95) and in each of 3 years at three sites, giving a total of nine data points.

The findings from the model were verified by plotting observed rates of population increase of arctic ground squirrels from 1992 to 1995 as a function of summer survival of juvenile female and male squirrels (emergence from the natal burrow to hibernation, estimated using Kaplan–Meier survivorship) (Figure 2). There was a strong significant relationship between survival and r for females ($r^2 = 0.64$, F = 12.29, df = 7, $p = 0.01$) but not for males ($r^2 = 0.004$, F = 0.03, df = 7, $p = 0.87$). This result may explain the observed synchronicity between arctic ground squirrel populations at Kluane and snowshoe hare population cycles. With the decline in snowshoe hare numbers, predation pressure on alternative prey increases dramatically, and arctic ground squirrels provide a substantial biomass of alternative prey during summer (Krebs et al. 2001). Rates of population increase in arctic ground squirrels were lowest when predator numbers were highest (Byrom et al. 2000) and predation during summer was largely responsible for the observed decline in arctic ground squirrel populations (Boonstra et al. 2001).

Conclusion

This study is one of the first to confirm the common assumption of predation risk models that individuals that expose themselves to risk will suffer higher losses from predation. Juvenile arctic ground squirrels with faster exploratory movement rates during dispersal were more likely to die from predation than squirrels with lower rates of movement. The behaviour of individual squirrels and the resultant effect on their survival (through predation) can be linked to observed cyclic fluctuations in squirrel numbers entrained by predators at Kluane during a snowshoe hare cycle. The link between behaviour of individual rodents and their population dynamics has implications for management of rodents both as pests and as threatened species.

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Strategies of aggressive fighting reflect degree of sociality in three species of gerbils

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Abstract. Animals living in communities should develop non-injurious ways of conflict resolution. A comparative study of aggressive fighting strategies in closely related species provides a good approach to investigating this statement. In the present study, we observed intraspecies male–male conflicts in a neutral arena for three species of gerbils, graded on their levels of sociality, from the least social, the pallid gerbil, *Gerbillus perpallidus*, to the much more social Mongol gerbil, *Meriones unguiculatus*, and great gerbil, *Rhombomys opimus*. From videotapes, we estimated winner–loser distances, and the duration of interactions and non-aggressive intervals between them, using 1 s scan sampling method. We found that patterns of aggression showed prominent interspecies differences. Great gerbils used a strategy of conflict delay—using, for the most part, very weak distant threats and standing immobile in static postures for a long time, with rare short blocks of contact threats or overt aggression. Mongol gerbils used a strategy of quick, short interactions, often in tactile contact. Rivals utilised threat postures or moved simultaneously, keeping the inter-individual distance unchanged. Pallid gerbils showed a very hard strategy of fighting, characterised by high levels of overt aggression, with fast changing of both distances between individuals and behavioural actions. We concluded, that male–male fighting strategies are in good agreement with species-specific social organisations in these gerbils.

Introduction

Gerbils (Gerbillinae) are a compact group of rodents, living in desert and semi-desert areas of Asia and Africa. This group has important agricultural and epidemiological significance, because they live on grazing areas, forage on grass and seeds, and are hosts of epidemical diseases that affect both humans and livestock. Gerbils represent a uniform group, possessing similar morpho-physiological adaptations for living in arid environments (Pavlinov et al. 1990). However, different gerbil species show high variability in their use of habitats, construction and use of hides, food, day/night activity and spatial-ethological structure. The discrepancy between similar external appearance and similar physiological adaptations to living in arid conditions, on the one hand, and high variability in social structures, on the other hand, makes this group very promising for comparative behavioural research, such as the evolution of sociality (Goltsman et al. 1994).

Extraction of stereotyped postures from behavioural observations is not the best approach to revealing interspecies differences, because most of important behaviours may be described only by using parameters of the entire behavioural continuum (Golani 1976, 1992; Moran et al. 1981). In our study, gerbils' ethograms are very similar, and behavioural differences are found mostly in kinematic characteristics, such as duration of behavioural actions, speed, and acceleration of speed during movements (Goltsman and Borisova 1993; Volodin and Goltsman 1998). In the present study, we tested aggressive conflicts in three species of gerbils differing in sociality—two social species, the great gerbil, *Rhombomys opimus*, and Mongol gerbil, *Meriones unguiculatus*, and a solitary species, the pallid gerbil, *Gerbillus perpallidus*, in order to compare differences in aggressive behaviour in these species in relation to their sociality.

Materials and methods

We videotaped intraspecies male–male conflicts in a neutral arena. We conducted 21 tests for the great gerbil, 26 tests for the Mongol gerbil, and 20 tests for the pallid gerbil. All of the 15 great, 26 Mongol and 20 pallid male gerbils were adult, captive-born animals, housed with 1–2 females or with females and their offspring (Volodin et al. 1996). Tests were made among unrelated and unfamiliar conspecifics in a plastic enclosure 76.5 cm × 58 cm × 65 cm.

A short time after the beginning of the test, one of the males becomes the winner and the second one becomes the loser, and this asymmetry is retained until the end of the test (Goltsman and Volodin 1997). From videotapes, we measured winner–loser distances, and the duration of aggressive interactions and non-aggressive intervals between them using a 1 s scan sampling method (Altmann 1974). In total, 34,022 s for great gerbils, 29,856 s for Mongol gerbils and 15,308 s for pallid gerbils were sampled. Thus, we analysed 355, 781 and 331 aggressive interactions and 340, 760 and 301 non-aggressive intervals for the great, Mongol and pallid gerbils, respectively.

Results

In all three species, male–male conflicts occurred as aggressive interactions interspersed by non-aggressive intervals (Figure 1). In turn, aggressive interactions could be broken down into distant threats, contact threats, and fighting and chasing.

The percentage of time spent in aggressive interactions decreases progressively in the order great > Mongol > pallid gerbils (Figure 2). However, the severity of the aggressive interactions showed a reversed pattern: fighting and chasing and contact threats took more time in the pallid gerbil in comparison to the Mongol gerbil, and more time in the Mongol gerbil in comparison to the great gerbil, which had the maximum percentage of distant threats. All the differences were significant ($p < 0.001$, White *t*-test).

Aggressive interactions were significantly longer in the great gerbil than both in the Mongol and in the pallid gerbils ($p < 0.001$, Mann–Whitney *U*-test), whose duration of aggressive interactions did not differ (Figure 3). Non-aggressive intervals were the shortest in the Mongol gerbil (Figure 3).

Distant threats were longest in the great gerbil, intermediate in the Mongol gerbil, and shortest in the pallid gerbil and all differences were significant ($p < 0.001$, Mann–Whitney *U*-test; Figure 2). The duration of contact threats and fighting and chasing were more similar between species, but the difference was still significant between the Mongol and pallid gerbils ($p < 0.01$, Mann–Whitney *U*-test) (data not shown).

During aggressive interactions, the great gerbil usually keeps a distance from 0.1 to 0.75 body lengths from his opponent, whereas the Mongol and pallid gerbils maintain a shorter distance of tactile contact. All the differences were significant ($p < 0.001$, White *t*-test) (Figure 4).

Figure 2. Total percentage of time the gerbil species spent displaying different behaviours during aggressive interactions—fighting and chasing, contact threats and distant threats—and non-aggressive intervals between aggressive interactions.

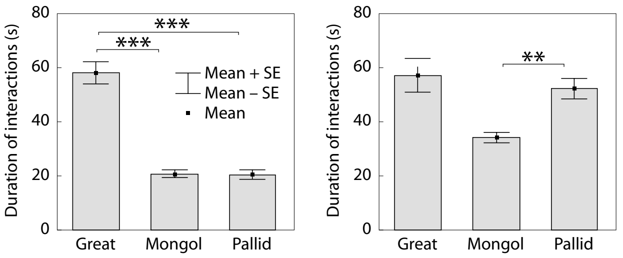

Figure 3. Duration of aggressive interactions and non-aggressive intervals (mean ± se) in the three gerbil species, where *** = $p < 0.001$; ** = $p < 0.01$.

Distance changing rates during non-aggressive intervals were similar in all the three species. In contrast, the distance changing rates during aggressive interactions did differ significantly between the species and graded from the most in the pallid gerbil, through intermediate in the Mongol gerbil, to the least in the great gerbil ($p < 0.001$, Mann–Whitney *U*-test) (Figure 5). It is interesting that in the great gerbil, the distance changing rate was much lower during aggressive interactions than during non-aggressive intervals ($p < 0.001$, Wilcoxon *t*-test); in the

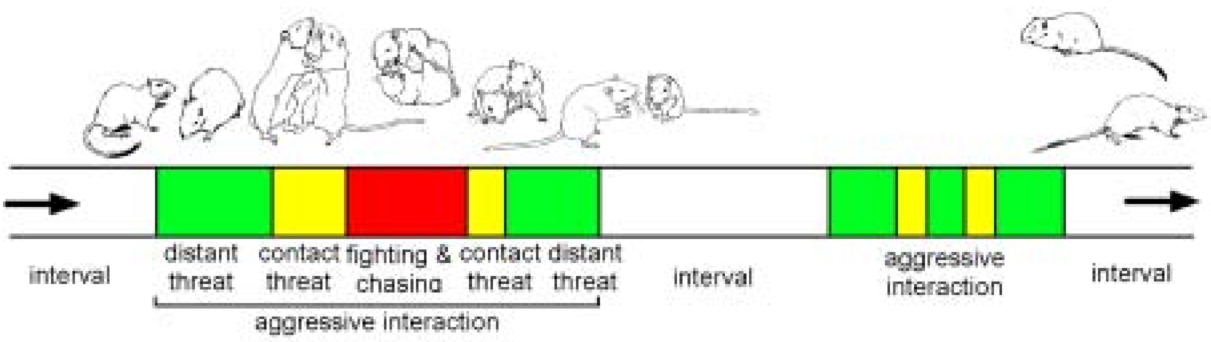

Figure 1. Schematic illustration of a sequence of actions among combatants during male–male conflicts in the three gerbil species observed in the study. Gerbil postures (from left to right): lateral threat posture (distant threat); boxing (contact threat); fighting; displacement (contact threat); frontal threat posture (distant threat); out of aggressive interaction (non-aggressive interval).

pallid gerbil, the relations were reversed ($p < 0.05$, Wilcoxon *t*-test); and in the Mongol gerbil, the rates were similar in both the cases.

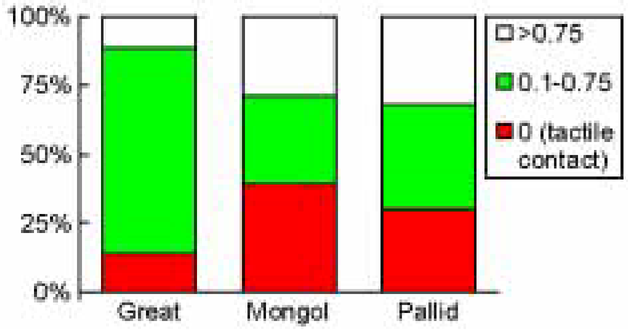

Figure 4. Total percentage of time keeping different winner–loser distances during aggressive interactions in the three gerbil species. Units of body length are the measure of distances.

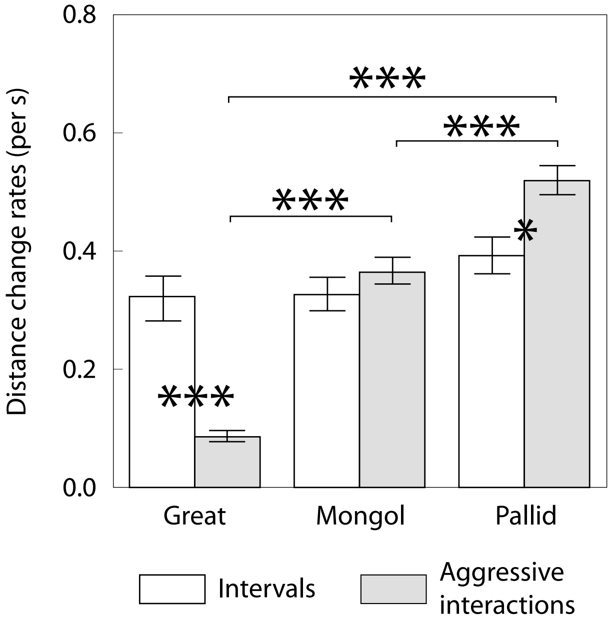

Figure 5. Rate of distance change during non-aggressive intervals and aggressive interactions (mean ± se) in the three gerbil species, where *** = $p < 0.001$; * = $p < 0.05$.

For the great gerbil, aggressive interactions were characterised by long immobility of both combatants, keeping a constant distance apart without body movement (static keeping of a constant distance apart) (Figure 6). In total, the great gerbils remained immobile more than 80% of the time during interactions. The aggressive strategy of Mongol gerbils was intermediate between the great and pallid gerbils: 39% of the time they were immobile, 22% keeping a constant distance by using synchronised movements (mobile but keeping a constant distance apart), and 39% of the time in changing the distance apart. In contrast, pallid gerbils mainly 'danced' around each other, changing the distance apart every 2 s of an interaction. Even when the distance apart was constant, pallid gerbils were immobile only 26% of the time, and spent nearly equal time in synchronised movements that maintained a constant distance apart. All the differences were significant ($p < 0.001$, White *t*-test, excluding mobile keeping of distances in the Mongol and pallid gerbils).

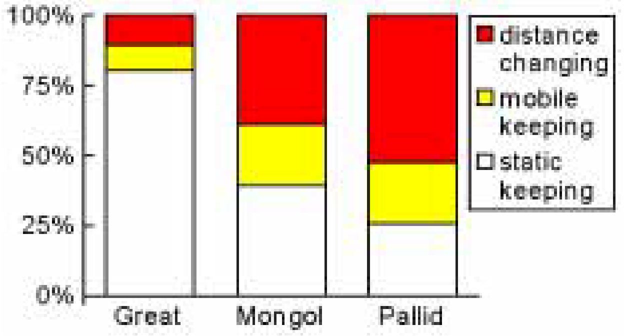

Figure 6. Total percentage of time gerbils spent with the winner–loser distance changing, mobile but keeping a constant distance apart, and static keeping of a constant distance apart during aggressive interactions in the three gerbil species.

Discussion

The differences we found in observing male–male conflicts represent distinctive species-specific strategies of aggressive fighting, graded in severity in accordance with degree of sociality in the species studied. The most social species, the great gerbil, used a strategy of a conflict delay, utilising for the most part prolonged distant threats, with rare, short periods of contact threats or fighting and chasing. Mongol gerbils used a strategy of quick and short aggressive interactions. Rivals showed threat postures or moved simultaneously, keeping a constant distance apart. The solitary pallid gerbils showed a severe strategy of aggressive fighting, with much fighting and chasing, and rapid changing of both distances and orientation.

Psychological intimidation is a very important aspect of aggressive fighting, and these interspecies differences may be discussed from the viewpoint of resistance to social suppression from a conspecific male (Goltsman et al. 1994; Goltsman and Volodin 1997). We hypothesised that more prolonged aggressive interactions demand more resistance from the participants. The time spent in aggressive interactions was the most in the great gerbil, intermediate in Mongol gerbil, and least in the pallid gerbil. Therefore, accordingly to our hypothesis, species-specific strategies of aggressive fighting show that the great gerbil possesses the highest resistance to social suppression, Mongol gerbil an intermediate resistance, and pallid gerbil the lowest one.

The enhancing of resistance may be among the mechanisms that promote the adaptation of animals to exist in social environments of high density. The differences we discovered in resistance to social suppression are in good agreement with the species-specific degree of social density in natural populations (Pavlinov et al. 1990; Goltsman et al. 1994). The observed data on differences in strategies of aggressive fighting in these three species suggest the existence of behavioural mechanisms correlated with social organisation in gerbils. In an ecological framework, these mechanisms may be among the factors that determine population density in gerbils in nature.

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The influence of predator odours and overcrowded mouse odours on regulation of oestrous cycles in house mice (*Mus musculus*)

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Abstract. We investigated the influence of chemical signals derived from different sources—urine of feral cats (*Felis catus*) and urine from overcrowded mice (*Mus musculus*) on regulation of oestrous cycles in *Mus musculus musculus* under laboratory conditions.

Cat urine and urine from mice housed in overcrowded conditions caused very similar effects. Application of urine from feral cats and from overcrowded conspecifics to the bedding of experimental animals for a period of 21 days caused a significant increase in numbers of animals with extended oestrous cycles. Application of cat urine or overcrowded mouse urine to the bedding of female mice caused an extension of oestrous cycles in 56.0% and 62.5% of tested animals, respectively.

The results of the present study and other experimental data from our laboratory may indicate that predator urine and urine from overcrowded conspecifics share the same chemical information.

Introduction

Mammals are known to avoid predator odours (Muller-Schwarze 1983; Weldon 1990; Ylonen et al. 1992; Eppli et al. 1993; Jedrzejwski et al. 1993). More than 10 years ago, the presence of predator urine was shown to decrease activity patterns in rodents (Sullivan et al. 1988). The mechanism of repellency is putatively a fear-induced avoidance response by rodents (potential prey) to the urine characteristics of predators on meat diets, i.e. the double-bonded sulfur and amino by-products of protein digestion (Nolte et al. 1994). In our investigations of the effects of predator urine on rodent behaviour, we found that exposure of rats (*Rattus norvegicus*), mice (*Mus musculus*), and voles (*Clethrionomys rutilus*) to predator urine significantly reduced the reproductive output of these rodents. Previously, we demonstrated that oestrous cycles were extended in Norway rats exposed to mink (*Mustela vison*) anal sac secretions (Voznessenskaya et al. 1992) and urine of feral cats (Feoktistova et al. 2001). Similarly, Kostela et al. (1996) found there was an extension of the duration of oestrous cycles in bank voles (*Cletrionomys glareolus*) exposed to weasel (*Mustela nivalis*) odours.

If food becomes limiting, rodents will begin catabolising their muscle protein and so their urine would contain larger amounts of protein digestion products (Swick and Benevenga 1977; Baracos et al. 1983). These signals could serve to trigger mechanisms that would curtail reproduction.

In the present work, we compare the effects of feral cat urine and urine from mice housed in overcrowded conditions on the regulation of oestrous cycles in house mice under laboratory conditions.

Materials and methods

Test subjects were 36 mice of 4–6 months of age from an outbred laboratory population. Before the experiments, females were housed singly in standard plastic cages. Each cage was placed in individual box (size 70 × 20 × 35 cm) with a separate ventilation system for every animal. Air-flow from different cages did not mix at any stage of the experiment.

Experimental rooms were illuminated on 12:12 hours light:dark schedule, and maintained at 20–22°C. Food and tap water were provided *ad libitum*.

Oestrous cycles were quantified by taking vaginal smears for 21 days before treatments (3–4 complete cycles). After the different types of treatments, oestrous cycles were monitored for a further 21 days. We used two basic treatments: (1) urine from feral cats (*Felis catus*) and (2) urine from overcrowded mice (*Mus musculus*). For the control group of animals (water treatment), we monitored oestrous cycles for the duration of the experiment (42 days).

Urine from feral cats (*F. catus*) was used as a source of predator chemical cues. The cats used in the experiment normally hunt for mice and have mice in their diet. If needed, additional meat was added to their diet. Freshly voided urine was frozen (22°C). Once defrosted, urine was used only 1–2 days. Non-predator urine was obtained from house mice (*M. musculus*). Individuals ($n = 12$) of both sexes were placed in a standard cage for 14 days before urine collection. Food and water were available *ad libitum*. Mice were placed into metabolic stainless steel cages, overnight, and urine was collected and stored using the method described above.

Urine (0.5 mL) (corresponding to specific treatment) or water was put directly onto the bedding of female mice every day for the duration of the treatment. For the first group ($n = 12$) water only was used. For the second group ($n = 12$) water was applied for the first 21 days, then cat urine was applied for the next 21 days. For the third group ($n = 12$) water was applied for the first 21 days, then urine from overcrowded conspecifics was applied for the remaining 21 days. The number of females with extended oestrous cycles relative to both of the controls was recorded. Also we recorded the number of times animals were in oestrus for each group for the period of manipulation (21 days).

Differences among treatment groups were determined using the *t*-test (Student criterion) and Fisher test (STATISTICA, StatSoft Inc., Tulsa, Oklahoma, 1999).

Results and discussion

Cat urine applied every day to the bedding of female mice for a period of 21 days caused a significant ($p < 0.001$) increase in the numbers of animals with extended oestrous cycles relative to control animals (Table 1). Urine from overcrowded conspecifics applied to the bedding of female mice on a daily basis had even greater effect. In this case, 62.5% of female mice had extended cycles relative to the control animals. For both treatments, the duration of the delay to the next oestrus ranged from 2 to 14 days. The average number of oestruses is shown in Table 1. We observed regular cycles for all animals in control group. The number of oestruses was significantly reduced ($p < 0.001$) in animals exposed to the cat urine and in the group treated with urine from overcrowded conspecifics ($p < 0.001$).

Conclusions

The results of the present study suggest that predator (feral cat) urine and urine from overcrowded mice may share similar information about unfavourable conditions for reproduction. The responses are similar to those reported in previous studies on rats, mice and voles (Feoktistova et al. 2001; Voznessenskaya 2002; Voznessenskaya et al., this volume). Mice respond to chemical cues of different origin in the similar manner: reducing numbers of cycling animals and lowering the probability of pregnancy.

The chemical cues of cat urine and urine from mice housed in overcrowded conditions may be due to each containing some similar chemical components as a result of protein digestion in carnivores and muscle catabolism in overcrowded rodents (e.g. sulfur-containing compounds, amino acids, and peptides) (Nolte et al. 1994).

Acknowledgments

This study was supported by the grant from Russian Foundation for Basic Research #01-04-48411 and Program of Presidium of Russian Academy of Sciences “Regulatory Systems”.

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Table 1. The influence of cat urine and urine derived from overcrowded conspecifics on the number of periods of oestrus during the treatment period in *Mus musculus*.

Treatment	Number of periods of oestrus pre-treatment (21 days)	Number of periods of oestrus during treatment (21 days)	Percentage of animals with extended oestrous cycles
Control (water only)	4.2 ± 0.1	4.3 ± 0.2	0
Cat urine	4.3 ± 0.2	3.0 ± 0.2	56.0
Overcrowded mouse urine	4.8 ± 0.3	3.0 ± 0.3	62.5

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Effectiveness of controlling fecundity and survival on rodents with different life history traits

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Abstract. The finite rate of increase of rodents is sensitive to changes in the key life history traits of fecundity and survival. We used matrix population models to manipulate fecundity (fecundity control) and survival (mortality control) and measured the effectiveness of these two alternative control approaches. Our results indicate that increased mortality through the use of rodenticides is more effective for rodents sensitive to survival, whereas fecundity control is more effective for rodents of high fecundity (frequent recruitment and long breeding seasons). Therefore, different life histories of rodents could influence the effectiveness of fecundity control and mortality control (e.g. use of rodenticides). Knowledge of life history characteristics of species should be considered in estimating population dynamics for management and conservation of different species of rodents.

Introduction

Life history traits of rodents vary considerably and are adapted to environmental influences. Vital rates such as fecundity and survival contribute differently to the population dynamics of rodents. For instance, the finite rate of increase can be more sensitive to changes in fecundity than survival in some rodents, whereas population growth rates are more sensitive to changes in survival in other species. Hereafter, we use the term ‘fecundity-sensitive’ to refer to the former, and the term ‘survival-sensitive’ to refer to the latter. The management or control of pest rodents is aimed to either reduce fecundity with contraception or increase mortality by applying rodenticides (Chambers et al. 1997; Sinclair 1997). However, differences in the sensitivity to changes in fecundity and survival to population growth rate may cause differences in the effectiveness of fecundity control (decreasing reproduction) and mortality control (decreasing survival) among rodent species. It seems reasonable to hypothesise that the fecundity-sensitive rodents would suffer greater reduction in population growth rate from fecundity control than from mortality control, but the survival-sensitive rodents would undergo a larger reduction in population growth rate from mortality control. This hypothesis has not been tested. Our objective was to test the above hypothesis using matrix population models. Mathematical models have been shown to be useful in formulating pest control strategies (Stenseth 1981).

Methods

Study species

We chose three rodent species, *Microtus californicus*, *Clethrionomys rufocanus* and *Mastomys natalensis*, for this study. *M. californicus* is a fecundity-sensitive species, whereas *C. rufocanus* and *M. natalensis* are survival-sensitive species (see the Results section). In addition, we created a hypothetical ‘super’ fecundity-sensitive species (SFS) using the 6-month wet season matrix of *M. californicus* for the monthly transition matrix of SFS. Thus, SFS is not only fecundity-sensitive, but also breeding-intensive (12 months a year). We also recreated a hypothetical species (HS) using the wet season matrix of *M. natalensis* as monthly matrix (A_m) for the entire year. As a counterpart of SFS, HS is survival-sensitive and has a long breeding season (12 months a year).

Model development and simulations

We used the stage-structured matrix model to project annual finite rate of increase (λ) for the three rodent species, HS, and SFS. Transition matrices (A) of the three species were obtained from Harding (2002), Yoccoz et al. (1998), and Stenseth et al. (2001), respectively (Figure 1). In a transition matrix,

$$A=\begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & a_{22} & a_{23} & a_{24} \\ a_{31} & s_2 & a_{33} & a_{34} \\ a_{41} & a_{42} & s_3 & s_4 \end{bmatrix},$$

f_1, f_2, f_3, and f_4 are the fecundity rates of females (number of female offspring per reproducing female) at each stage (e.g. juvenile, sub-adult, adult etc.), s_1, s_2, s_3, and s_4 are the survival rates of animals to next stage, and subscripts 1, 2, 3, and 4 represent stages. a_{ij} is the transition rate of animals from j stage to i stage. For instance, a_{22} is the rate, at which animals remain at stage 2, and a_{23} is the rate at which an animal changes from stage 3 to stage 2. In vertebrates, a_{31}, a_{41}, a_{32}, a_{42}, and a_{34} are zeros. The projection of population size in matrix models is the result of survival of animals and juvenile recruitment to the next time step.

We derived an average monthly transition matrix (A_{wm} and A_{dm}) for *M. natalensis*. Annual finite rates of increase of *M. californicus* (λ_{MC}), *C. rufocanus* (λ_{CR}), and *M. natalensis* (λ_{MN}), HS (λ_{HS}), and SFS (λ_{SFS}) were determined as follows. First, we derived annual transition matrices for the three species, HS, and SFS using equations:

$$A_{MC} = A_w * A_d$$

$$A_{CR} = A_f^{\,2} * A_s^{\,4} * A_w^{\,6}$$

$$A_{MN} = A_{dm}^{\,6} * A_{wm}^{\,6}$$

$$A_{HS} = A_m^{\,12}$$

$$A_{SFS} = A_m^{\,12}$$

And then, λ_{MC}, λ_{CR}, λ_{MN}, λ_{HS} and λ_{SFS} were computed as the dominant eigenvalues of annual transition matrices, respectively (Caswell 2001).

Sensitivity to vital rates were determined by elasticity analysis (Caswell 2001) using transition matrices of breeding seasons and the formula,

$$\text{Elasticity } (e_s) = \frac{s}{\lambda}\frac{\partial\lambda}{\partial s}$$

where s is a vital rate and $\partial\lambda/\partial s$ is a partial derivative of λ with respect to s. If the sum of elasticity of all stage-specific survival is greater than that of all stage-specific fecundity rates, we classified the species as survival-sensitive; otherwise, as fecundity-sensitive.

We simulated mortality control (applications of rodenticides) and fecundity control by reducing either survival or fecundity, respectively, to 80%, 70%, 60%, 50%, 40%, and 25% of the average values for entire effective periods. We assumed that lethal effects of rodenticides would last for one month (January) and assumed no multiple applications. The effects of contraception would last for the entire breeding season or year. Rodenticides and contraceptives had the same effects (or percentage reduction) on survival and fecundity to all age stages, respectively. We did not simulate fecundity suppression and application of rodenticides simultaneously. The effectiveness of fecundity control and mortality control was measured with the proportion of post-control finite rates of increase compared with the finite rates of increase of control populations that were not exposed to any chemicals and contraception agents. To demonstrate the influence of the length of breeding season to the effectiveness of fecundity control, we determined the proportional drop in the rate of population increase of *M. natalensis* with 20% reduction in fecundity rate for the breeding seasons of 4, 6, 8, 10, and 12 months, respectively.

Results and discussion

The sum of elasticity of all survival entries was greater than that of all fecundity entries in *M. natalensis* and *C. rufocanus*. On the other hand, the sum of elasticity of all fecundity entries was greater than that of all survival entries in *M. californicus* (Figure 2). In some rodent species, the elasticity might have seasonal changes (Haydon et al. 1999). In addition, biases in the estimation of survival and fecundity rates might undermine the effectiveness of elasticity analyses (Haydon et al. 1999).

Under mortality controls, fecundity-sensitive *M. californicus* and SFS underwent less reduction in population growth rate; however, survival-sensitive *M. natalensis*, HS, and *C. rufocanus* exhibited greater reductions in population growth rate (Figure 3a). Moreover, mortality control had similar effectiveness on *M. natalensis* and *C. rufocanus* (Figure 3a).

Fecundity control had similar effectiveness on *M. natalensis* and *C. rufocanus*, which have similar life histories (Figure 1), but fecundity control had a greater effect on HS compared with *M. natalensis* and *C. rufocanus* (Figure 3b). Although *M. natalensis*, *C. rufocanus*, and HS were all survival-sensitive (Figure 2), HS was more breeding intensive and had recruits 12 months a year. By contrast, *M. natalensis* and *C. rufocanus* had recruits only 6 months a year in our models. In fact, *M. natalensis* can have a greater fecundity than one in our model (Figure 1). *M. natalensis* can breed as early as in January and has an average litter size of 6.67. In our model, *M. natalensis* begins to breed in April and has an average litter size of 4.01. Stenseth et al. (2001) also found that fecundity control could effectively prevent the outbreak of *M. natalensis*. In our simulations, with a 20% reduction in fecundity, the population growth rate of *M. natalensis* was reduced to 0.769, 0.715, 0.661, 0.618, 0.602 of that of non-control populations for 4-, 6-, 8-, 10-, and12-month breeding seasons, respectively. The longer the breeding seasons, the greater reduction in population growth rate under the fecundity control. *M. californicus* had the least reduction in population growth rate under fecundity control (Figure 3b). This is probably because *M. californicus* had only one-time recruitment over 6 months in the matrix model. SFS, a hypothetical, fecundity-sensitive, and breeding-intensive species suffered the greatest reduction in the population growth rate (Figure 3b). SFS had recruits 12 months a year in our matrix population model. Therefore, fecundity control is more effective in rodents of high fecundity (long breeding season and frequent recruitment).

(a) Average monthly matrix of *M. natalensis*

Wet season

$$A_{wm} = \begin{bmatrix} 0 & 0 & 2.01 \\ 0.5 & 0.37 & 0 \\ 0 & 0.25 & 0.62 \end{bmatrix}$$

Dry season

$$A_{dm} = \begin{bmatrix} 0 & 0 & 0 \\ 0.5 & 0.37 & 0 \\ 0 & 0.25 & 0.62 \end{bmatrix}$$

(b) Seasonal matrices of *M. californicus*

Wet season

$$A_w = \begin{bmatrix} 1.33 & 1.33 \\ 0.58 & 0.58 \end{bmatrix}$$

Dry season

$$A_d = \begin{bmatrix} 0.49 & 0.49 \\ 0.2 & 0.2 \end{bmatrix}$$

(c) Seasonal matrices of *M. rufocanus*

Summer

$$A_s = \begin{bmatrix} 0 & 0.93 & 1.86 & 1.86 \\ 0.75 & 0 & 0 & 0 \\ 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0.75 & 0.75 \end{bmatrix}$$

Fall

$$A_f = \begin{bmatrix} 0 & 0 & 0.93 & 0.93 \\ 0.75 & 0 & 0 & 0 \\ 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0.75 & 0.75 \end{bmatrix}$$

Winter

$$A_w = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0.80 & 0 & 0 & 0 \\ 0 & 0.80 & 0 & 0 \\ 0 & 0 & 0.80 & 0.80 \end{bmatrix}$$

Figure 1. Projection matrices of stage-structured population models for *Mastomys natalensis* (a), *Microtus californicus* (b) and *Clethrionomys rufocanus* (c).

(a) Elasticity matrix of *M. natalensis*

$$\begin{bmatrix} 0 & 0 & 0.19 \\ 0.19 & 0.11 & 0 \\ 0 & 0.19 & 0.32 \end{bmatrix}$$

(b) Elasticity matrices of *M. californicus*

Wet

$$\begin{bmatrix} 0.81 & 0.09 \\ 0.09 & 0.01 \end{bmatrix}$$

Dry

$$\begin{bmatrix} 0.50 & 0.21 \\ 0.21 & 0.08 \end{bmatrix}$$

(c) Elasticity matrices of *M. rufocanuss*

Summer

$$\begin{bmatrix} 0 & 0.1 & 0.1 & 0.1 \\ 0.29 & 0 & 0 & 0 \\ 0 & 0.2 & 0 & 0 \\ 0 & 0 & 0.1 & 0.11 \end{bmatrix}$$

Fall

$$\begin{bmatrix} 0 & 0 & 0.07 & 0.13 \\ 0.21 & 0 & 0 & 0 \\ 0 & 0.21 & 0 & 0 \\ 0 & 0 & 0.13 & 0.25 \end{bmatrix}$$

Figure 2. Elasticity matrices of stage-structured population models for *Mastomys natalensis* (a), *Microtus californicus* (b) and *Clethrionomys rufocanus* (c).

We are aware that rodent populations are affected by density-dependent feedback and climate (Stenseth et al. 2001) as well as environmental and population stochasticity (Wang et al. 2001). One limitation of our study was that our model did not incorporate the effects of these factors. Also, lower fecundity could result in higher survival of those young that are recruited into the population (Sinclair 1997). Twigg and Williams (1999) found that the productivity of European rabbits (*Oryctolagus cuniculus*) decreased with increasing sterility levels, but the recruitment of offspring was enhanced with high levels of sterility. Thus, additional factors can be incorporated into the model that would affect population growth rates. This modelling exercise emphasises different responses of rodents with different life history traits to fecundity control and mortality control. However, in practice, the two alternatives are not always possible in some rodent species. In many cases, an integration of all available control techniques as a part of pest control strategy is needed (Twigg and Williams 1999).

Conclusions

Survival-sensitive and fecundity-sensitive rodents responded differently to manipulations of these two life history traits. Rodenticides are more effective in reducing population growth rate in survival-sensitive species, whereas reduced fecundity has a greater impact on reducing population growth rate in fecundity-sensitive species. Rodents that have large litter sizes and long breeding seasons should be effectively controlled by contraception. Additional factors, such as those subject to density-dependence, can be incorporated into the model to obtain a better predictor of population consequences of manipulating life history traits.

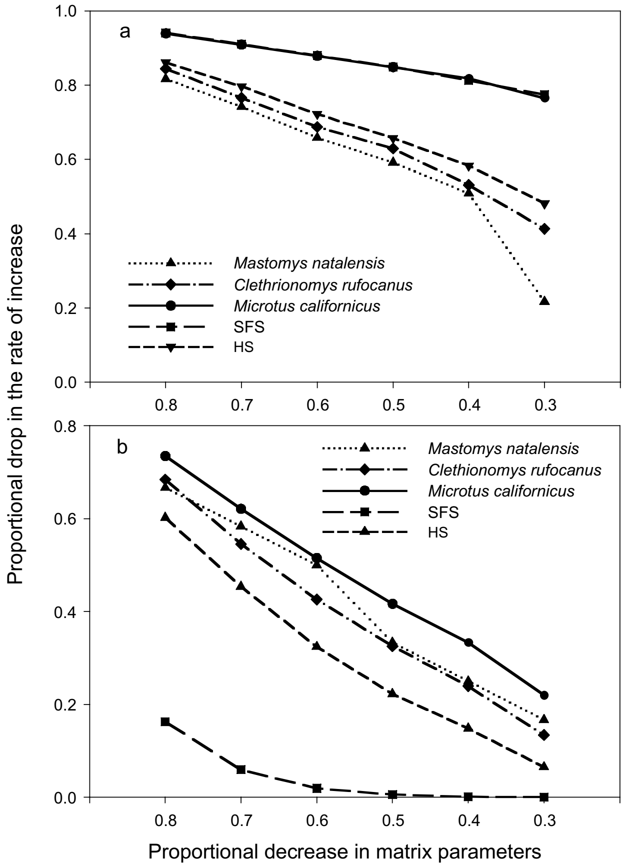

Figure 3. Effectiveness of rodenticides (mortality control) (a) and fecundity control (b) on *Mastomys natalensis*, *Microtus californicus*, *Clethrionomys rufocanus*, a hypothetical species using the parameters of the wet season matrix of *M. natalensis* (HS), and a hypothetical super-fecund species (SFS). The Y-axis represents the proportion of post-control finite rate of increase for experimental populations compared to that of control or pre-treatment populations.

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SYMPOSIUM 4: MANAGEMENT—FIELD

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Management of rodents in crops: the Pied Piper and his orchestra

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Abstract. Few rodent species do very well in agricultural fields, but with nevertheless dismaying consequences. The amounts of food that are lost due to damage by rodents in crops are large and there is a pressing need for effective in-field rodent management. A number of reasons make this a very difficult task. Some of these are related to the nature of the fields, which provide optimal habitats for the pest species. The ecology of those rodents, often with a very high fecundity that contributes to high population numbers, forms another but closely connected side of the problem.

The analysis of the ecology of rodent species that are a problem in crops in different parts of the world shows a considerable diversity of ecological traits. Ecologically based rodent management, aiming to reduce damage below an acceptable level, thus must be tailored to each individual species. This may mean that fundamentally different approaches, such as a focus on fecundity or mortality control, the attraction of predators, the reduction of dispersal, combined or alone, may be relevant for one species but not for another. Economic circumstances may render one strategy beneficial in some crops or regions, but not in another. Ecologically based management is a generic approach but its application is site- and species-specific. Management of rodents in crops cannot rely on a single Pied Piper's technique, but requires a directed and concerted strategy.

> "Please your honours," said he, "I'm able,
> "By means of a secret charm, to draw
> "All creatures living beneath the sun,
> "That creep or swim or fly or run,
> "After me so as you never saw!
> "And I chiefly use my charm
> "On creatures that do people harm,
> "The mole and toad and newt and viper;
> "And people call me the Pied Piper."
>
> R. Browning 1888,
> *The Pied Piper of Hamelin*

Introduction

The Pied Piper had a wonderful tool: a single flute to lure all vermin away. Alas, he was no more than the product of wishful thinking, but the tale remains a good illustration of the awe that rats have inspired for thousands of years. As long as history goes back, rodents have had a bad reputation as agricultural pests, on the field and in the store. Old Indian scriptures, dating back 5 millennia, testify to this (Prakash 1988) and myths and stories are found in all cultures.

Also in our day, rodents cause major losses to agricultural production, despite the availability of very effective rodenticides and other techniques to kill rodents. Estimates of damage vary widely: for a country like Tanzania, the average annual yield loss of maize is 5–15%. This corresponds to more than 400,000 tonnes of maize, equivalent to an amount that could feed 2.3 million people for a whole year, representing a financial loss of around US$40 million (Food and Agriculture Organization of the United Nations (FAO) 1998 data). In Indonesia, rodents cause annual losses in rice production between 10–20%, in Malaysia 2–5% (Singleton and Petch 1994), in Vietnam >10% (Singleton et al. 1999b), in Thailand 6–7% (Boonsong et al. 1999) and in India and Bangladesh 5–10% (Islam et al. 1993; Parshad 1999). Even when using a conservative estimate of 5% for the whole of South and Southeast Asia, the losses in that region amount to 16 million tonnes of rice, enough to feed almost 50 million people (Riceweb 2002).

Predictions about human population growth indicate that the world will have about one billion more mouths to feed by 2025. Regional food shortages will cost the lives of many people through starvation and cause social and political instability, with global consequences. Increasing world food production is a complex task, but it is obvious that rodent pests in agriculture will be a serious hurdle on the way. There is a pressing need for effective in-field rodent management.

After the first International Conference on Rodent Biology and Management in Beijing, China, in 1998, Singleton et al. (1999a) edited a book on ecologically based rodent management. This concept of using ecological knowledge to design management techniques, rather than just focusing on techniques for killing rats, has been picked up by a number of projects and researchers. One of the consequences has been the enthusiastic adoption of a number of ecologically based rodent management strategies that seem sustainable and environmentally friendly and are therefore attractive to the authorities. The question that I want to discuss in the present paper is whether it is such a good idea to use the same methods everywhere.

Agricultural fields as a rodent habitat

Rodents form a very diverse group of mammals, ranging from tiny pigmy mice to big capybaras, from arboreal flying squirrels to subterranean mole rats, from opportunistic omnivores (e.g. Norway rats) to specialist feeders (e.g. the North African fat sand rats that feed on a single family of plants only). It is therefore no surprise that some species thrive well under the conditions that are found in agricultural fields.

Generally, agricultural fields are fairly homogeneous patches in the landscape, with a plant community highly dominated by one or two crop species. The crop species that are grown have been selected for high productivity, and farmers attempt to increase soil fertility and water availability. As a result, plentiful amounts of energy-rich food become available in the fields. On the other hand, most crops are harvested every year, meaning that the availability of food and cover in the fields change drastically over the seasons. At the same time, these changes are closely linked to seasonal changes in light, temperature and precipitation, and thus are fairly predictable. Similar effects also occur in natural conditions, and many species have developed methods to use environmental clues for predicting seasonal changes (Boyce 1979). Rodent species that can take advantage of the temporarily abundant food, and at the same time somehow overcome periods when conditions are poor, make good candidates for agricultural pests.

The above general description holds best for fields with cereal crops, which take up the largest part of the total area used for agriculture in the world (FAO 2002). For some other crops, especially perennial crops like many root and tuber crops and tree crops, the temporal variability may be less strong. However, also here, the point remains that agricultural fields are very productive habitats. Rodent pest management in fields is limited by the fact that the same conditions that favour the presence of pest rodents are to a large extent also the conditions that farmers desire for their fields.

A rat is a rat is a rat?

There are almost 2000 species of rodents, but only a limited number of them cause problems in agriculture. In Africa, for example, with 406 species belonging to 11 families (Wilson and Reeder 1993), there are 77 species that have been reported to cause damage to agriculture, most of them in the Family Muridae (Fiedler 1988). But even in this group, most species only occasionally damage crops and just a handful (<20) cause serious damage over most of their distributional range. In Australia, only 4 out 67 species are clearly pest species, in India 12 out 128 species, and in Western Europe 5 out of 61. Still, being a pest species is not an inherent characteristic of these animals. Hamsters (*Cricetus cricetus*) are intensively controlled as pests in grain fields in eastern Europe, but in western Europe the species is endangered, and legally protected (Nechay et al. 1977). Understanding the diversity of the species that are involved in rodent damage, and those that are not involved, is crucial. There is no point in controlling an irrelevant species, and control strategies must target the right species.

A rodent species' status as a pest is a combination of its own biology and the nature of the agro-ecosystem in which it occurs. Although pest species are often thought to have a number of common features, such as a high fecundity and a fast rate of increase, there are some differences that are worth considering.

Rodent biology

The population dynamics of agricultural pest rodents can show at least three different basic patterns (Figure 1). Populations may be relatively stable or irregularly fluctuating, as in *Rattus tiomanicus* in oil palms; they may show strong seasonal fluctuations combined with interannual differences, as in the African multimammate mouse, *Mastomys natalensis*, in maize fields; or they may be eruptive with irregular peak years alternated with periods when there are hardly any mice (e.g. house mice, *Mus domesticus*, in Australia; see Singleton 1989; Singleton and Brown 1999; Davis et al., this volume). Regular cyclic populations seem to be rare in agricultural crops. I suggest that this could be due to the fact that feedback mechanisms in trophic interactions, a common explanation for cyclic population dynamics (Stenseth 1999), rarely occur in agricultural fields. Plant–herbivore interactions, where plant quantity and quality vary between years as a result of herbivory, can of course not be very important in annually planted crops. Predator–prey interactions are rare because predators are rare or even actively hunted in many agro-ecosystems (because they are considered pests themselves). Social regulation, an alternative explanation for cyclic population dynamics (Krebs 1996), is unlikely in agricultural fields because the instability of the environment, caused by frequent disturbances such as ploughing, weeding or harvesting, does not allow stable social structures to develop.

Different patterns of population dynamics are the result of differences in life history and interactions with the environment. The African multimammate mouse shows a strict breeding seasonality, closely linked to rainfall periods, probably through the stimulating effect of germinating grasses (Leirs et al. 1994). This induces maturation of sub-adult females, which then can produce a large number of young in a short period due to the high litter size (up to 24 young, with an average around 11). The young, however, do not start reproducing until the next wet season and in the meantime there is no reproduction while survival is low (Leirs et al. 1993, 1997). The usual demography of the Australian house mice is not well documented due to the very low densities that occur in most years, but particularly favourable conditions of food and cover lead to high population numbers that escape the normal density-dependent regulation and lead to an eruption (Pech et al. 1999).

Rodent management strategies are clearly dependent on the population dynamics of the targeted species.

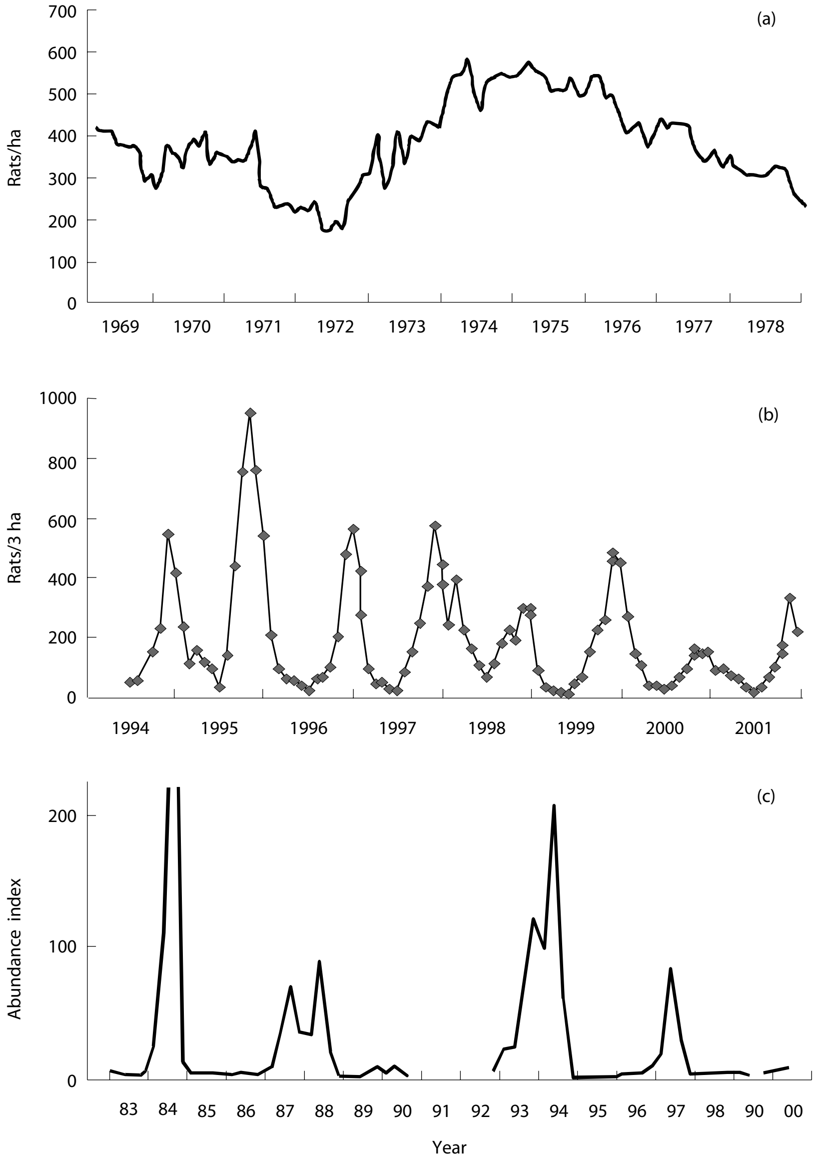

Figure 1. Multi-year population dynamics patterns in three different agricultural rodent pests: (a) wood rats, *Rattus tiomanicus*, in oil palm plantations in Malaysia, population size estimates (redrawn from Wood 1984); (b) multimammate mice, *Mastomys natalensis*, in a maize fields–fallow land mosaic in Tanzania, population size estimates based on robust design capture–mark–recapture (CMR) analysis (own data); (c) house mice, *Mus domesticus*, in cereal fields in Australia, abundance index based on adjusted trapping success (redrawn from Singleton et al. 2001).

Rodents with a stable pattern are kept within restricted limits by density-dependent mechanisms. In species with a clear seasonal pattern, density-independent environmental mechanisms cause the observed regular patterns, and the objective of rodent management will normally be to lower the long-term equilibrium around which population size fluctuates. Such a strategy seems irrelevant in eruptive species where population sizes are usually low anyway. In these species, rodent management will focus on avoiding the build-up of eruptions, or at least the initiation of control early in the build-up phase. It is worth noting that some species may have relatively high average population sizes and consequently cause considerable damage every year, but also in addition show irregular outbreaks (Leirs et al. 1996).

Diet is another aspect in which rodent species show considerable diversity. Many rodent pests are opportunistic omnivores. They can live on a variety of foodstuffs (green plant materials, seeds, fruits, or insects) and thus survive in many different types of crops, but they can also take advantage of a single food item, e.g grain seed, that becomes available in large amounts (e.g. multimammate mice in Africa (Leirs et al. 1994) or house mice in Australia (Bomford 1987)). However, this is not a general feature: other species, like the rice-field rat, *Rattus argentiventer*, have more specialised dietary requirements and thrive only in grasslands such as rice fields (Singleton and Petch 1994). Mole rats are specialised on roots and tubers and cause major problems in cassava fields (Sidorowicz 1974). Such variation means that some rodent species will be very sensitive to changes in crop choices, land use and field management, while others will be affected only marginally.

Crop ecology

Rodent damage is rarely uniform in time, but follows crop phenology. Rice-field rats cause more damage to some stages in the growth of rice than to others (Tristiani and Murakami 1998, 2000), multimammate mice dig up planted maize seeds but are no problem during the growth of maize plants until cobs start ripening (Makundi et al. 1999), and wood mice, *Apodemus sylvaticus*, are a threat to sugar beet fields only in the two weeks after they have been sown (Pelz 1989). In perennial crops, such as coconut or cocoa, rodent damage is more continuous but can vary, e.g. to coincide with fruiting (Williams 1985).

Changes to the phenology of the crop may exacerbate rodent damage. Damage by rodents in rice agro-ecosystems increased from 18,640 ha of total damaged area in 1992 to over 500,000 ha in 1999 (Brown et al. 1999; Singleton 2001). A major factor involved in this increase was the introduction of fast-growing rice varieties which allowed two or even three crops per year, rather than the traditional single crop. While rice-field rats earlier had to survive a long fallow period from mid-January to mid-August, that fallow period is now considerably shorter (from August to December, but during more than 3 months of this period the fields are flooded anyhow). Moreover, the rats now experience twice per year the good conditions provided by specific crop stages that are needed for reproduction (Brown et al. 1999). When irrigation is not synchronised over a large area, adjacent fields will have crops of different ages and rats may move between fields to benefit from the optimal crop stages during a prolonged period (Brown et al. 2001).

The way in which fields are managed will strongly affect the rodents living there, and the damage they cause. Integrated pest management schemes for rodent control rarely fail to mention how important it is to keep fields and field edges clear of weeds, and active weeding strategies have been promoted as rodent control measures (Green and Taylor 1975; Drost and Moody 1982). Maize fields in Tanzania that have been disc ploughed before planting show less damage by rodents than fields that are prepared with a slash-and-burn technique (Massawe et al., this volume). Moreover, fields are not isolated entities from which rodents can be excluded. The fields may be interspersed with different vegetation types and, even when they are large, they are associated with structural variation around hedges, fence lines, roads, irrigation canals, and wind shelters. Such elements increase the attractiveness but also the accessibility of the fields for rodents, since they may serve as refugia or dispersal corridors (Fenn et al. 1987; Brown et al. 2001). Large monocultures in Tanzania experience less rodent damage than smallholder fields that are interspersed with fallow land (Myllymäki 1987).

Rodent management strategies

Given the diversity among rodent pests and the agro-ecosystems where they occur, a number of management strategies have been designed in the past. Most of them have been very successful under specific conditions and this has encouraged people to also try to apply them elsewhere in very different ecosystems. However, none of them is a panacea, and while the people who designed those methods mostly are very well aware of that, policy-makers do not always appreciate the subtleties that make a strategy useful in one area but not necessarily elsewhere. Without presenting the strategies in detail, I want to present some examples and discuss why they seem appropriate for some combinations of pest rodents and agro-ecosystems, while they are less appropriate for other conditions. The list is not exhaustive, and strategies such as field sanitation, hunting in various ways, use of repellents, and control with pathogens are not discussed, although some may be very useful and effective under specific circumstances.

Rodenticides

Rodenticides provide a very effective tool for increasing mortality, one of the key demographic processes in population dynamics. A variety of compounds and ways of delivery exist, with second-generation anticoagulants giving the best results (Buckle 1994). Despite some public concern about the use of chemical compounds, rodenticides certainly will continue to play a role in rodent management in agriculture (Buckle 1999). When using rodenticides against different species, the most appropriate product should be chosen, based on information about toxicology and bait preference for the targeted species. Unfortunately, commercial compounds are largely designed to work optimally for a few commensal species of *Mus* and *Rattus*.

A common misconception with the use of rodenticides (and all other lethal control methods) is that the number of killed rodents is a relevant measure of success. An important reason why this does not hold is that density-dependent effects on recruitment and natural mortality may compensate for the mortality caused by the rodent control so that the population size as such is hardly affected. Another, and less often recognised reason, is that the relationship between rodent numbers and damage is not necessarily linear. In maize fields in Tanzania, it is sigmoidal, indicating that there are density ranges where a reduction in rodent numbers does not reduce significantly the level of damage (Mulungu et al., this volume).

In order to be effective, rodenticides must be applied at the correct point, both in space and in time. Rodenticides should be used at the appropriate places: for example, in macadamia orchards, rodenticides were broadcast on the ground until studies revealed that the rats doing the damage only foraged in the trees, and placing the rodenticides there led to a more effective control (Tobin et al. 1997). Likewise, the timing of rodenticide applications is crucial for their effect on a rodent population as, for example, clear in model simulations with *M. natalensis* (Stenseth et al. 2001).

Biocontrol with predators

Attracting predators is probably one of the oldest ways of controlling pests. Under field conditions, promising results using perches and nesting boxes to attract owls and raptors have been obtained in forestry (Munoz and Murua 1990), cereal fields (Kay et al. 1994) and in oil palm plantations (Smal et al. 1990). However, there are a number of questions to be raised. One misconception is that the trophic interactions between predators and prey are symmetrical; because mice are an important dietary item for a certain owl species, for example, does not mean that this owl is a significant mortality factor for the mouse population. Moreover, density-dependent mechanisms may compensate for the additional mortality that is caused by the attraction of predators. In Tanzania, keeping raptors and owls out of 0.5 ha field plots, or attracting them there, does not make a difference for the population size of rodents that is reached (S. Vibe-Petersen, unpublished data). In Kenya, on the other hand, experiments with nesting boxes in maize fields seem promising (Ojwang this Oguge, this volume). Predators also have problems in surviving periods with low rodent numbers. Studies with nest boxes for barn owls in oil palm plantations in Malaysia showed that, in the experimental phase, owls dispersed to neighbouring areas when densities of rats dropped and then reoccupied the nest boxes when densities of rats increased again. When more plantations took over the nest box idea, the density of owls became very large and when rat densities dropped, owls found no vacant territories, the owl population crashed and could not be re-established quickly when rat densities increased again (Smal et al. 1990; C.M. Smal, pers. comm.). Such mechanisms may actually lead to the introduction of cyclic population dynamics in the rodent pest.

Trap–barrier system

The trap–barrier system plus trap crop (TBS+TC) is an elaborate trapping method for the physical removal of rats from rice fields in Southeast Asia (for an overview, see Singleton et al. 1999b). Basically, a small plot of about 30 × 30 m is planted with a rice crop, a few weeks in advance of the surrounding fields. The plot is surrounded by a plastic fence in which holes with multiple live-capture traps are placed. Rats are attracted by the presence of the early crop and get caught. Large numbers of rats can be trapped and this reduces the damage to crops in the surrounding fields considerably. There is a lot of interest in promoting this method since it seems straightforward, does not require rodenticides, yields visibly high numbers of captured rats, and experiments have shown good results.

There are a few conditions, however, that must be met before this strategy can be used effectively. First of all, the cropping system must allow the planting of an early crop. In irrigated systems this may be feasible, but in rainfed systems, this might be difficult. Secondly, the targeted rodents must be attracted to the trap crop. This requires that they can detect the trap crop and are willing to actively move there over reasonably large distances. If those two conditions are not met, only rats accidentally entering the TBS plot will be trapped and although the plot itself may be protected, damage in the surrounding area will not be reduced and the cost of the fence and traps will not be economically justified. A complex situation may occur if the rodent fauna in the rice fields is diverse and only some of the species are attracted to the TBS+TC. This may result in the capture of many individuals of some species, but it may also reduce the competition for the other species that do not respond. The result could be that damage to rice is only slightly reduced.

Another point is that the TBS+TC plot provides protection to a relatively large area but only is economical if the damage reduction in that area is included. This means that the strategy will be sustainable only if farmers have large enough fields, or if a community-based approach is possible, where all those who benefit from a TBS+TC will contribute to it, even though it is not placed close to their own fields. This is not that easy to implement everywhere.

Diversionary feeding

Rodents cause damage because they select the food sources that at a certain place and time give them the best net benefit when balancing energy intake versus the cost of searching and handling food items (taking into account the risk for predation). This insight is the basis for diversionary feeding tactics, whereby the rodents are offered alternative food sources, which they will prefer over the crops to be protected. This has been tested in orchards and forestry (Sullivan 1979; Sullivan and Sullivan 1988) and is now a common strategy in sugar beet fields (Pelz 1989). In such fields, seeds are drilled in the soil in long rows, and wood mice, *A. sylvaticus*, simply go along these lines and dig up the planted seeds. The management method consists of providing alternative seed on the surface along the edges of the fields. The wood mice prefer to use the seeds on the surface and by the time these seeds are finished, the planted seeds have grown to a stage where they are no longer at risk.

The prime condition for having the diversionary feeding method work is that the economic cost of the alternative food is sufficiently low compared with the reduction of losses that can be realised. That condition is met when the crop has a relatively high value or when it has to be protected during a short time only. Surprisingly few experiments have been carried out with this technique. This may be because most crops need protection for a longer time, but also because the uneasy feeling that people may get because they are feeding rather than killing rodents. However, we must remember that the objective of pest management is reduction of damage, not necessarily reduction of rodent numbers.

Fertility control

Ecological theory predicts that reducing reproduction should be as least as effective as increasing mortality in order to reduce population size in the long term. Model simulations and experimental work confirm this for a variety of species (Chambers et al. 1997; Courchamp and Cornell 2000; Stenseth et al. 2001; Davis and Pech 2002; Shi et al. 2002). Fertility control has a number of advantages over lethal control for species with a high fecundity and a high natural rate of mortality, and at the same time can be considered to be a more humane management strategy than killing rodents. A number of different techniques for reducing fertility has been designed, but only immunocontraception seems to hold promise for real field efficacy (Chambers et al. 1999). Large efforts are under way to develop this strategy for the management of house mice in Australia.

Immunocontraception is based on the induction of an immunological response of animals (mostly females) to proteins of their own reproductive cells. This prevents successful fertilisation. The immune response is triggered by incorporating the protein in a virus which is then delivered to the animal as an infectious and self-disseminating organism, or as a deactivated oral vaccine. Ideally, both the protein and the mode of delivery should affect only the targeted rodent species, and hence the engineered micro-organisms cannot be used to control other species.

A more fundamental issue is that not all populations will be equally sensitive to fertility control. Recent analysis of survival and recruitment in the African multimammate mice, *M. natalensis*, and the South American leaf-eared mouse, *Phyllotis darwini*, shows that the annual population growth rate of these species is more affected by changes in mortality than by changes in fertility (M. Lima et al., unpublished results). This suggests that in order to keep these populations at a lower average density, mortality control may be more effective than fertility control. On the other hand, within-year population growth is dependent on reproduction and therefore fertility control may be an excellent tool to avoid the build-up of outbreaks. Again, how appropriate this strategy is will depend on the rodent species and the objectives that one wants to achieve.

Outbreak forecasting

Irregular eruptions of rodent populations come mostly unexpectedly and farmers are rarely well prepared. This has stimulated a lot of research on the causes of such outbreaks and the development of predictive models (see, for example, Leirs et al. 1996; Pech et al. 1999). Intuitively, it will be beneficial to be able to predict the outbreak and take preventative measures to reduce damage (e.g. order rodenticides in time, organise prophylactic control treatments, or plant a crop that is less prone to rodent damage).

However, the benefit of a predictive model is not necessarily clear cut. Due to stochasticity in the population dynamics of the rodents, any prediction will be probabilistic, meaning that there still will be outbreaks that are not predicted or predicted outbreaks that do not occur. Moreover, how advantageous it is to rely on predictions is not only dependent on the quality of the model, but also on economics. The cost of using the model and applying control measures whenever an outbreak is predicted must be outweighed by the benefit (i.e. reduced losses) that one can expect if action is undertaken and a predicted outbreak actually occurs. Depending on the relationship between costs and expected benefit, predictions should be more, or less, conservative. When control is cheap and the crop very valuable, it is better to apply control often. When control is expensive and the crop less valuable, then it may be better to accept losses caused by some outbreaks that were not predicted. The quality of the model depends on the biology of the rodents (and the skills of the researchers), while the economics depends on the agricultural system and the rodent biology (through the link between rodents and damage). We are currently working on a more formal analysis on the value of outbreak predictions. Preliminary results show, for example, that with house mice in south-eastern Australia, farmers may benefit more when they always apply control rather than never, while with multimammate mice in Tanzania, it would more beneficial never to do control than always (S. Davis et al., unpublished results).

Conclusion

The above examples have illustrated that smart strategies for rodent control do not necessarily work always and everywhere. The biology of rodents is diverse and complex and so is the ecology of the fields in which they live. Ecologically based rodent management is a sound concept, but it does not provide a ready-made solution. Specific approaches must be identified, based on the ecological characteristics of the agro-ecosystem and the pest species involved. Different techniques must be combined and fine-tuned to work optimally in each system. Management of rodents in crops cannot rely on a single Pied Piper's technique, but requires a directed and concerted strategy.

Acknowledgments

I thank Grant Singleton for stimulating discussions on many occasions and providing useful information for this review, and Charley Krebs and Roger Pech for their valuable comments.

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Ecologically based management of rice-field rats on a village scale in West Java: experimental approach and assessment of habitat use

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Abstract. A major constraint to rice production in Southeast Asia is pest rodents. In a large-scale replicated field study, we are examining the effect of ecologically based rodent pest management on rodent numbers, pre-harvest rodent damage, yield and the use of chemicals. This paper describes the rationale for including community rat campaigns as a management tool in this study. We present data on the spatial and temporal patterns of habitat use by rice-field rats (*Rattus argentiventer*), which are the major mammalian pests in lowland irrigated rice in Indonesia. Rat numbers showed similar fluctuations in rice fields, crop margins and village garden habitats. Most rats were caught during fallow and land preparation, possibly as a result of increased movements post-harvest. At this time, many more rats were captured in crop margins and village garden habitats than in rice fields. Similar numbers of rats were present in all habitats at tillering, ripening and harvesting of rice. We conclude that community rat campaigns targeted at refuge habitats (crop margins, village gardens) shortly before transplanting rice from nurseries into the rice fields should considerably decrease the founding population of rice-field rats for the next cropping season. This refuge campaign, combined with the application of community trap–barrier systems during the standing crop should minimise rat damage to rice crops and increase yield.

Introduction

Habitat use by pest rodents

Mobile animals select habitats actively to achieve maximum fitness (Fretwell 1972). Habitat choice of an individual takes into account intrinsic factors including intraspecific competition (Myllymäki 1977; Hodara et al. 2001), as well as extrinsic factors including interspecific competition (Hodara et al. 2001), predation (Newsome 1969; Lima and Dill 1990) and weather conditions (Vickery and Rivest 1992).

For rodent pests in agricultural systems, habitat use may be linked to patterns of land use (Twigg and Kay 1994; Leirs et al. 1997). Seasonal changes in food supply may cause movements of animals between refuge habitats and impact habitats (crops) (Hansson 1977; Redhead and Singleton 1988). Knowledge of the spatial activity of rodent pests is vital to developing appropriate management strategies because control should be conducted at key times in the source/refuge habitats where high numbers of the pest species are generated (Stenseth 1977; Singleton 1989; Twigg and Kay 1994).

The role of pest rodents in Southeast Asia

Rodent pests are a worldwide problem, and are responsible for considerable damage to crops, food stores and human property. Some rodents are also significant carriers of diseases transmitted to humans (e.g. leptospirosis, tularaemia, rickettsiosis, bubonic plague) (e.g. Gratz 1994), and thus have a further economic impact related to losses in worker productivity and health-care costs.

Rodents are one of the main causes of pre-harvest losses in Southeast Asian rice crops (Singleton and Petch 1994). In Indonesia, rodent pests are the most important pre-harvest pests, causing annual losses of 17% in rice crops (Geddes 1992). Generally, pre-harvest rodent damage is patchy with localised losses of 70% or even 100% occurring in particular fields. In other Southeast Asian countries, similar levels and patterns of rodent damage occur (reviewed in Jacob et al. 2002).

Ecologically based rodent management

Ecologically based rodent management (EBRM) aims to manage the target species based on sound knowledge of farming systems and natural factors, such as the availability of food and shelter, that contribute to the limitation of pest rodent populations. In manipulating these factors, control is spatially and temporally focused on the target species and non-target impacts are reduced. Key refuge habitats (banks of irrigation channels, irrigation levee banks) are modified to minimise the availability of food and shelter for pest rodents by controlling the growth of grasses and height and width of banks as well as by synchronising planting and harvesting (Leung et al. 1999).

Community trap–barrier systems (CTBSs) are simple, affordable structures used by farming communities in some Southeast Asian countries to control rats. A CTBS consists of multiple-capture cage-traps associated with a rectangular plastic fence, typically (25 × 25 m) that encloses a lure crop planted 2–3 weeks earlier than the surrounding crop. It is therefore more nutritious and attracts rats from the surrounding area, which are caught in the traps. In lowland flood-irrigated rice, one TBS protects up to 16 ha (Singleton et al. 1998). The CTBS method has significant advantages: it is environmentally sustainable because non-target species can be released and there are no residues left in the rice field after removal of the structure; and the technique is simple and can be easily transferred from scientists to extension officers and farmers (Singleton et al. 2001). However, the use of the CTBS entails a large maintenance effort (Jacob et al. 2002). Moreover, it is only effective until the surrounding crops reach their generative stage because the efficacy of the CTBS technology relies on the presence of an early-planted crop.

Best results in controlling pest rodents are likely if a combination of several management techniques—including CTBSs, community rat campaigns and habitat manipulations—are applied (Singleton et al. 2001). The choice of methods and timing of activities will depend on the biology and ecology of the target species. In contrast to lowland irrigated rice systems in Vietnam and Laos, where several rodent species occur, rice fields in West Java harbour almost exclusively rice-field rats (Singleton et al. 1998). Management in this ‘one-species system’ is therefore more easily targeted on the culprit and effects at the population level are more easily detected than in ‘multi-species systems’.

Effectiveness of ecologically based rodent management

Ultimately, farmers in Indonesia control pest rodents (and other pests that damage rice) in order to increase their net income. This can be achieved in two ways. First, if the cost of pest rodent management is lower than the monetary benefits from an increased yield, there is a direct increase in income. The cost of rodent management includes the materials and equipment use and the time spent conducting rodent control. Second, if improved management techniques are less time-intensive, then a farmer may spend the time gained in other cash-generating activities.

In addition, there may be an important environmental benefit if the use of EBRM measures results in a decrease in the use of poisons. In West Java and other regions in Southeast Asia, a large proportion of farmers use unregistered poisons (Sudarmaji, Rochman et al., these proceedings). These poisons include potent broad-spectrum chemicals such as endosulfan, aldicarb and dichloromethane.

A study of the effectiveness of EBRM should therefore include measurements of rodent damage to rice crops, crop yields, and the use of chemicals, as well as the time and money spent on rodent control.

Spatial and temporal scale

Pest rodents can be highly mobile (e.g. Krebs et al. 1995; Leirs et al. 1997). Despite relatively small home ranges of c. 1–2 ha during the breeding season (Brown et al. 2001) rice-field rats can travel large distances (>700 m) post-harvest (Jacob, Nolte et al., this volume). Rice-field rats are also thought to travel between refuge/nest habitats (channel banks, road verges) and impact habitats (rice crops). During the breeding season, there may be pronounced activity of pregnant and lactating female rice-field rats in rice fields (J. Jacob et al., unpublished data). These changes in spatial activity need to be considered for the management of populations of rice-field rats, but little is known about their spatial dynamics and habitat use.

A number of studies on large holdings not typical for Java have provided detailed information on the efficacy of certain aspects of EBRM such as the use of CTBSs and fumigation (e.g. Singleton et al. 1999). Studies at a village level are required to examine the effects of EBRM for traditional cropping systems. Implementation of EBRM there may lead to the application of additional techniques and to the temporal and spatial coordination of traditional and additional techniques.

In 2000, we began a replicated, manipulative village-level study of the efficacy of EBRM in lowland irrigated rice fields in Cilamaya, West Java. One management tool we planned to use was community rat campaigns instigated at key times. Therefore, as a prelude to the village-level study, we monitored the numbers of rice-field rats by capture–mark–recapture trapping during the wet season 1998/99 and dry season 1999. The aim of the study was to identify specific habitats and key times for community rat campaigns.

Materials and methods

The study was conducted in lowland irrigated rice crops near the town Cilamaya (06°14'51"S, 107°34'05"E), Subang province, West Java, Indonesia. The climate in the region is tropical. Annual variation of the average temperature (28°C) is low. About 75% of the annual rainfall (1450 mm) occurs during the wet season (November–April) but rain is also frequent during the dry season (May–October).

The West Javanese agro-ecosystem is characterised by smallholder lowland irrigated rice fields (average family holding of 1–1.5 ha). Individual holdings are partitioned by small distribution channels and larger rice-growing areas are separated by dikes and irrigation channels. Villages are located along roads. One rice crop is grown in each of the two seasons. Rice is transplanted from nurseries in the fields after 2–3 weeks. The main crop stages are tillering (55 days after sowing), booting (75 days), ripening (95 days) and harvesting (120 days).

We used a typical rice-growing area of about 750 ha for this study. Rice-field rats were trapped monthly for three consecutive nights from January 1999 until December 1999 in the vicinity of the villages Pasirukem, Sukatani and Tegalurung. We captured rats with multiple-capture wire-cage live-traps (20 × 20 × 50 cm). Six traps were set along a 120 m long drift fence (Leung and Sudarmaji 1999) in each of three habitats: rice fields, crop margins (irrigation channel banks and road verges) and village garden (Figure 1).

In rice fields, the drift fences were located either close to creeks or small irrigation channels that were 50–60 cm wide and 20–30 cm deep or about 50 m into the fields (Figure 1). Volunteer crops, which emerged from the stubbles after harvest, grew along the creek banks for 3–4 weeks after harvest. During the planting season, farmers usually did not manage the vegetation along these watercourses, but controlled weeds regularly in the fields. Drift fences with traps were also set along road verges and irrigation channel banks. In these habitats burrowing activity is usually high. Grassy vegetation 1–2 m wide occurred on either side of the channels and the roads, providing ground cover of 80–90%. Village garden habitats were located between villages and rice fields. In the village gardens, farmers grew bananas, mangoes, coconuts and vegetables.

In January, April, June and from August to November 1999 we set one drift fence in each of four rice fields, four crop margin habitats and in two village garden habitats. In February, March, May, July and October 1999 we set one drift fence in each of eight rice fields, eight crop margin habitats and in four village garden habitats.

The plastic drift fences were 60 cm high, stabilised by bamboo poles and dug into the ground about 20 cm deep. The openings of the traps were flush with holes at the base of the fence. The traps were on either side of the fence facing alternate directions and were held in place with bamboo sticks. The distance between traps was 20 m; the first and last trap along a drift fence were 10 m away from the ends of the fence. The distance between the drift fences was >300 m. Traps were checked every morning at sunrise. Rats were marked with a uniquely-numbered brass ear-tag (Hauptner, Germany) and released at the point of capture.

Rice-field rats are extremely trap-shy after first capture and can usually not be caught more than once, so that estimators of population size that rely on recaptures could not be applied. We therefore compared the minimum number of rats known to be alive (MNA) between seasons (wet and dry season), habitats (rice field, crop margin and village garden) and crop stages (tillering, maximum tillering, ripening, harvest and land preparation) using ln-transformed data in an accumulated analysis of variance (ANOVA) (general linear regression). MNAs at fallow

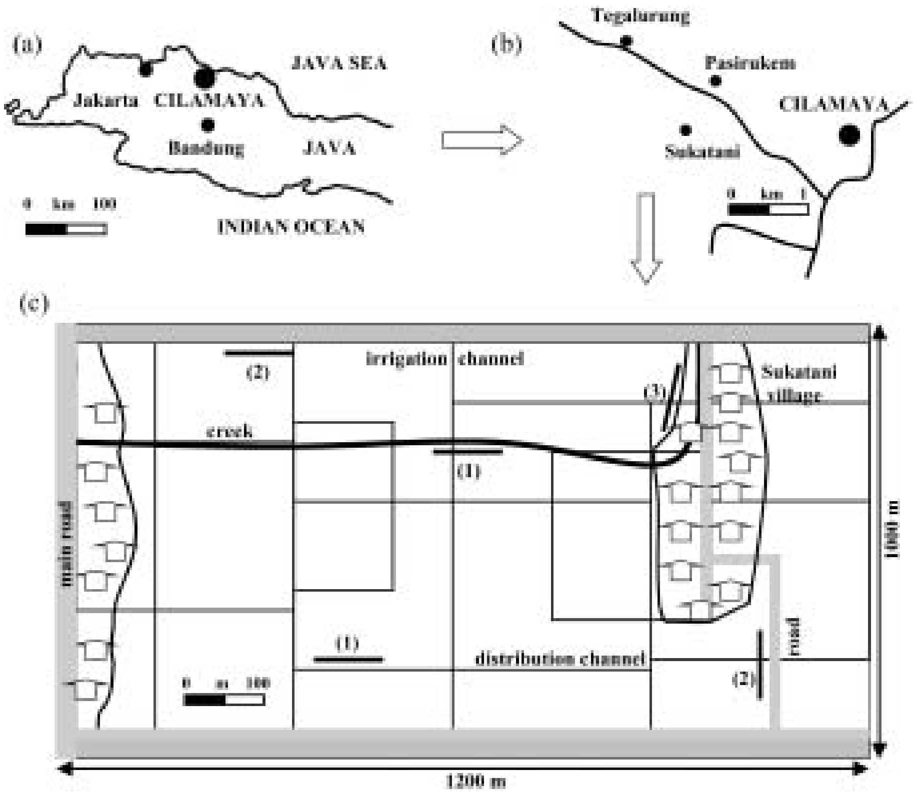

Figure 1. (a, b) Location of the study area in West Java, Indonesia. (c) Examples of the location of drift fences with traps (short black lines) for live-trapping rice-field rats in rice fields (1), crop margins along irrigation channels and roads (2), and in village garden habitats (3) near the village of Sukatani.

and transplanting were not considered in the statistical analysis because sampling at these crop stages was not conducted in both seasons. Variance is stated as standard error throughout the paper.

Results and discussion

We caught 1564 rice-field rats during 3060 trap nights. Captures of non-target mammals were rare (<2%) and included *Bandicota* sp., *Suncus* sp. and *Rattus rattus*.

There was no difference in the MNA between seasons ($F_{1,120}$ = 0.03, p = 0.862) (Figure 2). Across habitats, the average MNA was low (<10) at tillering, maximum tillering, ripening and harvesting, high (>26) at land preparation ($F_{4,120}$ = 37.18, p < 0.001) and highest (>37) at fallow (Figure 2). The breeding activity of rice-field rats commences about two weeks before maximum tillering (Leung et al. 1999) and should have led to recruitment of rats into the trappable population at ripening and harvesting. However, this was not reflected in the MNA. This could have been due to abundant high-quality food provided by the rice crop resulting in small home ranges and low trapping probability. In California voles (*Microtus californicus*), for example, plentiful food leads to small home ranges (Ostfeld 1986). High background food availability may also have reduced trappability because the rats' exploratory behaviour in their search for food may have been low.

The high number of rats caught at fallow and land preparation was probably due to increased movements activity of rats during and after the disturbance by harvest (Jacob, Nolte et al., this volume). Harvesting rice not only removed much of the food, it also removed the rats' shelter from predators. The reduction of shelter exposes small mammals to increased predation risk (Jacob and Brown 2000; Sheffield et al. 2001). Some small mammals such as common voles (*Microtus arvalis*) respond to the removal of shelter with decreased spatial activity (Jacob and Hempel 2002) but rice-field rats relocate quickly after harvest to unharvested rice fields (Jacob, Nolte et al., this volume). During fallow and land preparation, no unharvested patches were available and the rats may have been forced to move more often than in the standing crop in search for shelter and food. These movements and the relatively high number of rats at the end of the breeding season may have been the reason for the high MNAs.

In addition, trappability could have been influenced by the breeding activity because low MNAs coincided with the breeding season (maximum tillering until shortly after harvest) and high MNAs coincided with the non-breeding season (fallow and land preparation). When breeding, female rats may have stayed close to their offspring in the burrows, lowering the probability to encounter and enter a trap. This seems likely as several small mammals have relatively small home ranges in the breeding season compared to the non-breeding season (e.g. Krebs et al. 1995).

The number of rats caught was higher in crop margins and village gardens than in rice fields ($F_{2,120}$ = 6.63, p = 0.002) and the fluctuations in the MNA of rats showed similar trends in all three habitats (Figure 2). However, in contrast to crop stages when few rats were caught

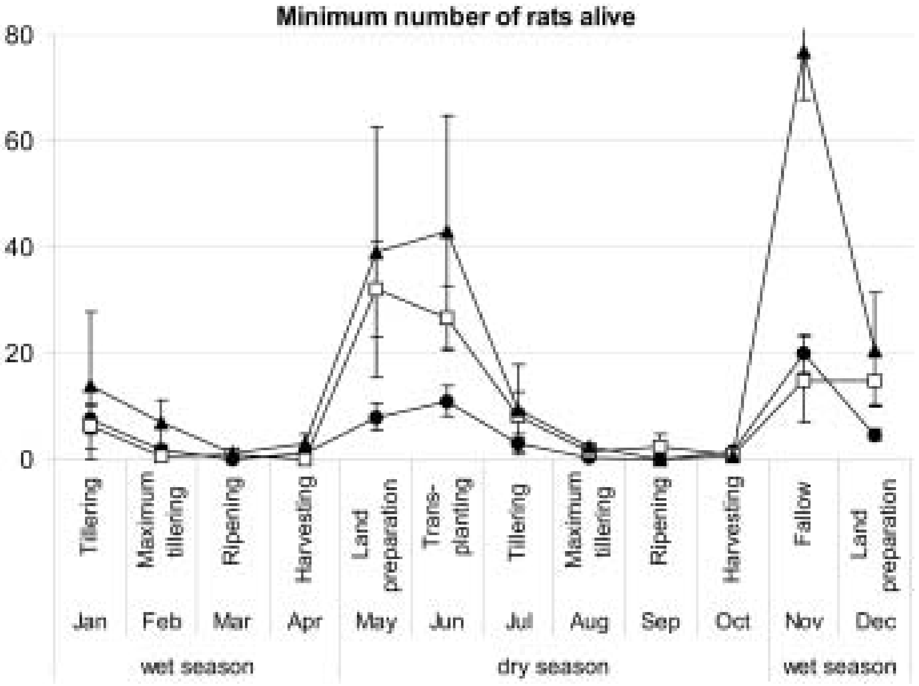

Figure 2. Relative abundance of rice-field rats as minimum numbers alive at monthly capture–mark–recapture trappings in rice fields (black dots), crop margin habitats (open squares) and village garden habitats (black triangles) in Cilamaya, West Java, Indonesia. Error bars are standard errors.

(maximum tillering, ripening and harvesting), there was a difference in MNAs between habitats at fallow, land preparation and transplanting (Figure 2) ($F_{8,120}$ = 2.01, p = 0.05). While few rats were caught at these crop stages in the rice fields, relatively high numbers of rats were usually caught in crop margin and village garden habitats. The latter habitats were relatively undisturbed during harvesting of rice and land preparation. In addition, shelter was not removed there and grass seeds and invertebrates may have been sufficient to sustain the rats until the next rice crop was transplanted.

The reproduction of rice-field rats usually ceases 2–3 weeks after harvesting of rice (Leung et al. 1999) and at that time the population size reaches its maximum. The high number of rats at that time does not pose a threat to the rice crop until transplanting because the only areas with rice plants present at this time—seed nurseries—can be successfully protected with fences (Sudarmaji, Rochman et al., this volume). Therefore, management actions to decrease rat numbers in crop margin and village garden habitats could be delayed until shortly before transplanting the rice from the nurseries into the fields. This timing would allow ‘natural mortality’ to decrease rat numbers for as long as possible before management actions are applied to minimise the founding population for the following planting season. However, management of rats in the crop margin and village garden habitats needs to be conducted before the rats recolonise and damage the freshly transplanted crop.

Rat management during community rat campaigns or bounty systems can remove high numbers of rodents from agricultural land within short periods of time. In these campaigns, rats are removed mainly by fumigation with sulfur gas and physical methods such as flooding burrows, digging, hunting, netting and trapping (Jacob et al. 2002). In Vietnam, a rat bounty scheme applied in 1998 in 47 provinces yielded 179 million rats (source: Plant Protection Division, Ministry of Agriculture and Rural Development, Vietnam). Bounty systems also are used occasionally in Indonesia. In regions where farmers are accustomed to rat campaigns on a community level, it may be relatively easy to conduct rat drives as a component of EBRM. We predict that the combination of traditional control methods applied during 2–3 week rat campaigns and follow-up control using CTBSs will result in lower damage to rice crops, higher yield and higher net income for farmers.

The cost of these management actions will have to be balanced with potential benefits. If rat numbers in refuges are low at early tillering of the rice crop, management actions may not be justified. However, one has to keep in mind that rats concentrate in refuge habitats at early tillering and, as a consequence, management can be targeted in smaller areas and possibly with much lower cost than at other times of the cropping cycle.

Conclusions

Based on our findings, we decided to use community rat campaigns in treatment areas in the village-level study as an additional tool for managing rice-field rats in lowland irrigated rice fields in West Java using EBRM. The campaigns are to be conducted in major refuge habitats (village gardens, channel banks, road verges) shortly before transplanting, when rat numbers are high at the end of the fallow. In conducting these studies, we will assess the effectiveness of using a combination of community rat campaigns and CTBSs for rodent pest management in lowland irrigated rice fields.

Acknowledgments

We thank Rahmini and Jumanta for help in the field and D. Grice for helpful comments on an earlier draft of the paper. The Australian Centre for International Agricultural Research supported the study (grant AS1 98/36).

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Impact of village-level rodent control practices on rodent populations and rice crops in Vietnam

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Abstract. In Vinh Phuc, Vietnam, data on the species composition, population abundance, breeding, and habitat use of the main rodent pest species were obtained. Four sites were selected for a replicated field experiment to examine the effectiveness of ecologically-based rodent management at a village-level scale. We present 14 months' data from the beginning of the experiment, the first 11 months of which were before any management actions were imposed. Live-trapping was conducted every month within three different habitats of the rice-growing area. The main rodent species present were *Rattus argentiventer* (58%), *R. losea* (22%) and *R. rattus* (12%). There were two main peaks in population abundance, each following harvest of the main rice crops. Captures of rats were very low from March to May, at the end of the winter crop season when vegetable crops were grown. Breeding was evident from maximum tillering to just after harvest for each of the spring rice crops and summer rice crops. The use of habitats was slightly different for *R. argentiventer* and *R. losea*, with more *R. argentiventer* trapped along big channel banks compared with small banks and big banks. When the abundance of *R. argentiventer* was low, more *R. losea* were trapped along big channel banks, and when more *R. argentiventer* were trapped, *R. losea* favoured small banks, which suggested interspecific competition. It will be important, therefore, that any practice imposed to manage *R. argentiventer* also manages *R. losea*. Based on our understanding of the rodent community and population dynamics, we developed a series of rodent management practices to reduce damage to crops. These included targeting rodent management within refuge habitats early in the growth of the rice crop and the application of a community trap–barrier system.

Introduction

Rodents are a significant problem for agriculture in Vietnam. Rats are considered the number one pre-harvest pest of lowland irrigated rice crops, especially in the Mekong and Red River Deltas. Recent changes in the economic structure of agricultural production have led to a doubling of rice production in the Mekong and Red River Deltas. An important factor behind these increases is intensification of cropping from two to three crops per year. Rodents have benefited from this because of the increase in food supply and an extension of the time that high-quality food is available (Singleton and Petch 1994). The latter would extend the period within each year that breeding occurs because the breeding season of the principal pest species of rats is linked with the availability of rice from its maximum tillering stage to ripening (Lam 1980, 1983; Tristiani and Murakami 1998). It is not surprising, therefore, that rat problems have been serious in Vietnam since 1995 (Figure 1).

The rice-field rat, *Rattus argentiventer*, is the single most important pest to rice crops in Vietnam, and it is an important pest of rice crops in other parts of Southeast Asia, including Malaysia and Indonesia. In Indonesia, it causes annual pre-harvest losses of around 17% (Geddes 1992; Leung et al. 1999). Other rodent species inhabiting rice fields in Vietnam include *Rattus losea*, *R. rattus* and *Bandicota indica* (Brown et al. 1999). Little is known about how these pest species interact within the rice-growing areas or how management should be implemented to mitigate damage to rice crops. Currently, most farmers are reactive in their actions, only implementing management once the rat problem is moderate to severe.

Methods for controlling damage caused by rodents in rice agro-ecosystems include the application of rodenticides (Buckle 1999), hunting, fumigation, physical barriers such as the trap–barrier system (TBS, Singleton et al. 1998, 1999), and cultural practices such as synchronised cropping, sanitation of fields and encouraging predators (such as barn owls) (Leung et al. 1999).

Our research is aimed at understanding the ecological factors influencing rodent populations in rice ecosystems in the Red River Delta, Vietnam. This ecological understanding has led to the identification of key management actions and the subsequent decision analysis of their feasibility and timing of application, their likely economic and environmental impact, and the required scale of implementation. The impact of integrating these management actions is currently under assessment at the village level through close cooperation with farmers in a replicated, controlled field experiment. As this study is in progress, the purpose of this paper is to (a) present background data on the species composition of the rodents inhabiting the rice fields of Vinh Phuc Province, (b) examine the population dynamics and breeding seasons of the most common species and relate these to the cropping system, (c) compare capture rates of rats in different habitats, and (d) describe the basic design and implementation of treatments for the village-level study.

Materials and methods

Study site

The study areas were all within Vinh Phuc Province, in northern Vietnam, 40 km north of Hanoi (21°08'N, 105°45'E). Four study sites were selected in March 1999 and comprised part of a main village or sub-villages. Each site was 0.5 to 1 km apart. The sites were set up to monitor the population dynamics of rats before implementation of ecologically-based rodent management. Each site was about 100–150 ha in size. Within each site, families manage small plots of land (called ‘sao’, which are 360 m^2). Each family generally owns 0.5–0.7 ha of land. The principal crop grown in the area is rice. There are two main rice-growing seasons each year, the spring rice season (transplanted late February and harvested mid-June), and the summer rice season (transplanted mid-July and harvested late September). Other crops grown are vegetables (broccoli, Chinese cabbage, kohlrabi, onion, pumpkin, tomato) and flower crops (chrysanthemum, rose). Summers are hot and wet, and winters are cool and dry. The annual average rainfall is approximately 1600 mm, most falling between May and September. Farmers irrigate their crops using water supplied by channels originating from large storage dams in nearby hills.

Monitoring of rat populations

Live-trapping for rats was implemented every month from April 1999 until May 2000 using single-capture wire traps (100 × 100 × 300 mm) baited with vegetables. Twenty traps were set for four nights across each of three trap-lines with two replicates of each line. The trap-line habitats investigated were: (1) ‘big channel banks’, large earth banks for transporting water, each bank 2 m high by 3 m wide; (2) ‘small banks’, 300 mm high by 300 mm wide for retaining water within paddies and for walking between fields; and (3) ‘big banks’, large earth banks for paths 1–2 m high and 2–5 m wide. There were 480 trap nights per census. Traps were placed at 10 m intervals, and trap lines were placed 50–100 m apart. Each captured rat was marked with an ear punch, identified for species, sexed, breeding condition determined for females (evidence of lactation or pregnancy), and measured (tail length, ear length, hind foot length, body weight). All animals were released at the site of capture.

Breeding samples were collected from 15 adult female *R. argentiventer* and 15 *R. losea* per month (the two main species caught). These animals were euthanased and assessed for uterus size, number of embryos, and size of embryos (trimester of development). These data were used to determine the commencement and cessation of breeding, percentage of adult females in breeding condition, and the average number of embryos per pregnant female.

Results and discussion

Species composition

The most common rat species caught was the rice-field rat (58%), followed by the lesser rice-field rat (22%) (Table 1). In total, seven species of rodent were captured, as well as an insectivorous shrew (*Suncus murinus*).

Population dynamics

There were two peaks in abundance—the first after harvest of the spring rice crop in July and the second after

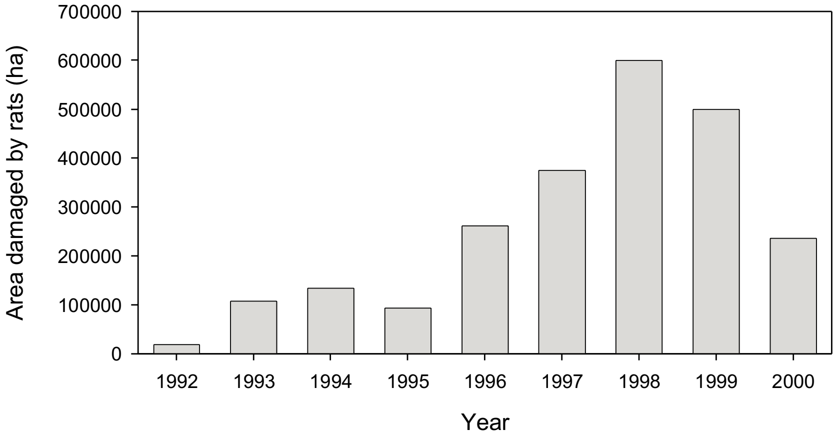

Figure 1. Area of rice crops (ha) damaged by rats in Vietnam since 1992. Data from Brown et al. 1999 and Ministry of Agriculture and Rural Development (2000).

harvest of the summer rice crop in October (Figure 2). *R. argentiventer* was more common than *R. losea* ($F_{1,60}$ = 9.38, $P < 0.01$), and the abundance of the rats was higher in July and October 1999 than other months ($F_{13,60}$ = 3.496, $P < 0.001$). The peak in abundance in October coincided with the damage observed to kohlrabi crops at that time (Tuan et al., this volume). Captures of rats were lowest during March, April and May after harvest of the winter crops and during the early growth phase of the spring rice crop. No marked animals were recaptured. *R. argentiventer* are well-known for their low recapture rate (Brown et al. 1999; Leung et al. 1999).

Breeding was evident from maximum tillering of the rice crop through to a few weeks after harvest during each rice crop. Very few adult female rats were in breeding condition during the winter period (<5% of captures). The average litter size of *R. argentiventer* was 9.0 pups (se = 0.30, *n* = 83), with 7.5 pups for *R. losea* (se = 0.30, *n* = 53).

Habitat use

Consistently more *R. argentiventer* were trapped on the big channel banks compared with the other habitats ($F_{13,90}$ = 3.693, $P < 0.05$) (Figure 3). Likewise, *R. losea* were more commonly trapped on big channel banks than other habitats ($F_{2,90}$ = 5.545, $P < 0.01$). The abundance of both *R. argentiventer* and *R. losea* was higher during June, July, August and October compared to other months ($F_{13,90}$ = 8.834, $P < 0.001$; $F_{13,90}$ = 8.480, $P < 0.001$, respectively), but the interactions were not significant ($F_{26,90}$ = 0.457, P = 0.987; $F_{26,90}$ = 1.403, P = 0.123, respectively). A Pearsons correlation analysis between captures of *R. argentiventer* and *R. losea* in each habitat showed that the highest correlation coefficient was for the relationship between the captures of *R. argentiventer* on big channel banks and captures of *R. losea* on small banks (R^2_{14} = 0.931, $P < 0.001$), and that the lowest correlation was for the relationship between

Table 1. Main small mammal species caught at Vinh Phuc Province, northern Vietnam, from April 1999 to May 2000.

Species	Common name	Vietnamese name	Number	%
Rattus argentiventer	Rice-field rat	Chuot dong lon	541	58.0
Rattus losea	Lesser rice-field rat	Chuot dong nho	204	21.9
Rattus rattus	Black rat	Chuot nha	110	11.8
Bandicota indica	Great bandicoot rat	Chuot lon	42	4.5
Mus sp.	Mouse	Chuot nhat	13	1.4
Rattus norvegicus	Norway rat	Chuot cong	5	0.5
Suncus murinus	Shrew	Chuot chu	2	0.2
Other rodent species not accurately identified		Cac loai chuoj chua xac dinh ten	16	1.7
Total			933	100

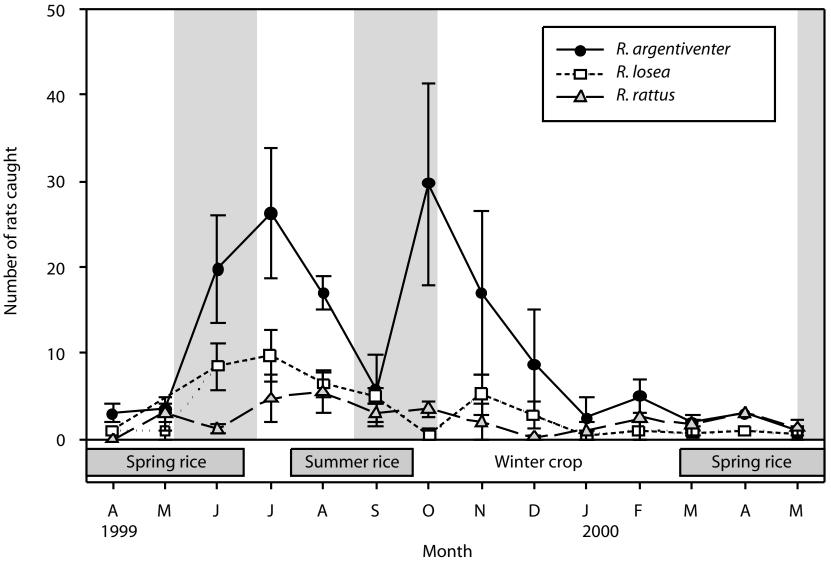

Figure 2. Population dynamics of the three common *Rattus* species at the Vinh Phuc study site from April 1999 to May 2000 in four sites trapped (means ± standard error). The shaded bars represent each breeding season. Crop stages are indicated for spring and summer rice crops and winter crops. The horizontal bars represent the duration of the rice crops.

captures of *R. losea* in small banks and *R. losea* in big channel banks ($R^2_{14} = 0.662$, $P < 0.01$). This suggests that when captures of *R. argentiventer* were low on big channel banks in September, there was a corresponding increase in captures of *R. losea*. *R. losea* favoured big channel banks only when fewer *R. argentiventer* were present. When relatively more *R. argentiventer* were trapped on the big channel banks, *R. losea* was predominantly found on small banks. These results indicate that interspecific competition for resources is occurring, with *R. argentiventer* considered the dominant species. Further research involving diet studies, monitoring habitat use through radio-tracking, and manipulative studies where only *R. argentiventer* are removed could assist our understanding of the interactions between the two species.

Development of village-level rodent control

Based on the results described above on the dynamics, breeding patterns and habitat use of the main rodent species, a series of management practices were developed for farmers to implement. From the four study sites, two treatment sites (farmers are encouraged to conduct the rodent management practices) and two untreated sites (farmers are not influenced in their rodent management practices) were selected. The selections were based on the abundance of rats and damage to rice crops and on discussions with village-heads on the willingness of farmers to conduct and implement the rodent control practices. This work is ongoing.

Before implementation of treatments, a meeting with farmers at the treatment sites was held to discuss the different rodent management practices available. These included routine actions (field sanitation, synchronous land preparation, TBS, reducing refuge around villages, and cleaning up after harvest), and actions if high numbers are forecast (trapping and hunting, using rodenticides, bounty on rats, and digging burrows). A survey of rodent control practices used by farmers at the Vinh Phuc study sites was summarised by Tuan et al. (this volume). Although various control methods are available to reduce the impact of rats on rice crops, the main control techniques traditionally used by farmers are poisoning and trapping (Tuan et al., this volume). The effectiveness of rodenticides is often compromised because the bait is not mixed properly, is placed in inappropriate locations, or is poorly timed to the rodent breeding cycle. Farmers frequently use poison baits after rodent damage has occurred rather than to prevent damage. Furthermore, the cost of chronic poisons is usually prohibitive for farmers, and there are serious risks of non-target poisoning (P.R. Brown and N.P. Tuan, personal observations).

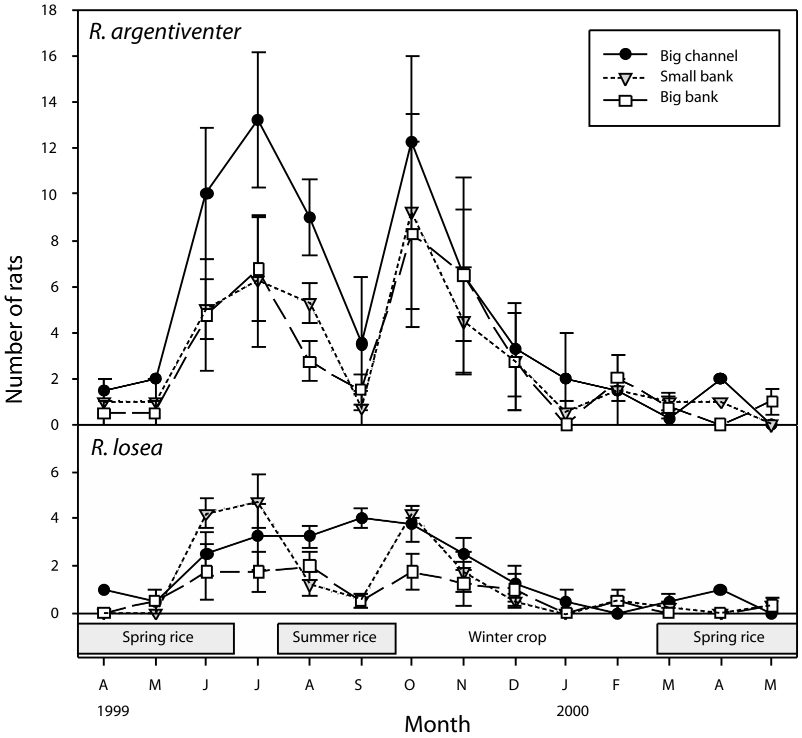

Figure 3. Habitat use of *Rattus argentiventer* and *R. losea* in Vinh Phuc Province from April 1999 to May 2000 as the average number of rats captured in trap lines set along big channel banks, small banks and big banks (means ± standard errors). Crop stages are indicated for spring and summer rice crops and winter crops. The horizontal bars represent the duration of the rice crops.

Table 2. List of farm management practices for managing rodents in the Red River Delta, Vietnam.

Management action	Timing[a]	Feasibility	Scale of adoption	Priority
Routine actions				
Field sanitation	LP	Yes	Farmer	High
Synchronise land preparation, seeding and planting	LP, SB, TP	Availability of labour	Village	Medium
TBS by farmer group[b]	TP	Yes	Village	High
Reduce bund size within rice fields	LP	Yes	Village	High
Encourage natural predators	All	?	District	High
Reduce refuge around villages	All	Yes	Village	High
Clean up after harvest	H, F	Yes	Village	Medium
Actions if high numbers are forecast				
Trap and hunt	All	Yes	Farmer	High
Apply chemical baits in field and houses	TP–MT	Yes	Village	Medium
Bounty system on rat tails/heads	LP–TP	? ($)	Commune	High
Dig burrows	LP–TP	Yes	Commune	Medium
Monitor rat activity in field	All	No	Village	Low

[a] LP = land preparation, SB = seed bed, TP = transplanting, MT = maximum tillering, H = harvesting, F = fallow.
[b] The trap–barrier system (TBS) needs to be planned in advance and set up 3–4 weeks before surrounding rice crops.

Research trials to develop rodent management practices for Indonesia (Leung et al. 1999) and the Mekong Delta region of Vietnam (Brown et al. 1999) indicated that a similar set of management actions for farmers in the Red River Delta would be appropriate (Table 2).

The management actions were assessed for their feasibility of implementation, including whether the action was economical, socially acceptable, environmentally friendly and sustainable, the scale of likely adoption, and its priority for farmers to implement. These management actions were developed by scientists and extension officers, through combining scientific knowledge on the biology and management of the rodent pest species with the concept of ecologically-based management defined by Singleton (1997).

Success of the rodent management practices will be assessed through comparing differences in the abundance of rodents between treated and untreated sites, the level of damage inflicted on crops, and differences in yields obtained by farmers. The use of chemical rodenticides and plastic barrier fences by farmers in the survey areas (without traps or a lure crop) is also under assessment.

Conclusion

The data collected are providing valuable information on the species composition, habitat use and abundance of the main rodent species in Vinh Phuc Province. This knowledge will help refine the rodent management practices that farmers will use, and to target key rodent habitats at key times. The benefits of this project will be demonstrated if there are increases in crop yields and less reliance on chemical rodenticides.

Acknowledgments

We thank all the village heads and farmers involved in the project for their support and willingness to participate in the project. Staff of the National Institute of Plant Protection (NIPP) provided excellent support while in the field and getting the project under way. In particular, we thank Dao Thi Hue, Phi Thi Thu Ha, Phung Thi Hoa, Pham Thi Lien and Pham Van Kien. We thank the reviewers who strengthened the paper considerably. This research is part of the ACIAR-funded project “Management of rodents in rice-based farming systems of Southeast Asia” (AS1 98/36).

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Rodent problems in India and strategies for their management

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Abstract. Rodents are major vertebrate pests due to their endemicity and propensity to damage major crops at the farm level and in storage in India. Analysis of the reviews on pre-harvest losses indicates a range of 5–15% damage to major cereal crops of rice and wheat. Instances of rodent outbreaks also occur due to bamboo flowering in the north-eastern states, and prolonged dry spells followed by heavy rains and flash floods in other states. Reports also exist on increased incidence of zoonotic diseases such as plague and leptospirosis. The lesser bandicoot rat, *Bandicota bengalensis*, is predominant in irrigated crops throughout the country including arable areas of the Thar Desert. The Indian gerbil, *Tatera indica*, soft-furred field rat, *Millardia meltada*, and field mouse, *Mus booduga*, are widespread in both irrigated dryland and dryland crops in the country, except in the north-eastern states. Due to the research support extended by the Indian Council of Agricultural Research (ICAR) All India Network Research Project on Rodent Control, Jodhpur, adequate technology for effective rodent management is available. The use of rodenticides is the most common approach to the rodent problem, but environmental and cultural techniques, such as clean cultivation, proper soil tillage and crop scheduling, have had long-lasting results. A National Programme on Rodent Pest Management, launched during 1976, with trainers' training, community preparation, technology and actual control operations, produced significant results in preventing rodent damage. With planning on rodent management by the Government of India, the emerging rodent-related problems could be controlled effectively. Currently, problems occur due to increases in intensive cropping in expanding irrigation areas, changing agricultural practices resulting in replacement of desert rodents with lesser bandicoot rats, increased coconut cultivation failing to follow proper spacing, cultivation of oil palm in rodent-endemic areas, and natural calamities like flash floods and drought spells followed by heavy rains.

Introduction

Indian agriculture has progressed a long way from an era of frequent droughts and vulnerability to food shortages to become a significant exporter of different agricultural commodities. This can be attributed to harnessing a larger portion of the land for agricultural purposes and introduction of new technologies. A spectacular rise in food grain production took place from 1949–50 to 1999–2000 (from about 55 to 206 million t). The thrust in intensive cropping, coupled with increased fertiliser use, resulted in an increase in pest problems with a crop loss of 10–20% annually, amounting to rupees (Rs)60,000 million in field and storage situations (Rajak 1993).

Economic importance of rodents

Agriculture

Rodents cause direct damage to various crops/commodities by gnawing and feeding, and indirect damage by spoilage, contamination and hoarding during on-farm and post-harvest stages (Rao and Joshi 1986; Parshad 1999). However, the pattern and level of rodent infestation, and the extent of damage, vary in different crops and geographical regions (Table 1). Most of the estimates of damage relate to isolated studies in smaller plots and extrapolated to larger areas. Hart (2001) reported that overall losses of grain to rodents in India were approximately 25% in pre-harvest and 25–30% in post-harvest situations, bringing the loss to at least US$5 billion annually in stored food and seed grain in India. Often chronic losses go unrecognised and these losses are economically more important.

Rodent outbreaks

Population explosions of rodents sometimes result in rodent outbreaks (Chauhan and Saxena 1985; Rao et al. 1998) (Table 2), on occasion resulting in famines. Reasons attributed to outbreaks are: (i) prolonged drought/dry spell followed by heavy rains increasing the reproductive propensity of the rodent pests, as happened in Saurashtra region of Gujarat state; (ii) failure of the monsoon in the preceding year, resulting in a favourable environment for rodent breeding, as in Cauvery Delta area of Pondicherry (Karaikal region) and Tamil Nadu (Tanjor and Nagapattinam districts) states; (iii) flash floods leading to unusual increases in the subsequent carrying capacity of the environment and to the absence of predators in the delta areas, as happens in Andhra Pradesh (East Godavari and West Godavari districts); and (iv) flowering of species of bamboo (*Melocanna bambusoides* and *Bambusa tulda*), leading to increased carrying capacity in *jhum*[1] cultivated fields in Arunachal Pradesh, Manipur, Mizoram and Nagaland states.

Cereal crops

Analysis of reviews on pre-harvest losses indicate a range of 5–15% damage to cereal crops like rice and wheat (Sridhara 1992; Chopra et al. 1996; Parshad 1999; Singleton 2001). The lesser bandicoot rat, *Bandicota bengalensis*, is the predominant rodent pest in these crops. The vulnerable crop period is the boot leaf stage, due to the availability of sweaty mucilage. Crop compensation does not occur after this stage.

Sugarcane

Gnawing lower internodes of sugarcane causes direct damage at the sugar formation stage of the crop. Even incisor injury to the cane is often associated with secondary losses in yield and quality because of red rot caused by *Physalospora tucamanesis*. Christopher (1987) reported a yield loss of gur (dark, unrefined sugar) at 45.6 kg/ha with 20.7% damage in Andhra Pradesh. While regularly propped and detrashed fields resulted in totally erect crops, improperly maintained ones resulted in lodging of cane. Neglected fields had a staggered damage of 63%. Bindra and Sagar (1975) and Srivastava (1992) also reported similar damage patterns. *B. bengalensis* is the predominant rodent pest species in the crop. In Punjab, *Nesokia indica* also inhabits sugarcane fields. Rodents

Table 1. Extent of crop losses due to rodent pests, the pest species involved, and their distribution in India.

Crop	Extent of loss (%)	Rodent pest species	Habitat/distribution of species
Rice	1.1–44.5	*Bandicota bengalensis*	Irrigated fields
		Millardia meltada	Semi-irrigated fields
		Mus booduga	Irrigated fields
		Rattus nitidus	*Jhum* fields in the north-east
		Rattus rattus brunneusculus	*Jhum* fields in Mizoram
Wheat	2.7–21.3	*Bandicota bengalensis*	Irrigated fields
		Millardia meltada	Irrigated dry fields
		Tatera indica	Rainfed fields
		Meriones hurrianae	Desertic soils in Indian desert
Sugarcane	2.1–31.0	*Bandicota bengalensis*	Irrigated fields
		Nesokia indica	Irrigated fields in Punjab
		Millardia meltada	Irrigated fields
Groundnut	2.9–7.3	*Tatera indica*	Irrigated dry fields
		Millardia meltada	Irrigated dry fields
		Bandicota bengalensis	Irrigated fields
Coconut	4.5–55.0	*Rattus rattus*	Throughout India
Cocoa	30.0–50.0	*Rattus rattus wroughtoni*	Southern India
		Funambulus palmarum	Andhra Pradesh and Tamil Nadu
		Funambulus tristriatus	Kerala and Karnataka
Oil palm	11.2–57.3	*Bandicota bengalensis*	Fruits in southern India and Andaman
		Hystrix indica	Seedlings in nurseries
		Tatera indica	
Vegetables	1.4–30.6	*Bandicota bengalensis*	Irrigated fields
		Millardia meltada	Irrigated dry fields
		Tatera indica	Dry fields
		Meriones hurrianae	Indian desert soils
		Funambulus pennanti	Northern India
Fruits	Varied	*Funambulus pennanti*	Northern India
		Funambulus palmarum	Southern India
Storage	2.5	*Rattus rattus*	Residential premises and farm level storage
		Mus musculus	
		Bandicota bengalensis	

Source of damage data: Rao and Joshi (1986) and Parshad (1999).

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[1] '*jhum* cultivation' is shifting cultivation in which the forest is burnt periodically in different places.

colonise cane fields because they provide an undisturbed habitat for burrowing, feeding, breeding activities and protective cover from avian predators for most of the year. Further, the crop affords an alternative site for rodent activity during the inter-cropping period in surrounding fields, especially rice/wheat.

Pulse and oilseed crops

The high protein content of seeds results in moderate rodent damage to the pods of lentil, arhar, moong, soybean and Bengal gram. Changing patterns of agricultural practices, such as introduction of summer pulses between the *rabi* (winter crop) and ensuing *kharif* (rainy season crop) seasons, made availability of food continuous for rodents, increasing their population and rendering the area endemic for these pests. Awasthi and Agarwal (1991) reported a yield loss of 16.5 kg/ha in soybean crop at the green pod stage.

Groundnut is grown as an irrigated dry crop in most areas in the country. Rodents damage and remove the pods at sowing time and at maturity (4–7%) and hoard sometimes up to 320 g/burrow (Patel and Nayak 1987; Mittal and Vyas 1992). Indian gerbil, *Tatera indica*, and soft-furred field rat, *Millardia meltada*, along with *B. bengalensis*, cause the major damage in irrigated fields. During the rodent outbreaks in Gujarat in 1976 (Shah 1979) and 1988–89 (Vyas et al. 2000), rodents damaged up to 85.42% of the crop in the Saurashtra region.

The area under oil palm cultivation is increasing and there are reports of rodent damage in several parts of the country, although documentation of the damage was done only in the Andaman islands. Rodents damage the female flowers while feeding on the oil-bearing tissue. Subiah (1983) and Advani (1985) reported up to 57.3% damage to oil palm fruits.

Plantation crops

Coconut is one of the major plantation crops affected by rodents, with damage done at the point of attachment of the nuts and to the pulp. Most of the damaged nuts fall to the ground after 2–4 weeks of damage (Shamsuddin and Koya 1985; Rao 1995). Most coconut palms are infested by *Rattus rattus* and 10–32% damage often occurs to tender coconuts (Subiah and Shamsuddin 1992; Rao 1995; Gandhi 2001). The bunch size class with 6–10 nuts was reported to be more affected (36%), suggesting placement of baits at the base of such bunches (Gandhi 2001).

Rodents also affect the shrub plantations of cocoa and cardamom. Squirrels and rats make irregular holes in the cocoa pods (sometimes up to 50%) to feed on their contents (Bhat 1992). Injured pods are not fit for use due to black pod disease caused by a fungus, *Phytophthora palmivora.* Cardamom capsules are damaged by *B. bengalensis* and five-striped palm squirrel, *Funambulus palmarum*, at the ripening stage when they begin to emit the typical cardamom odour (Srihari and Chakravarthy 1992).

On-farm damage after harvest

Malhi and Parshad (1987) reported a loss of 4.31% panicles, equivalent to 1.11 quintals per hectare of wheat and 4.64% loss of rice panicles, equivalent to 1.72 quintals of coarse rice after harvest and before the produce was lifted from the field.

Post-harvest losses

Farmers retain 60–70% of their produce in storage. A committee constituted by the Government of India for assessment of storage losses in 1996 estimated a total loss

Table 2. Rodent outbreaks in India during the last 10 years

Year	State/Union territory	Area (and crops affected)	Estimated loss
1990–91	Gujarat	Saurashtra region (groundnut, wheat, gram and cotton)	Not available
1994	Pondicherry	Karaikal region (rice, gram and soyabean)	Not available
1994	Tamil Nadu	Cauvery Delta (rice and gram)	Not available
2001	Tamil Nadu	Cauveri Delta (rice)	Not available
1997–98	Andhra Pradesh	210,000 ha in Godavari Delta (rice)	3301.85 million t
2001	Andhra Pradesh	31,000 ha in East Godavari district (rice)	Not available
1999–2000	Arunachal Pradesh	7000 ha (rice and maize)	Not available
1999	Manipur	1000 ha (*jhum* rice)	Not available
2000	Manipur	1264 ha (*jhum* rice)	Not available
1999–2000	Mizoram	53,945 ha (rice, maize and vegetable crops)	Not available
1999–2000	Nagaland	1000 ha (rice)	Not available

Source of information: Directorate of Plant Protection, Quarantine and Storage, Department of Agriculture and Cooperation, Ministry of Agriculture, Government of India.

of 9.33% for food commodities, and rodents accounted for 2.5% of this. A national study made by the Indian Grain Storage Management and Research Institute (IGMRI) revealed a total post-harvest loss of 4.75% of wheat with rodents accounting for 0.59%. Rodents contaminate food with their hair, urine and faecal droppings, the level varying in different situations. The daily rate of defecation was reported as 22 pellets for *B. bengalensis* and 13 pellets for *M. musculus* (Nimbalkar 2000). Due to this, the Government of India stipulated that food commodities should not have hair and excreta in excess of five pieces per kg sample under *Prevention of Food Adulteration Rules 1956* and amended from time to time.

Public health

Rodent-related problems exist in public health due to their role as vectors and reservoirs for bacterial diseases such as leptospirosis, murine typhus and salmonellosis, in addition to plague. As humans and livestock are in regular contact with rodents, the potential for transmission of zoonotic diseases is high. Limited investigative work exists on the exact role that rodents play in the epidemiology and transmission of human and animal diseases.

Plague

Although plague has been present in India since the 16th century, the mortality attributed to it in British India from 1896 until 1994 was 12,657,077 lives (Viliminovic 1972; John 1996). During 1994, 54 fatalities were reported among 876 cases (WHO 2000a). During February 2002, a confirmed report of plague was received from Himachal Pradesh.

In India, sylvatic plague foci are recognised at the foothills of the Himalayas (Jammu and Kashmir, Himachal Pradesh, Uttaranchal and Bihar), in the watersheds of the Vindhyas (Madhya Pradesh) and in the Deccan Plateau covering Andhra Pradesh, Karnataka, Maharashtra and Tamil Nadu states (John 1996). Rodents are primary hosts of *Yersinia pestis* (the causal agent of plague), which is transmitted by the oriental flea, *Xenopsylla cheopis.* The primary species of wild rodent infected with *Y. pestis* in India is the Indian gerbil, *Tatera indica.* This gerbil is susceptible to infection, but resistant to disease and consequently acts as a permanent reservoir host. When gerbils frequent fields around human habitations, peri-domestic rodent species like *B. bengalensis* in these fields become infested with the plague-infected flea. This transmits in turn to *R. rattus* in ruderal habitats. Both *R. rattus* and *B. bengalensis* are susceptible to infection, disease, and rapid mortality. This can lead to increased incidence of human plague.

Leptospirosis

Leptospirosis is a zoonotic disease which occurs worldwide in warm humid tropical countries. The International Leptospirosis Society opined that greatly in excess of 100,000 severe cases of leptospirosis occur annually worldwide (WHO 1999). This survey and available information indicate human leptospirosis-infected areas in Andamans, Gujarat, Kerala, Maharashtra, and Tamil Nadu. The animal hosts for leptospirosis are cattle, rodents, pigs, dogs and cats. The common sero group is *icterohaemorrhagiae.* Pathogenic species of *Leptospira* survive for long periods in the convoluted tubules of the kidney in natural hosts, mostly rodents. The organisms multiply and up to 100 million leptospires/mL urine may be shed. The infectious bacillus is transmitted to man by skin contact, particularly contact with broken or abraded skin, in stagnant waters. Hence, rice and sugarcane field workers are particularly vulnerable to this disease because of their working conditions.

In India, three rodent species (*Rattus norvegicus*, *R. rattus* and *B. bengalensis*) are known to be associated with this disease (Gangadhar 1999), which is more common than ordinarily diagnosed—many so-called ‘fevers of unknown origin’ being caused by it (John 1996). Leptospirosis was reported in Orissa (WHO 2000b) after the 1999 cyclone and affected at least 14.1% of the population due to the closer interaction between humans and reservoir animals. Leptospirosis is often ignored or undiagnosed due to lack of awareness, misdiagnosis, and a lack of diagnostic services (WHO 2000b).

Other diseases

Since 1990, a variety of typhoid fever caused by *Salmonella typhi* and resistant to most of the existing antibiotics has been prevalent in many parts of India (John 1996). Human infections with the virus causing Kyasanur forest disease were reported in Karnataka state. The disease is transmitted by ticks belonging to the genus *Haemaphysalis* and is maintained in small mammals, such as *Suncus murinus* and *Rattus* spp., while monkeys in forest areas serve as amplifying hosts (Rajagopalan 1966).

Major rodent pest species

The rodent fauna of the Indian sub-continent is represented by 46 genera and 128 species (Roonwal 1987). Among them, 13 species are predominant pests requiring attention (Table 1). The lesser bandicoot rat, *B. bengalensis*, is predominant in irrigated crops throughout the country, including arable areas of the Thar Desert, but is not present on Lakshadweep and Andamans islands (Rao 1993). Due to its ferociousness, it replaced other species and became a major pest in storage situations and other premises in metropolitan cities like Mumbai, Calcutta and Delhi.

The Indian gerbil, *T. indica*, soft-furred field rat, *M. meltada*, and field mouse, *Mus booduga*, are widespread in both irrigated dryland and dryland crops in the country except in the north-eastern states. The Indian crested porcupine, *Hystrix indica*, is widely distributed in hillock or arid habitats, occasionally inflicting severe damage to crops, orchards and reforestation plantations.

Other rodent species have restricted distribution, namely: the desert gerbil, *Meriones hurrianae*, in desert areas; the Himalayan rat, *Rattus nitidus*, in the north-eastern region; the short-tail mole rat, *Nesokia indica*, in the north-western plains; the three-striped squirrel, *Funambulus palmarum*, on the southern peninsula; the five-striped squirrel, *F. pennanti*, on the northern peninsula; the western Ghat squirrel, *F. tristriatus*, on the west coast of the southern peninsula; and the Norway rat, *R. norvegicus*, in port areas.

The house rat, *R. rattus*, and the house mouse, *Mus musculus*, are the major commensal pests (Prasad and Rao 2000). At least 14 subspecies of *R. rattus* have been reported from India (Biswas and Tiwari 1969). Of these, *R. r. rufescens* Gray occurs in premises throughout the country, *R. r. wroughtoni*, Hinton and *R. r. blanfordi* Thomas are restricted to plantation crops like coconut, oil palm and cashew on the southern peninsula (Bhat 1992), *R. r. andamanensis* Blyth occurs on Andaman and Nicobar Island (Subiah and Mathur 1992) and *R. r. brunneusculus* occurs in Mizoram (Chauhan and Saxena 1985).

Existing technical know-how

Due to the research support extended by the Indian Council of Agricultural Research (ICAR) All India Network Research Project on Rodent Control, Jodhpur, adequate technology for effective rodent management exists (Rana and Tripathi 1999).

Environmental and cultural methods

Several agronomic measures used in raising crops in the country contribute indirectly to reduction of rodent populations. Deep ploughing, bund trimming and other land preparation measures reduce the carrying capacity of the habitat for rodents. Routine weed removal by farmers in crops also deprives rodents of shelter and alternative food sources. Sharma and Rao (1989) reported a decline in rodent infestation in rice fields with reduction in bund dimensions. Sabhlok and Pasahan (1985) also reported migration of gerbils from about 65–78 m away after removal of wild vegetation from the fields. Christopher et al. (1984) reported that periodic removal of garbage and nesting material in animal/human dwellings, stores and godowns discourages rodent habitation. Alley planting of rice also reduces rodent damage (Anon. 1959–69).

Physical elimination of field rats is in vogue with communities in Irulas of Tamil Nadu and Erukulas of Andhra Pradesh where rats are used for food. Rodents, especially *T. indica* and *B. bengalensis*, are caught physically by digging the burrows. Sometimes, fumigation of burrows using smoking straw is employed. However, this physical killing is done often around the time of ripening of the crop after maximum rat damage has already occurred. Staff at Acharya N.G. Ranga Agricultural University, Hyderabad, developed an improved smoke generator for effective control of burrowing rodents. Paddy straw is burned, leading to the generation of smoke, which is pushed into the burrow tunnel with the help of a blower (Rana and Tripathi 1999).

Trapping

Although trapping is one of the oldest methods, there is little proof in the scientific literature that it is an effective method of reducing rodent numbers (Reddy 1999). *Tanjor kitties* (bamboo palmyra traps) are effective in maintaining rodent numbers at a low level once they have been reduced by other methods. Indigenous bamboo snap-traps are laid on the periphery of *jhum* cultivated fields in the north-eastern states to trap rodents immigrating from adjoining forest areas and resemble the trap–barrier system of rodent management (Singleton et al. 1999).

Role of predators

Biological control existed in the country before the 1970s due to the presence of natural predators. Cats in domestic situations, and snakes and owls in field situations, are the predominant vertebrate predators. Whitaker and Dattatri (1986) reported that rodents constitute prey items for the cobra (75%), Russels viper (75%), krait (29%) and scaled viper (22%). However, the feeding rate of captive snakes is one rodent every three days. This predatory pressure on rodents is very low compared to the faster breeding propensity of rodents. Hence, snakes alone may not be able to control rodent populations in nature.

Kumar (1985) reported that 61% of the total estimated biomass of the pellets of spotted owlet was *R. rattus* and *M. musculus.* Neelanarayanan (1997) reported the consumption of 1–6 rodents/night by the barn owl, with an average of 1.58 rodents/day. *B. bengalensis* (40%) and *M. musculus* (33%) constituted the major prey items. Provision of nest boxes (91.4 × 45.7 × 53.3 cm) and T-shaped owl perches provided alternative sites for barn owls for predatory activity (Neelanarayanan 1997). However, declining rodent populations post-harvest resulted in predators leaving the area**.** The T-shaped owl perches are currently popular in cereal crops as one of the integrated pest management (IPM) practices. However, their use is not desirable after the flowering stage of crops because granivorous birds use the perches during their feeding activity in the grain crops.

Use of microbes

Salmonella and murine typhus bacteria were found to be ineffective against *R. rattus* and *B. bengalensis* in India (Deoras 1964). Bindra and Mann (1975) reported that the murine typhus bacterium cause <40% mortality of *M. musculus* and *T. indica*. Studies with the trichostrongloid nematode, *Hepatojarakus bandicoti*, are yet to explore the potential for rodent control. Studies on virally vectored immunocontraception (Hinds et al., this volume) are yet to be considered in India.

Ultrasound devices

The sense of hearing among rodents is above 20 kHz, thus extending well into the ultrasonic range. Ultrasound devices are being used as deterrents to rodent immigration but to date evidence has found them ineffective.

Chemical repellents

There is no effective chemical repellent to rodents available that is not also toxic to humans. Field rodents often damage the imported rodent-repellent cables installed in telecommunication networks. Although pheromones appear to be promising, scientific work is lacking to identify, isolate and introduce pheromones for extension purposes.

Rodenticides

The use of rodenticides is the most common approach to tackle the rodent problem in the country. Among the seven rodenticides registered under the *Insecticides Act 1976*, those able to be marketed and used commonly include aluminium phosphide, zinc phosphide, bromadiolone and coumatetralyl.

Zinc phosphide is the most commonly used acute rodenticide. Used at 2% in cereal baits, it detoxifies rapidly in carcasses and baits, and thus is relatively safe and economical (Prakash and Mathur 1992). Development of bait shyness and the lack of an effective antidote are limitations to its use. The control success that can be achieved is usually around 60% (Rao et al. 1998). ICAR recommends use of zinc phosphide in rice, wheat, jowar, millets, sugarcane, pulses, oilseeds and vegetable crops. However, due to toxicity problems in non-target species, its use is advocated primarily in situations where rodent infestations are at high levels, i.e. 50 active burrows per hectare. Efforts are in progress to develop a ready-to-use formulation of this rodenticide for effective application in different situations.

Among first-generation anticoagulants, coumatetralyl is used in cereal-mixed baits at 0.0375%, mostly in storage/domestic situations. Low toxicity level, chronic action and availability of vitamin K_1 as an antidote make it an effective anticoagulant. It is also recommended in controlling *B. bengalensis* in crops of Punjab (Rana and Tripathi 1999).

The second-generation anticoagulant bromadiolone has been available commercially in ready-to-use formulation since 1988 for use in crops and storage/domestic situations. It is recommended as a component of the IPM packages for rodent control in crops with moderate levels of rodent infestation. It is used in cereal bait at 0.005% and applied inside burrows at 15 g per burrow. It is advocated for use in bamboo bait stations in *jhum* fields of the north-eastern states. Bait shyness does not exist with this chemical, hence a second application is recommended after 15 days to address the residual rodent infestation (Rana and Tripathi 1999).

Application of aluminium phosphide pellets at two per active burrow is recommended for effective field rodent control. Due to easy handling, application and immediate kill of rats inside burrows, the farming community prefers this fumigant rodenticide. However, because of the higher toxicity of the chemical to non-target species and the absence of an antidote, the Government of India has restricted the use of this rodenticide.

Timing of rodent control

Farmers normally resort to symptomatic treatments, i.e. controlling rodents after damage is seen in their crop. Mostly, these measures lead to partial success due to poor bait intake in the presence of food crops in the fields. Most of the states of the country adopt prophylactic or lean-period rodent control. It is presumed that bait intake will be high during the interval between two crop seasons and farmers will have free time to participate in the control operations on a community basis. However, analysis of implementation of this approach showed that farmers were not keen on rat control in this period due to the absence of rodent infestation in their fields (Rao et al. 1998).

Cereal crops exhibit compensatory growth if pests inflict damage in the initial stages, but not if damage occurs after the vegetative stage (Rao 1992). Hence, rodent control is advocated during the vegetative stage of cereal crops when rodents immigrate to and try to establish in the crop. Treatment during this stage resulted in effective rat control (Rao et al. 1998).

Strategies for rodent management

National Programme on Rodent Pest Management

Recognising the increasing rodent problems, ICAR launched a National Programme on Rodent Pest Management (Anon. 1976) from 1976 in collaboration with the Directorate of Plant Protection, Quarantine and Storage (DPPQ&S) and Union Department of Food. The program has four components: preparation of the community, training of personnel, control operations, and prophylactic strategies. The primary aim is to undertake rodent control at the community level on a continuous basis.

In view of the dearth of qualified extension personnel in rodent management, training of trainers (ToTs) through Apex Level Training programs was given priority. The Central Arid Zone Research Institute, Jodhpur, IGMRI, Hapur and National Plant Protection Training Institute (NPPTI)/Acharya N.G. Ranga Agricultural University, Hyderabad to date have trained about 4000 extension personnel and university scientists. In addition, the NPPTI, a training wing of DPPQ&S, organises All India training programs for extension personnel of states/union territories (UTs)/other organisations. To date, 305 extension personnel from the states have been trained in 17 programs in the institute. This institute also organised *in situ* training programs in the states/UTs of Andhra Pradesh, Arunachal Pradesh, Assam, Goa, Karnataka, Lakshadweep, Manipur, Meghalaya, Mizoram, Nagaland, Pondicherry, Uttar Pradesh, Tamil Nadu and Tripura as needed.

A ‘rodent control week’ was observed by the states/UTs every year until the early 1990s to expose large areas to the control of rodents through a community approach. This was discontinued because rodent control was incorporated as an integral component of the IPM activity of the states/UTs.

Inputs for rodent management

To encourage rodent control by states/UTs, the Government of India formulated a centrally sponsored scheme for control of special pests of agricultural importance from 1976–77 with a subsidy of 50% on the cost of rodenticides. Until 1992, the scheme provided an assistance of Rs20.4 million for rat control, covering an area of 13.76 million ha. After 1992, central assistance was provided through identified crop-based central sector schemes. During 2000, with the amalgamation of the crop-based central sector schemes into a Macro Management in Agriculture Scheme, states/UTs were given flexibility to incorporate the rodent control component under the crop-based central sector schemes. There is an increasing trend in the country to use anticoagulant rodenticides (Table 3).

Rodent management in the post-harvest situation

To protect food grains in storage at the farm level, the Ministry of Consumer Affairs, Food and Public Distribution, Department of Food and Public Distribution (erstwhile Department of Food under Ministry of Food and Agriculture) launched the Save Grain Campaign (SGC) scheme with 14 regional and 3 sub-regional SGC offices. Training, demonstration and publicity programs in scientific preservation of food grains and pest control techniques were given by these units (Anon. 2002). The research support was extended by IGMRI, Hapur.

Research support and documentation

ICAR extended research support initially with a project, All India Coordinated Scheme for Research on the Study of Field Rats, from 1959 until 1969 with four centres in the country. Subsequently, ICAR launched a major scheme All India Coordinated Research Project (renamed as Network Project) on Rodent Control from 1977. It has 10 centres covering the major agro-climatic zones of the country. The project scientists developed new information on different aspects of ecology and management of major rodent pest species of crops, and also suitable location-specific packages of practices. The research information in the country is being disseminated periodically by the ICAR bulletin *Rodent Newsletter.* Effective interactions among rodent researchers are also organised through biennial workshops/group meetings.

To fine-tune the field-based extension technology for rodent management, the DPPQ&S organises national workshops at NPPTI, Hyderabad, bringing together senior extension personnel of the states/UTs, ICAR project and agricultural university scientists, and representatives of the rodenticide industry. The extension-based recommendations finalised in these workshops are circulated to all states/UTs for their adoption. Four workshops have been conducted to date. NPPTI also undertakes limited research activities to fine-tune the research results produced by various research organisations.

Planning for rodent pest management

During 2001, the Government of India formulated planning for IPM with rodent control as one of the components for implementation by all relevant extension agencies. The available technology is being advocated to the states/UTs. In addition, challenges were identified, critical suggestions to address them were developed, and a strategy planned by relevant technical organisations.

Challenges for integrated rodent management

Intensive cropping due to increased irrigation fosters invasion by rodent pests and causes increased problems.

Table 3. Amounts of rodenticides (technical grade) used (t) in India.

Year	Rodenticide consumption (t)		
	Aluminium phosphide	Bromadiolone[a]	Zinc phosphide
1990–91	700	–	300
1991–92	650	–	250
1992–93	600	–	300
1993–94	850	116	300
1994–95	875	158	300
1995–96	900	195	300
1996–97	1050	223	250
1997–98	865	284	230
1998–99	955	266	250
1999–2000	1400	489	285
2000–01	2000	697	330

[a] Amount of formulated product.
Source of information: Pesticide Information (magazine issues in different years).

These changing agricultural practices also influence the density of rodent populations. The Indira Gandhi Canal in desert tracts brought more cultivable land under irrigation, but also increased rodent problems due to replacement of desert rodents with the lesser bandicoot rat, a dominant rodent pest. Similarly, failure to follow proper spacing in increased coconut cultivation has led to significant rodent damage to the nuts. Cultivation of oil palms in rodent-endemic areas also naturally decreases the productivity of oil palms due to their vulnerability to these pests in the initial bearing years. Natural calamities like flash floods and drought spells followed by heavy rains etc. also foster irruption of rodent populations in these areas, contributing to significant crop losses. However, monitoring the rodent situation in the regular pest monitoring systems of the states is lacking in the country. A survey of sporadic bamboo-flowering areas, rodent surveillance in the flowering areas, training of trainers, creation of awareness among the farming community, and rodent control measures are in progress to arrest major outbreaks in the north-eastern states anticipated from 2005 to 2007. However, actual causal factors responsible for such rodent outbreaks in this region are not known. There are endemic areas for rodent pests due to continuous availability of food and shelter in irrigated crops. Intensified monitoring efforts are not occurring after prolonged drought/dry spells and subsequent floods. As a consequence, early signs of irruptive rodent populations are not detected and the opportunity for timely action is missed. The existing linkage of extension and rodent research is inadequate for proper translation of research recommendations to the farm level.

Reports of an increased incidence of leptospirosis and the reappearance of plague are of major public health concern. Epidemiological surveys and studies on the biology of ecto-parasite populations in different areas are lacking. Such studies would indicate the actual reservoir/vector species responsible for disease transmission, indicate factors responsible for arthropod propagation in the rodent burrow, and may lead to appropriate management of the vector species.

Conclusion: critical suggestions for avoiding rodent-related problems

The states/UTs need to: popularise a non-chemical and community approach among the farming community; include rodents in pest/disease surveillance activities; train more personnel in rodent pest management; create awareness through the media; make available safer rodenticides in vulnerable places; liaise with public health authorities for coordinated action; and ensure quality control. The activities in the central sector include extending timely guidance to the states/UTs on appropriate control operations. The pesticide industry may supply rodenticides in a more timely manner in vulnerable places and develop safer formulations through research and development.

Revitalising research activities is the prime requirement in the development of rodent surveillance and ecologically based rodent management strategies. Microbiological expertise and epidemiological surveillance require updating in public health systems in India. Simultaneous toxicological studies of both rodent and flea populations should be undertaken.

A species-based approach to rodent management is desirable. During plague prevention activities, the main reservoir species, *T. indica*, is not targeted because it lives far away from human habitation. In view of this, planning of rodent vector management is desirable for preventing human disease. Even a small residual rodent population may lead to propagation of the bacteria and transmission of the disease to more animals/people. Hence, with the linkage between various extension agencies and central IPM centres, and the technical expertise of IGMRI, the ICAR project should be strengthened. More technical personnel must be trained to undertake management of the rodent pests and their plague vectors more effectively.

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Habitat manipulation and rodent damage control: reducing rodent damage in Australian macadamia orchards

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Abstract. This paper examines the relationship between adjacent non-crop vegetation and rodent (*Rattus rattus*) damage in Australian macadamia (*Macadamia integrifolia*) orchard systems. Orchards adjacent to structurally diverse, non-crop vegetation dominated by woody weeds exhibited significantly higher damage when compared to orchards adjacent to managed grasslands. This relationship formed the basis for a rodent damage reduction strategy utilising habitat manipulation. Structurally diverse, non-crop habitats were modified to grasslands leading to a reduction in rodent damage of 65%. This strategy was cost-effective and has the potential to be long-term with minimal effort needed to maintain sites in a modified state. Habitat manipulation is a process whereby the resource load in a system is reduced and hence rodent densities cannot reach levels where they cause significant crop damage. This paper provides empirical evidence to support habitat manipulation as a practical, cost-effective control strategy for rodent pests.

Introduction

Rodents cause significant damage to crops throughout the world and hence have been a target for control for most of our modern history. Rodent control methods have largely focused on manipulating the mortality of a population in order to suppress the population to a point where damage is acceptable. Unfortunately, mortality-based control often does not address the cause of high rodent densities and hence high damage to crops. When populations are reduced through mortality-based control, the remaining animals are exposed to increased resource levels and may in fact compensate for reductions in population size with an increase in reproductive output. This is ultimately expressed as the population 'bouncing back' post control. Caughley and Sinclair (1994) suggest that such control can be likened to a sustained-yield harvesting exercise where the off-take is never utilised.

In more recent times, the reliance on mortality-based control has been questioned. New methods of control are being sought that address the cause of rodent populations reaching high densities in crop systems. These new methods of control are conceptually different, with research directed towards: (1) reducing the fecundity of populations and hence reducing the populations' ability to respond to high resource availability (Chambers et al. 1999); and (2) reducing the resource availability (e.g. shelter and alternative food) in crop systems so that populations cannot build to high densities (habitat manipulation). Both these approaches aim to prevent populations from reaching densities where they have the potential to cause significant damage, as opposed to conventional, mortality-based methods where control is often not initiated until damage has occurred.

This paper examines the potential for habitat manipulation as a rodent damage mitigation strategy. A case study of rodent damage in Australian macadamia orchard systems is provided to highlight the approach to developing such a strategy. A more detailed analysis of the approach can be found in Horskins et al. (1998) and White et al. (1997, 1998).

Materials and methods

These studies were conducted on the Sunshine Coast in south-eastern Queensland, Australia. All orchard sites were at least 20 years old, were dominated by two macadamia varieties (HAES508 and HAES246) and were spaced at 5 m × 10 m intervals.

Twenty-one orchard sites were chosen on the basis of the type of adjacent non-crop habitats:

- six large, temporally stable sites (at least 10 m wide and consisting of a thick ground layer with a dense cover of woody vegetation);
- five small, temporally stable sites (less than 3 m wide and consisting of dense woody vegetation);

- four modified sites (grassland sites which were intermittently slashed when machinery access was possible);
- three highly modified sites (grassland sites routinely slashed throughout the year); and
- three sites which were surrounded by macadamia orchards.

To determine the spatial pattern of damage, tree selection for damage assessments was based on distance from the adjacent habitat. Five trees were randomly selected every two rows into the orchard (20 m), from the front row to the ninth row (80 m into the orchard). Five second-row trees were sampled also. All nuts that fell within a 2.5 m radius from the base of each tree were collected by hand and the numbers of both potentially harvestable mature nuts and mature nuts damaged by rodents were recorded, thus providing an estimate of economic loss for each tree.

Trapping

Of the 21 sites used for the analysis of damage, seven sites were randomly selected for kill-trapping of rats. Four sites were adjacent to large, temporally stable habitats and three sites were adjacent to temporally unstable sites (two modified and one highly modified). Each trapping site consisted of a block of 63 trees (seven rows by nine trees per row). Sixty large traps (Supreme rat snap traps) were placed at each site on a 10 m × 20 m trapping grid, with 40 traps in the orchard (20 ground layer and 20 tree layer) and 20 traps in the adjacent habitat (trapping was conducted at least 50 m away from damage estimation sites). All traps were baited with a mixture of rolled oats, peanut butter and linseed oil. Trapping was conducted over a 12-month period, with three consecutive nights of trapping at each site per month. The location of each animal was recorded and the animals' stomachs were removed for dietary analysis.

Habitat manipulation

Eight sites from the damage distribution study were selected for a trial of habitat manipulation—five with temporally stable (large) adjacent habitats and three with highly modified adjacent habitats. Three of the five large, temporally stable adjacent habitats were cleared of all vegetation greater than 10 cm in height. The area manipulated at each site had an orchard frontage of 125 m (25 tree frontage) and extended 20 m into the adjacent habitat. The adjacent habitats were sprayed with Grazon™ (the active ingredient of which is picloram), a dicotyledon-specific herbicide, during the growing season to minimise regeneration of shrubs and trees.

To determine the effect of habitat manipulation, damage estimates were conducted at all sites using the methodology outlined in the damage distribution study. Damage estimates from the previous year were compared to assess the success of habitat manipulation.

Results and discussion

Distribution of damage

The mean number of damaged nuts per tree across all study sites was 93 (5% of mean yield), however damage per tree ranged from 0 to 1522 nuts (0% to 83.4% of mean yield). The distribution of damage was skewed with the majority of trees (98.5%) sustaining some damage and the median damage was 40 nuts per tree (2.2% of mean yield).

Damage varied with the type and size of adjacent habitat ($F_{(4,543)}$ = 110.96, p < 0.001)(Figure 1). Damage was significantly higher in orchards adjacent to large, temporally stable habitats (mean damage per tree 9.9%). Orchards adjacent to small, temporally stable habitats and modified habitats sustained significantly less rodent

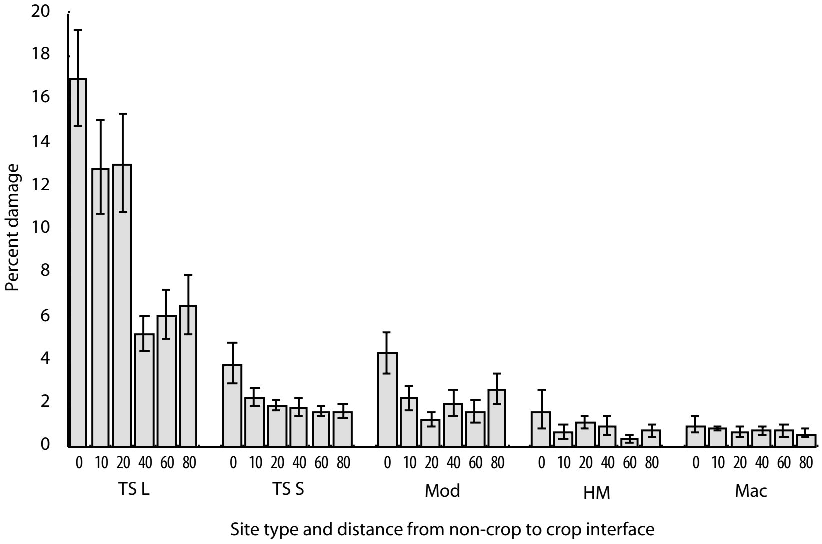

Figure 1. Percentage (1 se) of macadamia nuts damaged in association with adjacent habitat types and the distance (m) from the crop/non-crop interface, where: TS L = temporally stable (large); TS S = temporally stable (small); Mod = modified; HM = highly modified; and Mac = other macadamia orchards (after White et al. 1997).

damage (mean damage per tree 2.2%). The lowest level of damage was associated with orchards adjacent to highly modified and macadamia habitats (mean damage per tree 0.8%).

Distribution of damage within the site was associated with the distance from and the type of adjacent non-crop habitat ($F_{\text{Habitat (4,532)}} = 100.49$, $p < 0.001$; $F_{\text{Distance (5,532)}} = 7.19$, $p < 0.001$; $F_{\text{Interaction (20,532)}} = 2.39$, $p < 0.001$) (Figure 1). Sites adjacent to temporally stable habitats (large and small) sustained higher front-row damage (LSD < 0.05). Sites adjacent to large, temporally stable non-crop habitats sustained high levels of damage for the first three rows, whilst damage in orchards adjacent to small, temporally stable habitats was only high in the first row. This trend was not observed in orchards adjacent to temporally unstable (modified and highly modified) or macadamia habitats, with damage being evenly distributed throughout the orchard. Ultimately, the level of damage in a crop was directly related to the size, structure and temporal stability of the non-crop habitat.

Rodent distribution and diet

A total of 696 *Rattus rattus* was captured. Rodent captures were not uniformly distributed throughout the orchard system. Highest trap success occurred in large, temporally stable adjacent habitats. Trap success in temporally unstable adjacent habitats (mean = 1.4%) was significantly lower than trap success in temporally stable adjacent habitats (mean = 12.9%) ($t = 4.66$, df = 5, $p = 0.006$). Orchard trap success (mean = 2.2%) was similar regardless of the temporal stability of the adjacent habitat ($t = –0.65$, df = 5, $p = 0.542$). Damage levels in orchards were positively correlated with the number of rodent captures in the adjacent non-crop habitats ($r = 0.794$, $p = 0.033$, $n = 7$).

Of the 363 rodents captured within the adjacent habitat, 218 (60.1%) had consumed macadamia nuts along with 94.1% of the 204 rats caught within the orchard. These results suggest that a large rodent population utilises the temporally stable adjacent non-crop habitats and move into the orchard to feed. This supports the damage distribution studies, which suggest that the majority of damage occurs in the first few rows of crops adjacent to large, temporally stable adjacent habitats. These results also indicate that there may be a second, smaller population that lives within the orchard component of the system causing the low baseline damage that is seen in all orchards, regardless of adjacent habitat type.

Habitat modification

The damage and dietary results confirm that adjacent non-crop habitats play an important role in crop damage in macadamia orchards. The large difference between damage in orchards adjacent to large, temporally stable non-crop habitats and those adjacent to highly modified non-crop habitats suggested that a habitat manipulation strategy could be appropriate for reducing rodent damage. The process used involved simplification of the large, temporally stable adjacent non-crop habitats, from largely dense weedy vegetation providing high vertical structure, to large, highly modified grasslands, providing limited structure.

There was no significant difference in the level of damage between years in orchards adjacent to highly modified habitats ($F_{(1,166)} = 2.301$, $p = 0.131$) or unmanipulated sites adjacent to temporally stable adjacent habitats ($F_{(1,110)} = 0.101$, $p = 0.751$). Before habitat manipulation, there was no significant difference in damage levels between the temporally stable sites that were manipulated and those that were to remain unmanipulated ($F_{(1,93)} = 0.534$, $p = 0.467$). However, orchards adjacent to habitats that were manipulated showed a significant reduction in damage compared to unmanipulated, temporally stable sites ($F_{(1,178)} = 38.04$, $p < 0.001$) (Figure 2). Manipulation of the adjacent habitat reduced damage from 13% (±1.8%) to 4.6% (±0.4%), a reduction of 64.6%.

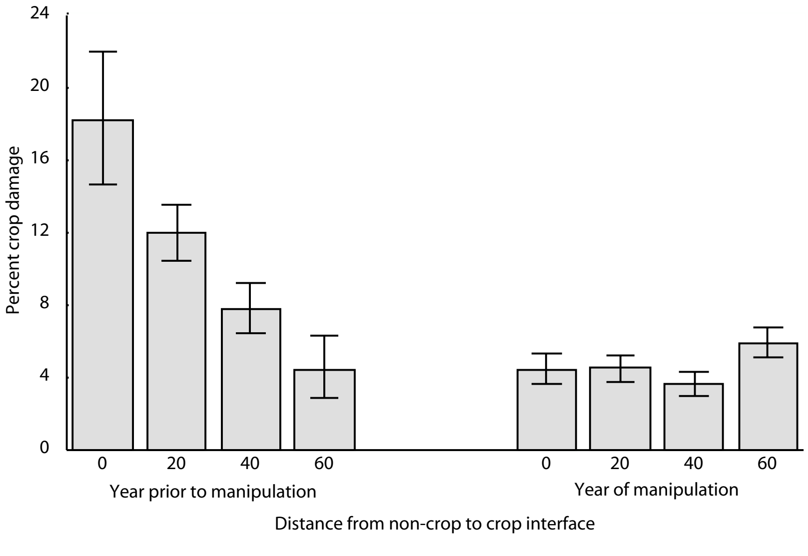

Figure 2. The effect of manipulating large, temporally stable, structurally complex non-crop habitats on the distribution of macadamia nut damage (mean, ±1 se) in adjacent orchards (after White et al. 1997).

The high edge damage associated with temporally stable non-crop habitats was significantly reduced by the manipulation of the non-crop habitat. This effect was most likely the result of the non-crop population of rodents significantly declining in number due to reduced availability of structural resources. The resultant damage in the orchard was likely associated with the small component of the population that lived within the orchard itself.

The cost of manipulating the adjacent habitat along an orchard frontage of 25 trees (120 m) was calculated at US$164 in the initial year. This figure represents the estimated cost of clearing the vegetation (US$54) and applying two rounds of herbicide to control regrowth (US$105). The average tree yield of the orchards examined in this study was 20.5 kg of nut in shell (NIS). At the time of this study, NIS sold for US$1.65/kg. The losses due to rodent damage were calculated on the basis of a frontage of 25 trees and extending 7 rows into the orchard. The losses due to rodent damage in the year before manipulation at sites adjacent to temporally stable habitats was US$820 (±$170). At sites which had been manipulated, the losses were US$271 (±$23). Habitat manipulation reduced crop losses by US$549 at a cost of US$164, resulting in a saving of US$385/site to the grower. The profit associated with control should increase in subsequent years due to reduced costs in maintaining previously manipulated adjacent habitats.

Conclusions

Habitat manipulation operates by removing or altering the critical resources that give rise to high reproductive success and/or survival. The method has been described as one of the few control methods that does not operate against a negative feedback loop (Caughley and Sinclair 1994). This method of control has the potential to be implemented in many crop–rodent systems, but requires a sound understanding of the system in which control is to be implemented. The main aspect of habitat manipulation is determining the habitat features that give rise to high damage levels and also identifying habitat features that lead to limited damage levels. Ultimately, reducing the size of habitats and replacing them with habitats that lead to low damage is the objective of such control.

Habitat manipulation is one of the few rodent damage control strategies that has been shown to be cost-effective. The other main advantage of such a strategy is that it is not technically challenging to conduct and does not require access to rodenticides that are often expensive. A difficulty associated with habitat manipulation is that environmental damage may occur as part of the strategy. Habitat manipulation may also impinge upon biodiversity values of the areas in which they are implemented. These issues should be examined in subsequent research examining habitat manipulation.

Acknowledgments

This project was generously funded by the Australian Macadamia Society and Horticultural Research and Development Corporation (HRDC), and was conducted on a Queensland University of Technology Postgraduate Scholarship.

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Patterns of rodent pest distribution in a maize cropping system in the Kenyan Rift Valley

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Abstract. We studied the small mammal community structure in a maize cropping system in the Kenyan Rift Valley. Using the capture–mark–recapture (CMR) method, we set in maize fields four permanent trapping grids each with 100 box-traps. Traps were opened for three consecutive days every 4 weeks for 20 months. Eight hundred and thirty-seven individual small mammals were captured 1240 times in 20,100 trap-nights. The rodents included six murids (*Aethomys* cf. *kaiseri*, *Arvicanthis* cf. *neumanni*, *Lemniscomys striatus*, *Mastomys* cf. *erythroleucus*, *Mus minutoides* and *Rattus rattus*) and a cricetid (*Tatera* cf. *robusta*), while the shrews were all soricids (*Crocidura* species). *Mastomys* was the most dominant species within and across the entire grids, accounting for 71.0% of all captures. Other common rodents were *Arvicanthis* (14.1%) and *Mus* (8.0%). *Aethomys* and *Rattus* were rare, being captured only at the highest altitude (1922 m) while *Tatera* was restricted to the lowest altitude (1712 m). Rodent pests were not uniformly distributed in maize fields even though the maize cropping agro-ecosystem was continuous here. *Mastomys* remains the most important pest species due to its distribution and abundance in the study area.

Introduction

In Kenya, almost half the acreage used for food crops in the small farm sector is planted to maize (Rundquist 1984). More than 1 million ha of maize, with a production of between 1.4 and 3 million t, are cultivated. Large-scale farms produce 13% of the total production on 10% of the area and supply 45% of the maize sold in local markets. The remaining 87% of the Kenyan maize production is subsistence for the farming population and only a small surplus is marketed for profit (Dissemond and Hindorf 1990), yet it is the basic foodstuff for about 90% of the population (Gerhart 1975).

Reports of rodent damage are recorded annually in Kenya with serious outbreaks every few years and some areas experiencing up to 90% loss. In April 2001, 2833 ha of land under maize was reported destroyed by rodents in Kwale district of Kenya. This constituted 30% of the total area under maize in the district. With a population of 28.8 million (Goliber 1997), likely to double by the year 2020, a steady loss of even few per cent of production must be checked. Moreover, the region has 70 million inhabitants requiring food aid (FAO 2000).

Although rodents have received relatively little attention in Africa as vertebrate pests (Fiedler 1994; Bekele and Leirs 1997), their capacity for crop depredation and transmission of diseases introduces an applied aspect of rodent ecology. Where rodent outbreaks have been reported, control measures have favoured application of toxic chemicals often at a time too late to be effective. The contemporary approach to rodent problems is that of ecologically based management. This has received fewer considerations due to insufficient basic field and experimental data in support of their efficacy (Makundi et al. 1999). Thus, strategies in management of rodents both in the field and in stores are poorly developed. Effective control needs information on accurate pest identity, ecological theory and field data to provide vital ingredients in the design of sustainable management strategies (Singleton et al. 1999). Our knowledge of rodent pests in Kenya is inadequate, while issues on pest problems remain anecdotal. Thus, we developed a study to provide information towards breaching this gap.

Materials and methods

The study was carried out in Nakuru district in the Kenyan Rift Valley at latitudes 35°28'–35°36'E, longitudes 0°13'–1°10'S, and altitudes of between 1720 and 1800 m above sea level. The climate in this area falls between semi-arid (annual rainfall less than 760 mm) in the lower areas and dry subhumid (annual rainfall of 1270 mm) regions at the higher altitudes. Rainfall is bimodal with peak precipitation (70–80%) in March to May and late August to October, although great variations may occur from year to year. The maximum temperature is about 30°C, with December to March being hottest and July being coolest at an average of 23.9°C.

Trapping was done on four permanent grids (1 ha each) in maize crop fields along an altitudinal gradient: (i) Mugo (1922 m); (ii) Beth (1895 m); (iii) Kurt (1823 m); and (iv) Moto (1712 m). The capture–mark–recapture (CMR) technique was used in sampling small mammal populations. Rodents were live-trapped using Sherman's LFA traps measuring 23 × 8 × 9 cm, between May 2000 and December 2001. Each grid consisted of trapping stations laid at 10 m within and between rows, giving 100 traps per grid. Trapping in Mugo and Beth grids commenced in May 2000, at Moto grid in July 2000, and at Kurt grid in April 2001. Primary trapping was made every 28 days and secondary trapping for three consecutive days and nights during each primary trapping session. Traps were baited with a mixture of peanut butter, corn oil and fried coconut cubes.

Results and discussion

A total of 1240 captures of 837 individuals were made of seven rodent and undetermined shrew species in 20,100 trap-nights. This gave a trap success of 6.2%. The low capture rates were attributable to prolonged drought before the study and inconsistent precipitation during the work. Rodents captured included six murids (*Aethomys cf. kaiseri* (Noack 1887), *Arvicanthis cf. neumanni* (Matschie 1894), *Lemniscomys striatus* (Linnaeus 1758), *Mastomys* cf. *erythroleucus* (Temminck 1853), *Rattus rattus* (Linnaeus 1758), *and Mus minutoides* Smith 1834) and a cricetid (*Tatera* cf. *robusta* Cretzschmar 1826), while the shrews were all soricids (*Crocidura* species) (Table 1).

The most dominant species in all the trapping grids was *Mastomys*, accounting for 71% of all captures. Reasonably common were *Arvicanthis* (14.1%) and *Mus* (8.0%). The distribution of *Mastomys* was uniform (χ^2 = 4.855, P = 0.182, n = 594) in all the grids. Distribution of other species varied significantly among the four grids: *Arvicanthis* (χ^2 = 28.529, P = 0.000003, n = 119), *Mus* (χ^2 = 64.632, P < 0.00001, n = 67), *Lemniscomys* (χ^2 = 20.538, P = 0.0001, n = 13), *Tatera* (χ^2 = 81.000, P < 0.00001, n = 27) and *Crocidura species* (χ^2 = 15.000, P = 0.0001, n = 13) (Table 1). Three and one individuals represented *Aethomys* and *Rattus*, respectively.

The importance of *M. erythroleucus* in eastern African agriculture has been documented previously in maize fields of Ethiopia (Bekele and Leirs 1997). Although it was not reported in the early rodent outbreaks in the Kenyan Rift Valley (Taylor 1962, 1968; Taylor and Green 1972), this may have been due to misidentification. Moreover, the multimummate rats—especially *Mastomys natalensis*—are the most important murid pests in eastern Africa (Fiedler 1994; Martin et al. 1989; Leirs et al. 1996). Other important murid pests previously recorded in our study sites include *Arvicanthis*, *Lemniscomys* and *Rhabdomys pumilio* (Sparrman 1784) (Taylor 1962, 1968; Taylor and Green 1976). During our study, *Arvicanthis* was captured in fair numbers (14%), *Lemniscomys* was recorded only at the higher altitudes in low numbers, while *Rhabdomys* was not recorded in over 20,000 trap-nights. Despite its pest status elsewhere, *Tatera* has never been reported as a pest in this area where it was restricted to the drier, lower altitude (the Moto grid).

Conclusions

Our study has shown that rodent pests are not uniformly distributed in maize fields, even within a continuous maize cropping agro-ecosystem in Kenya. Patterns in rodent pest distribution may be attributed proximally to

Table 1. The community structure, number of individuals, and distribution of rodents and *Crocidura* captured in four trapping grids in maize fields in the Kenyan Rift Valley between May 2000 and December 2001.

Species	Study grids				
	Mugo	Beth	Kurt	Moto	Total
	Trap nights				
	6000	6000	2700	5400	20,100
(a) Rodentia					
Mastomys cf. *erythroleucus*	151	152	164	127	594
Arvicanthis cf. *neumanni*	32	8	30	49	119
Mus minutoides	45	4	8	10	67
Tatera cf. *robusta*	0	0	0	27	27
Lemniscomys striatus	10	3	0	0	13
Aethomys cf. *kaiseri*	3	0	0	0	3
Rattus rattus	1	0	0	0	1
(b) Insectivora					
Crocidura species	3	9	1	0	13
Total	245	176	203	213	837
Trap success (%)	6.0	5.8	11.2	5.1	6.2

localised conditions driven by land use and altitude. Since rainfall here varies with altitude, climate is perhaps of ultimate importance in determining the distribution of the pest species. Due to ease of capture of *Rhabdomys*, its absence during this study was surprising given it had been a major pest here previously. It would appear that the species is locally extinct for reasons beyond the scope of current findings. *Mastomys* is the most important pest species with uniform distribution in all maize fields.

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Prey selection by barn owls in rice fields in Malaysia

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Abstract. Prey selection of the barn owl, *Tyto alba,* in rice fields in Malaysia was measured using feeding pellets collected in and around nest boxes and perching sites from September 2001 to February 2002. Analysis of the feeding pellets showed that rats constitute 94.7% of the barn owls' food (*n* = 160), while shrews (6.3%, *n* = 5) and birds (7.4%, *n* = 4) constitute the remainder. The rice-field rat, *Rattus argentiventer,* constitutes 85.7% of the identifiable rat prey species and the remainder (14.3%) is the wood rat, *Rattus tiomanicus*. Pellets collected in January showed that 61.1% of the prey consist of juvenile rats, compared with 12.2%, 25.8% and 42.8% in the preceding months of October, November and December, respectively. The higher percentage of juvenile rats in the prey can be associated with the rice-field rat's reproductive cycle, which in turn is influenced by the phenology of the rice paddy plant. Pellets collected in October, November and December showed a high proportion of headless prey, i.e. 51.2%, 54.8% and 76.2%, respectively. Fewer pellets were collected in January and February, with a relatively lower proportion of headless prey, i.e. 22.2% and 50%, respectively. These findings can be explained by association with the owl's breeding period that lasts from October to December, during which male barn owls usually decapitate and consume the head and bring home headless rat carcasses to the females and their young.

Introduction

The barn owl, *Tyto alba*, is a cosmopolitan species occurring on all continents and in a wide range of habitats, except Antarctica and the smaller Pacific islands (Smith and Cole 1989). In recent years, there has been increasing public interest in the potential for owl predation to control rats. In Peninsular Malaysia, the first confirmed breeding of the barn owl was recorded on Fraser Estate, Kulai, Johore, in 1969 (Wells 1972), and these owls are believed to have originated from Java and Sumatra (Lenton 1985). The spread of *T. alba* in Malaysia was closely associated with extensive oil palm cultivation, as these plantations harbour a bounteous supply of rats. The provision of artificial nest boxes in oil palm plantations has succeeded in boosting local *T. alba* populations to effectively reduce rat infestations (Smal 1988). The barn owl feeds exclusively on live prey, preferring small rodents and birds, which it swallows whole or in parts (Harrison 1991). After digesting the softer tissues, it regurgitates the remains in compact oral pellets, which usually contain bones, claws, teeth, fur and feathers.

Several studies on the food selection of *T. alba* in oil palm plantations show that rats constitute a major prey. Lenton (1980) and Smal (1988) found, from analysis of oral pellets, that rats comprised more than 98% of the owls' food. The objective of this study was to evaluate prey selection of *T. alba* in rice-field areas. Monthly variations in prey items, with particular reference to adult versus juvenile rats and the presence or absence of skulls in pellets, were also recorded to determine whether feeding behaviour is influenced by the owl's breeding cycle and the rat's reproductive cycle.

Materials and methods

Pellets were collected from September 2001 to February 2002 in and around nest boxes and perching sites in a paddy-field area in Sawah Sempadan, Tanjung Karang, Selangor, and pooled into monthly samples. Individual pellets were dried at 60°C for at least 48 h, then soaked in 0.5 M NaOH. The pellets were than teased apart and the contents recorded. If a skull was present, the following measurements were made to 0.1 mm using a caliper (Mitutoyo Series 505): (1) skull length (from the posterior-most point of the supraoccipitals to the anterior tip of the upper incisor socket, (2) upper tooth row, and the length of the (3) palatine foramen, (4) lower jaw (mandible), (5) femur, and (6) humerus. The identification of *Rattus argentiventer* and *Rattus rattus diardii* follows Harrison (1962). For *R. argentiventer,* the anterior palatine foramine is longer than the upper tooth row and extends between the cheek teeth, while that for *R. r. diardii* is usually variable (Figure 1). *Rattus tiomanicus* is identified by the presence of anterolabial stylid on the second lower molar (Lekagul and McNeely 1977). Smaller skulls were designated as juveniles. If a skull was lacking, measurements of the femur and humerus were used to distinguish juveniles from adults.

Results and discussion

Prey items

A total of 169 prey items were identified from 160 pellets (nine pellets had two prey items in them) collected during this study. Of these, 160 or 94.7% contained rats. The other prey identified from the pellets were the common shrew, *Suncus murinus* (2.9%, *n* = 5) and birds (2.4%, *n* = 4). Lenton (1980) analysed 2839 pellets from oil palm plantations and determined that 99.1% of the prey items were rats. He also determined that shrews were the most common non-rat prey in the plantations but from a much wider range of prey, which included birds as well as arthropods and amphibians. The far fewer pellets analysed in this study may explain the lower range of prey items. The overwhelming dominance of rats in the diet of the owls nonetheless was striking.

Rat species were determined from pellets in which skulls were present. Only two species, *R. argentiventer* and *R. tiomanicus*, were identified based on the measurements and designated features of the skull. *R. argentiventer* formed the primary diet with 85.7% of the identifiable rat prey (*n* = 77) as compared to *R. tiomanicus* with 14.3%. In oil palm plantations, Lenton (1980) determined *R. tiomanicus* as the most common rat species, accounting for 89.78% of the prey items, whereas *R. argentiventer* was only 6.22%; the rest being occasional *Rattus exulans*, *R. annandalei*, *R. rajah* and *R. surifer*. The rat species composition from both Lenton's and this study suggests that the diet of *T. alba* is influenced by the rat species' composition, although this needs to be substantiated with live trappings. However, it is fairly well established that *R. tiomanicus* is more common in oil palm plantations (Han and Bose 1978; Wood and Liau 1984) and *R. argentiventer* is more common in rice fields (Lam 1982, 1988). The presence of *R. tiomanicus* in the owls' diet in the present study can be attributed to owls hunting in oil palm plantations adjacent to the rice-field area (Figure 2).

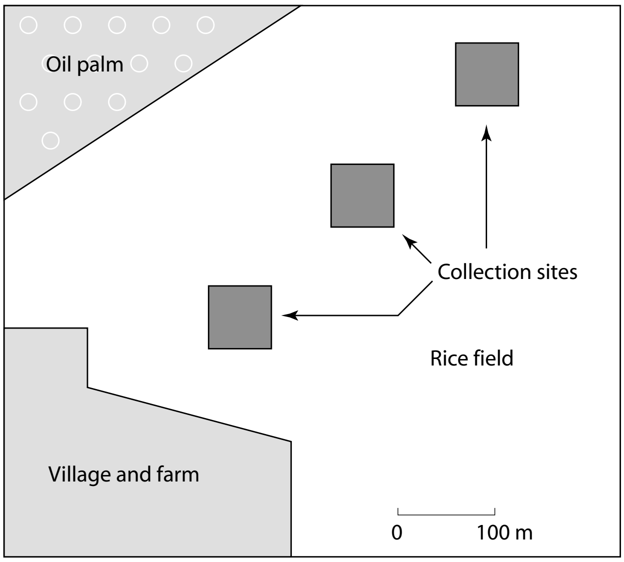

Figure 2. Sites for the collection of oral pellets around nest boxes and perching poles.

Analysis of a higher number of pellets should give a better picture of the rat species' composition in the diet of *T. alba* in rice fields. Occasional trappings in the area, especially near farmers' houses and other buildings,

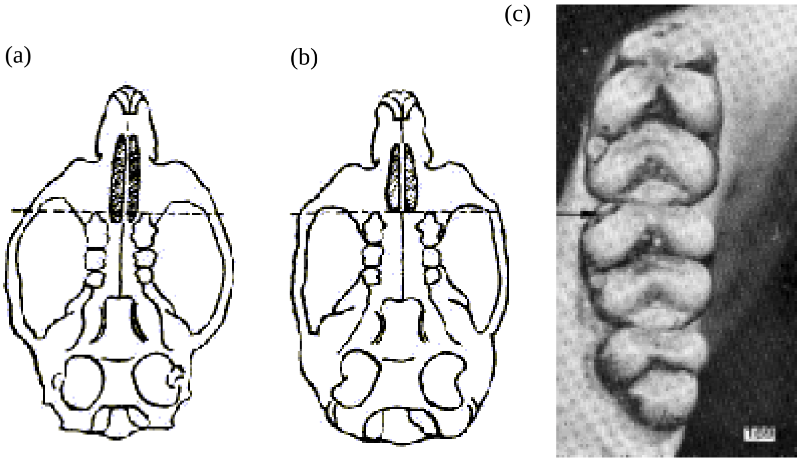

Figure 1. The anterior palatine foramina (dark shaded) is longer than the upper tooth row and extends between the cheek teeth in *Rattus argentiventer* (a); while that of *Rattus rattus diardii* (b) is variable. *Rattus tiomanicus* (c) possesses an anterolabial stylid on the second lower molar.

revealed that *R. r. diardii* is quite common and it may also constitute an occasional prey of *T. alba*. Lam (1988) conducted a trapping study in another rice-field area in Malaysia at Bumbung Lima, Perak, and caught a small number of *R. r. diardii* among the predominantly *R. argentiventer* rodent population.

As an oligophagous predator with a narrow prey range (Lim 1999), this study reaffirms the suitability of the barn owl as a natural predator in a rice agro-ecosystem as it is unlikely to prey on poultry or other non-target species.

Rat prey selection of barn owls

Barn owls in this study took both adult and juvenile rats. On average, juvenile rats constituted only 28.1% of the total rat prey (Table 1). However, the proportion of juveniles varied from month to month. The highest proportion of juveniles occurred in December and January, comprising 42.8% and 61.1% of the total number of pellets with rats, respectively. The largest number of pellets collected was in November, but juveniles comprised only 25.8% of that month's uptake. These figures suggest that the prey composition is influenced by the rice-field rat's reproductive cycle, which peaks around harvesting time (Lam 1983), the period when new cohorts join the above-ground population. At Tanjung Karang, rice is harvested in December and January, and this explains the higher proportion of juveniles in the diet during those months. Although *T. alba* prefers to take smaller rats (Harrison 1991), this preference is largely influenced by the availability of the range of prey sizes. This study did not attempt to estimate the relative availability of each size class of rats, but the data suggest that *T. alba* takes mostly adults rats, varying juvenile prey uptake according to their availability.

Table 1. Monthly percentage of *Tylo alba* pellets containing juvenile rats and rats without heads.

Month	% juvenile	% rat prey without head	Total number of pellets containing rats
September	0	33.3	6
October	12.2	51.2	41
November	25.8	54.8	62
December	42.8	76.2	21
January	61.1	22.2	18
February	33.3	50.0	12

Proportion of pellets without skulls

Pellets were categorised according to whether or not they contained a skull. The highest proportion of pellets not containing skulls was collected in December (76.2%, n = 21). The proportion was also high in October and November (51.2%, n = 41; and 54.8%, n = 62, respectively), but substantially lower in January (22.2%, n = 18). In February, the percentage was 50% but this could be due to the small sample size (n = 12) (Table 1). The presence or absence of skulls in pellets can be associated with the owl's breeding cycle. In Tanjung Karang, *T. alba* starts to breed in October. Most of the chicks hatch in November and December. Male barn owls have been observed to decapitate their prey and bring the headless carcasses to feed the females and her chicks (Lenton 1984). During the time that chicks are in the nest, female barn owls rarely leave their nest. Therefore, the higher percentage of skull-less pellets in the nest box during the breeding period is the consequence of males taking home headless meals for the chicks. In January, most of the owlets have fledged, and therefore males take less food home, resulting in a lower percentage of skull-less pellets.

Conclusion

The food of the barn owl in the rice-growing area of Tanjung Karang is mainly *R. argentiventer.* Other rat species may also be taken subject to availability, particularly *R. tiomanicus*. Shrews and birds were also preyed upon but comprised little of the prey eaten. Prey preference is associated with the rice-field rat's reproductive cycle as reflected by the higher proportion of juvenile rats in the diet as these become available. The proportion of pellets without skulls was higher during the owl's breeding season because males usually feed on the head and bring home the headless portion to feed the females and chicks.

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Robustness of techniques for estimating rat damage and yield loss in maize fields

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Abstract. Four sampling techniques for estimation of maize damage and yield losses due to rodents were compared. We determined the actual rodent damage in 15 maize fields in Tanzania by counting damaged and undamaged maize plants and calculated the actual yield loss. The techniques of (a) non-stratified systematic row sampling, (b) non-stratified systematic Z-sampling, (c) stratified random square sampling, and (d) non-stratified simple random sampling were compared for robustness in terms of precision and accuracy, and time spent on damage and loss estimations. Our results showed clearly that non-stratified systematic row sampling is the most robust technique for assessing rodent damage and yield loss in the study fields. We provide a standard curve for sampling density and precision for this technique.

Introduction

Rodent damage is a serious impediment for agriculture (Fiedler 1988; Singleton et al. 1999). Survey reports in Tanzania, relying on data from questionnaires, have shown that, on average, rodents cause about 15% loss of maize crop annually (Makundi et al. 1991). Precise estimates are rarely available though obviously needed (Judenko 1973; Mwanjabe and Leirs 1997). There are many reasons for making more precise assessments, including: to establish the economic status of specific pests; to justify expenditure on control; to estimate the effectiveness of control measures; to measure the effects of environmental factors on the loss of yield caused by pest attack; to give information to manufacturers and distributors of pesticides to enable them to decide what action should be taken; and to give a basis for directing future research and agricultural planning (Judenko 1973; Buckle 1994). Clearly, many of these requirements are important in planning a strategy for field rodent control.

Unlike insects, rodents are secretive and not easily observed; many are nocturnal. Often, the investigator must rely on various signs such as tooth marks, missing plants parts and characteristics of the damage, burrows, and traps to identify rodent species (Fiedler 1988). Also, to assess rodent damage, a larger area must be investigated than is the case with insects, since rodents are more mobile, far from homogeneously distributed in the crop, and a single individual typically can cause damage to several plants in one night. Estimation techniques for insect damage, therefore, would be not be adequate for assessing rodent damage.

Several sampling techniques for estimating rice damage and yield loss caused by rodents have been evaluated in southern Asia, and this research has suggested that a stratified or clustered approach is the most reliable (Benigno 1979; Rennison and Buckle 1988). Hoque et al. (1986) evaluated three damage-estimation sampling techniques in maize fields one week before harvest and found that they gave similar results but differed considerably in efficiency. Benigno (1980) reported that stratified, random quadrat sampling is suitable for maize-damage evaluation. In Africa, Mwanjabe and Leirs (1997) used a systematic row sampling approach in their study in Tanzania to estimate rodent maize damage at planting, while Key (1990) used transects of 50 planted points within a maize plot to estimate rodent damage at the seedling stage and rodent cob damage at the maturity stage.

In the present study, we compared the actual rodent damage and yield loss in maize fields with four different estimation techniques. We investigate which technique is most robust in terms of precision and accuracy and most efficient in terms of technical complexity and time. This research aims to provide a sound basis for future work, which requires damage and yield loss estimation for pest monitoring, surveillance and forecasting and management evaluations.

Materials and methods

Locations and seasons

Field experiments were carried out during the cropping seasons in 1999 and 2000, in two farms at Sokoine University of Agriculture, Morogoro, Tanzania. The farms are located at 6°50'S, 37°38'E at an altitude of 510 m above sea level (asl) and 6°46'S, 37°37'E at 480 m asl, respectively. The area has a bimodal rainfall pattern and the study was conducted during the long rains maize-growing season each year. The seeds were sown in March, although the exact timing depends on rainfall, while the harvesting was done at the end of July.

Treatments

The study was carried out in 15 plots for damage assessment at the seedling stage and 8 plots for assessment of cob damage at maturity, 70 × 70 m each. Actual damage was assessed for comparison with estimations made using the sampling techniques described below. Rodent densities during the damage assessments ranged from 0 to 140 animals per ha (L.S. Mulungu et al., unpublished data). All fields received similar standard agronomic treatments, i.e. early ploughing, application of triple superphosphate (TSP) fertiliser (20 kg P_2O_5/ha) before planting, and nitrogen fertiliser (40 kg N/ha) twice as a top dressing, three weeks after the sowing and booting stages. Three seeds of maize (variety Staha) were planted per hole, at a planting space of 90 × 60 cm. Weeding was carried out twice. Harvesting was carried out by hand picking of the cobs when all cob silks were dry.

Sampling procedures

Crop damage assessment was carried out at the seedling stage, 10 days after planting, and at maturity, 1 week before harvesting. At the seedling stage, the number of seedlings was recorded at each sampled planting hole (since three seeds were planted per hole, damage was expressed as the proportion of missing seedlings). At maturity, the damaged proportion of each sampled cob was estimated. We used four different sampling methods, based on Mwanjabe and Leirs (1997), Rennison and Buckle (1988), Hoque et al. (1986), Benigno (1979, 1980):

- (a) *Non-stratified systematic row sampling*, where the sampling unit is a maize row; four rows apart and leaving out the two outer rows in order to reduce inter-field effects and prevent sampling of abnormal rodent movement behaviour in relation to barriers (Kaukeinen 1984). The assessor walks along maize rows across the field, recording damage at each plant hole in the row. In our fields, 15 rows were sampled per field.
- (b) *Stratified random square sampling*, in which the fields first are surveyed superficially in order to determine the distribution of rodent damage. Parts of the field with relatively similar damage intensity are then grouped in strata as low, medium, and high damage. Within each stratum, three squares of 5 × 5 holes are selected randomly in an area of similar damage intensity. From there, mean percentage damage is calculated for the whole field on the basis of the proportion of the different strata in the field.
- (c) *Non-stratified systematic Z-sampling*, in which the samples are systematically taken from nine points (2 × 5 holes) at fixed distances along a zigzag line in the maize field, running along two sides of the fields, connected by a diagonal line. Thus, a total of 90 holes (270 plants) are examined per field. In our fields, the distance between any two sampling points in the parallel lines was 27.5 m apart, while that between points on the diagonal line was 21.0 m.
- (d) *Non-stratified simple random sampling*, in which each individual sample unit (a planting hole) is drawn independently and with equal probability using the random-pair technique (Gomez and Gomez 1984). We selected the holes as follows: the total number of rows per field and holes per row was determined leaving two rows out around each field (e.g. 75 rows per field and 114 holes per row); then 120 pairs of random numbers was selected, each with a random row number and an independent random hole number in that row. These pairs formed the coordinates of the sampling points and were located and inspected in the field.

We also measured the actual damage by sampling every planting hole in a number of fields at the seedling stage (15 fields: 2 fields in 1999 and 13 fields in 2000) and at maturity (8 fields) to compare the robustness of the sampling methods. Cob damage at maturity was not observed at the first farm. In eight plots at the second farm in both years, only non-stratified systematic row sampling was used at seedling stage but the four sampling techniques and the actual counting of all plants were employed at maturity because maize cobs in this farm were damaged by rodents.

Yield loss

After harvest, the maize was threshed, cleaned by hand winnowing, and sun dried. The grain was weighed and the weight, adjusted to a common moisture level of 15.5% (Moyal 1998), was taken as the actual yield for the plot. The potential yield for the plot was calculated as the product of the total number of seeds planted times the mean actual yield per unattacked plant (surrounded by other unattacked plants), assuming no compensation. The total yield loss for each plot (Y_t) was calculated as the difference between potential and actual yield. The yield loss during the maturation period (Y_m) was calculated by using a difference between mean actual yield per unattacked plant and mean yield per attacked cobs. The yield loss due to damage at planting was then $Y_t – Y_m$.

Evaluation of techniques

The four sampling techniques were compared with regard to time use (time spent for completing the estimate for a plot), complexity for the observer, and reliability (correlation between estimated damage versus actual damage and yield loss, at planting as well as at maturity).

Sampling intensity

Since the non-stratified systematic sampling technique turned out to perform best (see Results), we investigated which sampling row interval at planting time would give an optimal balance between effort and accuracy. Using a computer, we simulated sampling intensities, re-sampling data from the 15 plots for which actual damage was recorded for all plants. Different sampling intervals (every 2nd, 3rd, 4th, 5th, ...20th row) were chosen and, for each sampling interval, we ran all possible simulations by choosing a different starting line every time. Simulated sample size decreased with increasing interval between sample rows. Obviously, choosing every single line corresponds to counting all plants, i.e. the actual damage. The variation between estimates was plotted against sampling interval.

Results and discussion

Comparison of sampling techniques

The average time spent per plot for each sampling technique is shown in Table 1. Non-stratified systematic row sampling was the fastest method, while non-stratified simple random sampling required the most time. In terms of complexity, the non-stratified systematic row sampling technique was the easiest. Previous studies in maize and rice in Asia also indicated a preference for similar methods, mainly because of the technical complexities of random sampling (Hoque et al. 1986; Rennison and Buckle 1988; Bailey 1994).

The correlation analyses between estimated and actual damage during seedling stage and harvest period show that for all sampling techniques, estimates and actual damage were highly correlated (Table 2). The non-stratified systematic row sampling technique had the highest correlation values both at the seedling stage and at maturity (r = 0.99 and r = 0.98, respectively). The non-stratified simple random technique had relatively lower correlation values (r = 0.95, r = 0.88) in all crop growth stages. In theory, stratified sampling should give at least as good an estimate as a non-stratified one. That was not the case, and probably is an indication that it is difficult to keep track of the boundaries of the strata and estimating their relative proportion of the field (Hoque et al. 1986).

Our study also showed that the four tested techniques gave good predictions of yield loss due to rodent damage at crop seedling and maturity growth stages. However, at maturity, stratified random square sampling again provided the weakest relationship (Table 2). This suggests that this sampling technique is not robust at this crop growth stage. Non-stratified systematic row sampling gave the highest correlation of crop damage and yield loss at both seedling and maturity stages of the crop. At the seedling stage, the regression coefficient (r^2) is lower than that at maturity, probably because many things can happen in the period between seedling and maturity stages, such as attack by other pests, disease, effects of weeds, and change in weather conditions. Buckle (1994) and Judenko (1973) pointed out that crop damage at the planting stage is compensated from better growth caused by reduced competition for growth resources following the death of neighbouring plants. However, Myllymäki (1987) pointed out that, in maize, compensation was minimal. Maize damage at the ripening stage is not compensated for, since kernels have completed growth by then.

Our computer simulations for different sampling intensities allowed us to quantitatively describe the intuitively assumed relationship between sampling intensity and estimate accuracy for the systematic row sampling. The standardised variance, which is the ratio of variance of the estimated damage values to the actual damage, gives a measure of the proportional variance of the estimates. An increase of estimate variation is observed when the interval between rows becomes larger (Figure 1). In other words, estimates become less reliable.

Table 1. Average time used to collect samples and degree of complexity for each sampling technique.

Sampling technique	Time (h) spent per plot (mean ± sd)	Complexity
Non-stratified systematic row sampling	1.09 ± 0.05	Simple, little training required on how to count and select rows, no special equipment required
Stratified random square sampling	1.37 ± 0.19	Complex, requires training to identify and weigh strata
Non-stratified Z-sampling	1.99 ± 0.08	Complex, requires measuring quadrats and distance between sample points
Non-stratified simple random sampling	3.34 ± 0.07	Very complex, requires understanding of the concept of randomness and availability of random tables or something similar

Table 2. Linear relationship between estimated damage at different crop growth stages and the actual damage or yield loss.

Sampling technique	Actual damage (%)			Yield loss (kg)			Sample size (*n*)
	Regression equation	R^2	*p*	Regression equation	R^2	*p*	
Seedling stage							
Non-stratified systematic row sampling	$0.957x + 3.436$	0.99	0.001	$12.20x + 38.46$	0.73	0.001	15
Stratified random square sampling	$1.132x – 7.149$	0.94	0.001	$12.731x + 11.204$	0.69	0.001	15
Non-stratified Z-sampling	$1.082x + 1.992$	0.93	0.001	$11.997x + 57.109$	0.60	0.001	15
Non-stratified simple random sampling	$0.851x + 9.201$	0.90	0.001	$12.041x + 48.598$	0.69	0.001	15
Maturity stage							
Non-stratified systematic row sampling	$1.505x – 0.005$	0.95	0.001	$1.1696x + 0.1728$	0.91	0.001	8
Stratified random square sampling	$1.789x – 0.269$	0.90	0.001	$31.358x + 174.23$	0.10	0.440	8
Non-stratified Z-sampling	$1.654x – 0.652$	0.90	0.001	$94.068x + 23.094$	0.90	0.001	8
Non-stratified simple random sampling	$3.556x + 0.180$	0.78	0.001	$49.301x + 62.711$	0.76	0.01	8

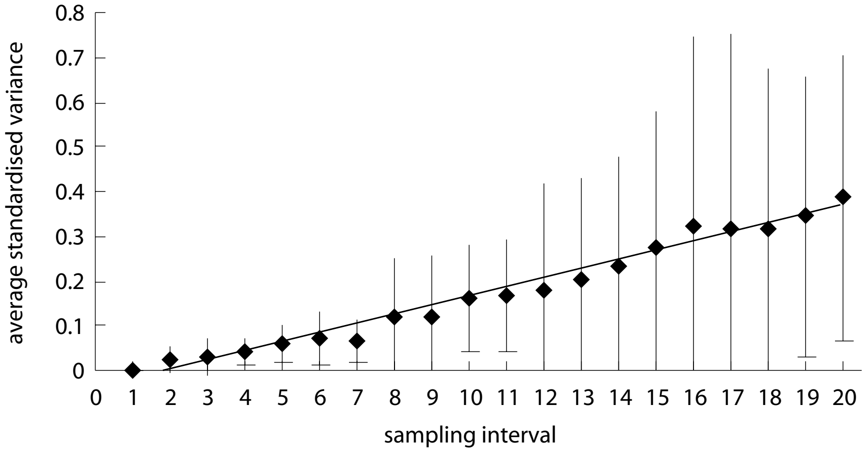

Figure 1. Average standardised variance for each simulation of 15 plots versus sampling interval for each plot.

On some plots, this effect was more dramatic than others, illustrating that damage is not equally distributed in all fields. When a sampling interval of less than six rows is used, the variation of an estimate stays below 10% of the actual damage (Figure 1). Therefore, the curve can actually be used as a standard curve for future studies to decide what sampling row interval should be chosen for obtaining a desired accuracy, or what kind of accuracy can be expected for a given sampling row interval. To sample each 5th row in the maize field, as used by Mwanjabe and Leirs (1997), seems to be a reasonable balance.

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Effect of land preparation methods on spatial distribution of rodents in crop fields

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Abstract. A mark–capture–release (CMR) study was carried out in Morogoro, Tanzania, from April 1999 to August 2000 to investigate the effect of slashing and burning versus tractor ploughing on the population of rodents in agricultural fields. We found that the spatial distribution of individuals was significantly affected by the land preparation method. The coefficient of dispersion values (based on variance-to-mean ratio calculations) indicated that more animals clustered around the edges in tractor-ploughed fields whereas in the slashed-and-burnt fields, animals were randomly distributed. Before land preparation, animals were randomly distributed everywhere. This suggests that the slashing-and-burning practice does not affect the rodent population distribution in crop fields while tractor ploughing does affect rodents, probably by reducing cover and food availability or even by killing some individuals. Yet, it seems useful as a management tool when it is practised over a large area and if the surrounding fallow lands, which act as donor habitat, are cleared.

Introduction

Rodents are responsible for substantial damage to food and cash crops and play an important role as reservoirs and carriers of zoonotic diseases in East Africa (Fiedler 1988). A mosaic of small plots of various crops, intermingled with patches of fallow and permanent grassland, combined with minimum land preparation and subsequent flourishing of weeds, creates favourable conditions for opportunistic and prolific species such as *Mastomys natalensis* and results in a high degree of damage to crops (Taylor 1968; Myllymaki 1989; Mwanjabe 1993).

Various studies have been carried out in Tanzania to establish the relationship between ecological parameters and rodent population dynamics. Most studies have largely involved research in areas with natural and semi-natural vegetation (Leirs et al. 1989, 1996; Telford 1989; Leirs 1994; Makundi 1995).

An understanding of factors that influence the population dynamics of rodent pests can provide an indication of the type of strategy that should be employed in their management. This study aimed to establish how cropping systems and land preparation methods influence the abundance and spatial distribution of *M. natalensis.* Here we discuss the effects on spatial distribution.

Materials and methods

The study area is located at 6°46'S, 37°37'E and 480 m above sea level at Solomon Mahlangu Campus (Mazimbu), Sokoine University of Agriculture, Morogoro, Tanzania. The area has a bimodal rainfall pattern with short rains between October and January and long rains between March and May. Two crops per year, depending on the amount and distribution of rainfall, are cultivated.

A capture–mark–recapture (CMR) study was conducted during the 1999–2000 cropping seasons. Eight 70×70 m grids were prepared, consisting of seven parallel lines, 10 m apart, and seven trapping stations per line (total of 49 trapping stations/grid), also 10 m apart. One Sherman live-trap ($7.5 \times 9.0 \times 23.0$ cm, HB Sherman Trap Inc, Tallahassee, USA) was placed on each trapping station. A 200–300 m wide zone of fallow land separated the grids from each other. The grids were subjected to two types of cropping systems (mono-cropping, inter-cropping) and two land preparation methods (tractor ploughing, slashing and burning). The mono-cropping system consisted of a monoculture of maize and the inter-crop consisted of a mixture of maize and beans. The experimental design was a completely randomised design (CRD) with 2×2 factors replicated twice. The grids were ploughed in November 1999 and February 2000 during the short and long rain seasons, respectively. Tractor ploughing was done using a disc plow at a depth of 30 cm—a normal rooting depth for most annual crops. Slashing was done manually close to the surface of the soil and the weeds were left to dry for one or two days, depending on weather conditions, after which they were burned. Maize sowing followed a standard procedure (planting lines 90 cm apart, plant holes 60 cm apart, and three seeds per planting hole). The bean crop was sown 3 weeks after the maize, at a spacing of 50 cm × 10 cm. All necessary agronomic practices such as fertiliser application and weeding were carried out equally on all the plots. Triple superphosphate (20 kg/ha) and nitrogen (40 kg N/ha) were applied before sowing and 3–4 weeks after sowing, respectively.

Trapping was conducted in each grid for three consecutive nights at intervals of 4 weeks. Additionally, trapping was conducted before land preparation (tractor ploughing or slashing and burning), after land preparation, and after seed emergence. Traps were baited with peanut butter mixed with maize bran and were inspected early in the morning. Animals were marked by toe-clipping. The trapping station, sex, weight, and reproductive status of captured animals were recorded. Animals were later released at the station of capture.

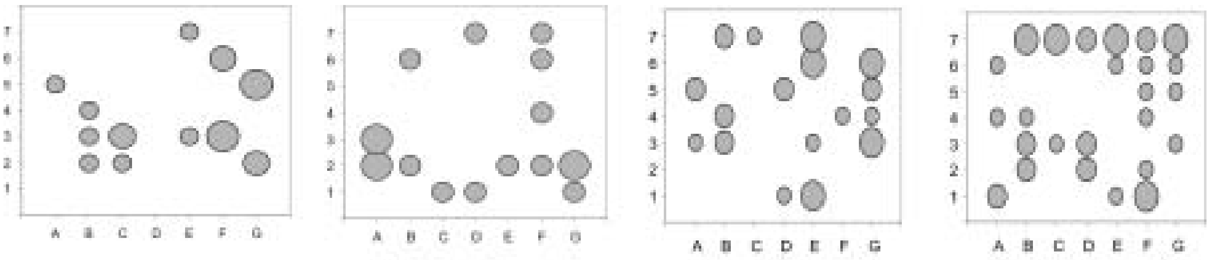
Population size was estimated for each 3-day trapping session using the M(h) estimator of the program CAPTURE for a closed population, which allows for individual variations in trapping probability (White et al. 1982). Spatial distribution of animals was established by means of capture maps showing the intensity of captures at different trapping stations. The pattern of distribution of individuals over the different trapping stations was established by determining the coefficient of dispersion (CD) by calculating the variance-to-mean ratio. These ratios indicate whether animals are aggregated, random or regular in their distribution (Kranz 1993). The distribution was considered random when the CD values were 0.7–1.3, aggregated (clustered) when CD values were >1.3, and regular when CD values were <0.7.

Using the established maps, the percentage of animals captured at the centre grids (40 × 40 m from lines 2–6 and trapping stations B–F) was compared between treatments. Since the central grid consisted of 5 × 5 of the 7 × 7 traps of the whole grid, we expected a proportion of 25/49 if animals were evenly distributed throughout the field. Statistical analysis using GLM Factorial ANOVA (analysis of variance) was performed in STATISTICA to compare the effect of the different land preparation methods and the cropping systems on the distribution of animals.

Results and discussion

The population abundance of rodents was influenced by the land preparation method and, to some extent, the cropping system. Trapping after land preparation showed a drop in population size in the slashed-and-burnt fields, but not in the tractor-ploughed fields (data not shown here). After seed emergence, the rodent population increased in all the grids, but a greater increase occurred in the slashed-and-burnt fields than the tractor-ploughed fields. During the long rain season, very few animals were captured and there was no clear pattern in the population trend.

The immediate effect of slashing and burning and tractor ploughing was a drastic drop in the rodent population, but it increased fast in the slashed-and-burnt fields after germination and emergence of weed and maize seedlings. The increased population size was probably due to recolonisation from the surrounding fallow land, but this needs to be investigated further. Figures 1 and 2 show typical examples of the spatial distribution of individuals in tractor-ploughed and slashed-and-burnt fields, respectively, during various growth stages of maize. The animals were randomly distributed in both the treatments before land preparation (Table 1). However, at the seed emergence and vegetative stages of the maize crop, animals occurred in clusters in the tractor-ploughed fields in both the short and long rainy seasons, while they remained randomly distributed in the slashed-and-burnt fields (variance-to-mean ratio, Table 1); the clusters in the ploughed fields were situated near the field edges. The land preparation methods, cropping systems and the season significantly affected the distances occupied by individuals from the centre of the grids. The mean distances were 27.8 m and 21.6 m for tractor-ploughed and slashed-and-burnt fields, respectively, and were significantly different (Tukey HSD test; $p < 0.001$).



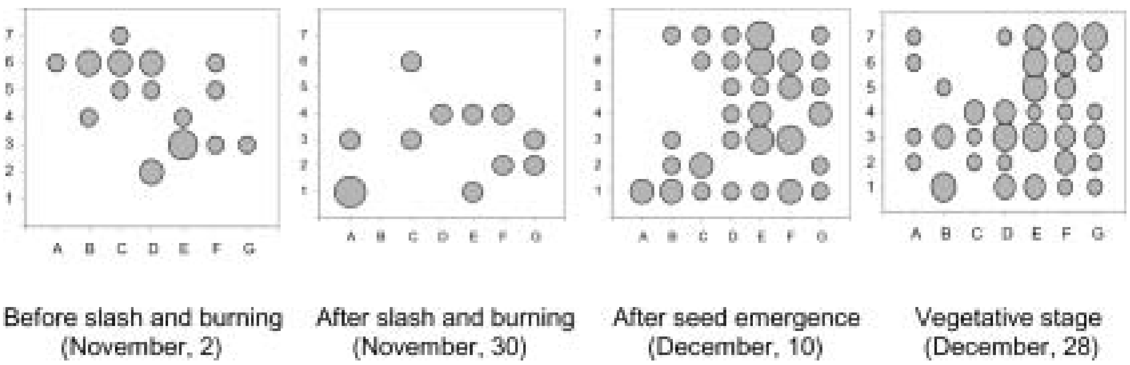
Before ploughing (November, 2)

After ploughing (November, 30)

After seed emergence (December, 10)

Vegetative stage (December, 28)

Figure 1. Distribution of trapped individuals over the different trapping stations in the tractor-ploughed fields (mono-crop) during the short rainy season 1999. Dot size increases with number of captures (1–3). Scale: trapping stations A–G and trapping lines 1–7 were 10 m apart. Lines with trapping stations were 10 m apart; the field extended 5 m beyond the outer trap lines; the fields were surrounded by fallow land.



Before slash and burning (November, 2)
After slash and burning (November, 30)
After seed emergence (December, 10)
Vegetative stage (December, 28)

Figure 2. Distribution of trapped individuals over the different trapping stations in the slashed-and-burnt fields (mono-crop) during the short rainy season 1999. Dot size increases with number of captures (1–3). Scale: trapping stations A–G and trapping lines 1–7 were 10 m apart. Lines with trapping stations were 10 m apart; the field extended 5 m beyond the outer trap lines; the fields were surrounded by fallow land.

Table 1. Coefficient of dispersion (CD) values (variance (s^2) to mean ratio calculations) and pattern of spatial distribution of rodents before and after land preparation and during growth of maize.

Cropping stage	Tractor-ploughed				Slashed-and-burnt			
	Mean	s^2	CD	Distribution[a]	Mean	s^2	CD	Distribution[a]
Before land preparation	0.65	0.65	0.99	Random	0.24	0.23	0.94	Random
After land preparation	0.51	0.75	1.48	Clustered	0.42	0.54	1.20	Random
After seed emergence	0.67	1.09	1.63	Clustered	0.95	0.87	0.91	Random
At vegetative stage	0.61	1.04	1.58	Clustered	1.20	1.08	0.89	Random

[a] Coefficient of dispersion scale: random distribution = 0.7–1.3; aggregated (clustered) distribution = >1.3; regular distribution = <0.7.

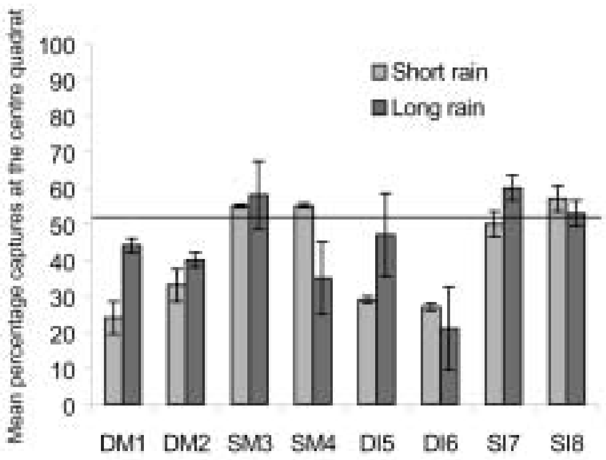


Figure 3. Mean percentage (± se) captures at the centre grid during the short (1999) and long (2000) rain seasons (the mean percentages are for the sum of captures before ploughing, after ploughing, after seed emergence and at vegetative stage). Abbreviations on the X-axis refer to land preparation (D = tractor ploughing; S = slashing and burning) and cropping system (M = mono-cropping; I = inter-cropping). Numbers refer to different replicates. The horizontal line at 51% indicates the expected value if animals were evenly distributed over the grid and the periphery.

For the two cropping systems, the mean distances were 26.0 m and 23.4 m for mono-cropped and inter-cropped fields, respectively, and also varied significantly (Tukey HSD test; $p = 0.007$). In the short and long rain seasons, the distances also differed significantly (Tukey HSD test; $p = 0.041$) (25 m for short rains and 23.8 m for long rains). The concentration of the animals along the edge of the tractor-ploughed grids is probably due to a combination of mortality in the ploughed grid, movement from the centre to the edges, and possibly recolonisation from the surrounding fallow land. Survival analyses, which can elucidate this, will be presented elsewhere. Deep ploughing using a tractor most likely reduces survival within the fields, because weed seeds, which are consumed by rodents, are ploughed under, while the nesting sites and burrow systems are destroyed. Ploughing may also have caused direct mortality of some individuals. Studies in China also showed that ploughing reduced the population of *Cricetulus triton* (Zhang et al. 1999).

Significantly, more animals were captured in the centre (40 × 40 m) grid in the slashed-and-burnt fields than in the tractor-ploughed fields during the two cropping seasons (Tukey HSD test; means, tractor-ploughed = 36.25%, slashed-and-burnt = 51.00%, $p = 0.03$) (Figure 3). The percentage of animals captured at the centre grid in the tractor-ploughed fields was significantly different from the expected value of 51% (equivalent to the ratio of 25/49 traps at the centre) ($\chi^2 = 8.5$; df = 1). In the slashed-and-burnt fields, the centre grid had 51% of the captures which corresponds to the expected proportion of captures for 25/49 traps. This suggests that in the slashed-and-burnt fields there were no differences in the distribution of animals between the centre and the periphery, while in the tractor-ploughed fields there was a tendency for more animals in the periphery than would be expected by chance. Cropping system and season had no significant effect on captures at the centre grid and there was no interaction between ploughing, cropping system and season on the distribution of animals. The observed distribution of animals in the different fields suggests that the slashed-and-burnt fields provided better protection and more resources than the tractor-ploughed fields. It could also be argued that the maize seeds provided more favourable food than weed seeds in the adjacent fallow land. This is consistent with Taylor and Green's (1976) observations that, when there were no cereal crops in the fields, rodents depended on weed seeds and the leaves of dicotyledonous plants, but as soon as the cereals became available, they formed a major part of the diet of *M. natalensis.*

The influence of cropping system on spatial distribution and population abundance of *M. natalensis* is not quite clear in the current study. However, it is plausible that there was increased activity of rodents in both types of cropping system because the weed density increased in the fields. It is also apparent that the population density within the inter-cropped fields increased, which could be attributed to better cover, or an alternative food was available when maize crop was not very attractive for the rodents. Therefore, it will be interesting to investigate how repeated weed control in both types of cropping system, and how the method of land preparation will affect the distribution pattern and population abundance of rodents and whether this could be part of an integrated approach for management of *M. natalensis*.

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Current approaches towards environmentally benign prevention of vole damage in Europe

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Abstract. Voles are the most important field rodent pest in Europe and farmers need benign means of reducing damage to crops. In this paper, I review ideas discussed during a recent meeting in Braunschweig, Germany, on *Prevention of vole damage in organic farming*. Measures suggested include the installation of migration barriers, the use of secondary plant compounds specifically acting against voles, support of vole predators, diversionary feeding, and physical devices for early detection of vole infestations. These approaches show some potential but require further investigation before they can be recommended for practical use. A successful strategy for the prevention of vole damage will probably have to integrate several of the suggested methods.

Introduction

Prevention of vole damage is still one of the prominent challenges facing European rodent control officers. Cyclic vole species like *Microtus agrestis, M. arvalis, M. subterraneus* and *Arvicola terrestris* cause significant damage throughout their wide geographical range during peak years of abundance. Besides taking grain from fields, voles debark trunks of young trees and destroy their root system by gnawing. Fruit trees in orchards and afforestations in forestry mostly suffer this type of damage. In 1998/99, damage by *Arvicola terrestris* in German forests occurred on more than 1000 ha with losses of up to 50% of trees and an estimated cost of 1.5 million Euro (Schneider 2001). In the same years, *M. agrestis* and *Clethrionomys glareolus* accounted for further damage on up to 9900 ha per year (Müller and Heidecke 2002). Furthermore, huge areas of grassland may be devastated when voles occur in high numbers (more than 1000 per ha in *A. terrestris* and up to 5000 in *Microtus* species) (Meylan 1977; Lauenstein 1979).

In conventional agriculture and forestry, voles are usually controlled by distributing anticoagulant or zinc phosphide baits. Due to restrictions in the use of pesticides, however, these poison baits cannot always be applied. These pesticides are mostly non-specific and effects on non-target species cannot be completely ruled out (Zahner 1996; Saucy et al. 2001). In organic farming, synthetic pesticides are not allowed, thus trapping and gassing remain the only applicable measures, requiring a lot of time and personnel skills (Malevez 2002; Popow 2002).

Here, I review the ideas presented during a meeting organised by the Federal Biological Research Centre for Agriculture and Forestry in Braunschweig, Germany, in June 2001 on *Prevention of vole damage in organic farming* in the context of *Plant protection in organic farming—problems and solutions*. The presentations of the meeting are documented in Federal Biological Research Centre for Agriculture and Forestry (2002). I refer to the papers contained therein by Gago (2002), Müller and Heidecke (2002), Pelz (2002), Saucy (2002), Sommer (2002), Wieland (2002) and Wink (2002).

Suggested approaches

Migration barriers (fencing) and trapping

Dispersal constitutes an important element in the population dynamics of small mammals. It is assumed that immigration and emigration will usually level out unequal population densities in uniform habitats, with juveniles dispersing after weaning in order to establish their own territories. This dispersal behaviour has the potential to limit the success of vole management strategies.

Control measures targeting rodent populations usually cover restricted areas and thus result in vacancies that will quickly be re-colonised from neighbouring populations, especially if the overall population density is high. Saucy (2002) and Wieland (2002) suggest the use of migration barriers to protect valuable crops from vole immigration.

Saucy and Schneiter (1997) observed extensive above-ground dispersal of young water voles during rainy nights. Based on this experience, Saucy (2002) recommends semi-permeable fences equipped with one-way exit doors that allow voles to leave the plots, but prevent them from re-colonisation. In connection with other control measures, like frequent grass mowing, traditional trapping and measures favouring natural enemies, Saucy thinks semi-permeable fences are likely to provide long-term protection against vole damage.

Wieland (2002) demonstrated in a field experiment that immigration of the field vole, *M. arvalis*, into a carrot field was totally stopped using a 4 mm plastic fence, 16 cm above-ground and 8 cm below-ground in combination with poison bait stations along the fence. Even a ploughing furrow equipped with poison bait stations blocked migration considerably, achieving an 80% reduction of immigration.

Potential significance of secondary plant compounds

More than 360,000 plant species, forming the base of the food chain, produce in addition to primary compounds (e.g. amino acids, carbohydrates, fatty acids) a large number of secondary compounds. About 80,000 of those secondary metabolites are already known from plants, although no more than about 20% of all plants have been investigated to date, and most of these investigations have been incomplete. Secondary compounds play an important role in the chemical defence of plants against herbivores. During evolution, plants have succeeded in developing specific substances targeting important organ systems of herbivores (e.g. the central nervous system, the digestive system, heart and blood circulation, respiration, muscle contraction or reproduction). Among the mechanisms underlying the toxic effects are the inhibition or modification of cell structures including deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), and the functional processes during protein biosynthesis (for an overview, see Wink 1993, 2000).

Polyphagous herbivores are capable of evaluating the quality of potential food plants and to detect and avoid secondary substances and the plants containing them (Bernays and Chapman 1994). They prefer plants with low content of or harmless secondary substances, like our cultivated plants that have lost most of their poisonous secondary substances. Most of the polyphagous species also use mechanisms for a fast detoxification and elimination of secondary substances. Mono- and oligophagous herbivores, on the contrary, are adapted to specific secondary substances that stimulate consumption by these species. They often store the poisonous secondary substances and utilise them for their own defence against predators.

Several secondary compounds are already known to have an effect on voles (Lindroth and Batzli 1984; Bucyanayandi et al. 1990). Wink (2002) suggests locating potential compounds by a systematic screening of the biological effects of secondary compounds on voles. Additional experiments would then be required to find a practicable way to apply these substances on cultivated plants to protect them. If these secondary compounds cannot be used as a repellent, there might also be a chance to find a more vole-specific poison in contrast to the non-specific rodenticides used today.

Tree species differ greatly in their palatability or repellence and even varieties vary in their palatability to voles. However, in years of high vole abundance, these properties seem to be insufficient to keep voles completely away from trees (Rousi 1989).

Müller and Heidecke (2002) report promising preliminary results using extracts from *Echinops sphaerocephalus* as a repellent. This plant contains echinorin, an alkaloid with a bitter taste but of low toxicity. In laboratory and field trials to protect shoots of apple twigs from gnawing damage by *M. agrestis*, the repellence of the echinops extract was on the same level as the standard thiram repellent used for comparison (HaTe-PELLACOL®). In the field trials, after 80 days the bark area gnawed in echinops-treated twigs was still less than 25% compared to the untreated (control) twigs. Investigations to further strengthen the effectiveness of the echinops extract are currently in progress.

Supporting vole predators

In peak years of abundance, *A. terrestris* makes up 80% of the diet of the barn owl, *Tyto alba*, in the French Jura (P. Delattre, pers. comm., 1981). *Asio otus* and *Falco tinnunculus* are other examples of birds of prey that specialise on voles. Among the mustelids, *Mustela nivalis* and *M. erminea* mostly depend on voles as their principal prey, with *Arvicola* and *Microtus* species making up more than 50% of their diet (Debrot 1981; Erlinge 1981). From an applied point of view, it would be highly desirable to support predators in such a way as to increase their influence on vole populations. There are a few examples where predators have been used to solve vole control problems—the best known being the successful attempt to expel *A. terrestris* from the Dutch island of Terschelling (Van Wijngaarden 1961). However, specialised predators are restricted in their numbers by the minimum density of the prey species during the low phase of their cycle. Since predators are regarded as principal factors driving the cycles of small mammals (e.g. Henttonen 1999; Klemola et al. 1999; Sittler 1999), there is sufficient reason to believe that a diversely-structured landscape and provision of shelter—such as heaps of wood or stones to support mustelids, and nesting places and perches for birds of prey—could assist in keeping vole populations at a low level and to dampen outbreaks. However, experimental data for voles to support this idea are still missing. The scientific challenge would be to provide evidence for the ecological benefits of predator support.

Provision of alternative food

Provision of diversionary food is a method of habitat modification designed to temporarily satisfy part, or a majority, of the food requirements of a problem species in a localised area (Howard 1967; Sullivan 1979). A good example how such a system can work has been the diversionary feeding of mice that has been successfully applied for the prevention of damage by *Apodemus sylvaticus* to pelleted sugar beet seeds (Pelz 1989). From an energetic point of view, it is much more efficient for these mice to take the seeds provided instead of digging up hundreds of seeds that farmers have planted in the soil.

Although the requirements of a bark-consuming vole may not be directly comparable with those of a seed-consuming mouse, the key question to be answered is identical: What makes up the relative attractiveness of the target cultivated plant? Can the basic nutritional needs of the rodents be satisfied alternatively and in this way the cultivated plants be protected? Laboratory and field studies on nutritional requirements of voles revealed that the need of certain minerals like sodium, calcium or phosphorus may have an influence (Hansson 1991), but also the conversion of starch to glucose at low temperatures (Murneek 1942) may trigger the debarking behaviour of voles. Reduced availability of preferred food plants during autumn and winter is indicated by a higher proportion of less preferred grasses in the diet of voles at this time of year (Cengel et al. 1978). Servello et al. (1984) found that the digestibility of apple tree root bark for *Microtus pinetorum* was 15–30% lower compared to the proportion of digestible dry material and digestible energy usually found in the stomachs of this vole species caught in apple orchards. But sugar content of root bark was significantly higher in winter than in summer. These findings suggest that a bark diet helps voles to get through times of food shortage during winter, and that the palatability of tree bark derives from its sugar content.

Experiments with diversionary feeding to prevent voles from debarking trees have been conducted by Sullivan and Sullivan (1988) in Canadian apple orchards and in forest plantations (Sullivan et al. 2001). They distributed alfalfa-, wood- or bark-pellets formed to blocks with wax and sunflower oil. Although a significant reduction of damage could not be achieved in all of these trials, the results do show that diversionary feeding is a method deserving further exploration (Pelz 2002).

Physical detection of vole infestations

Due to their subterranean and crepuscular habits, it is sometimes difficult to be aware of the presence of voles in plantations. In woody plants, damage caused during winter often does not become obvious before the next spring when buds are not put forth. The ability to detect vole populations while they are at low density is important for the success of any vole management strategy. New techniques are now available that may make the early detection of voles possible. These include the use of infrared cameras and sound detectors.

Infrared cameras

These may be useful tools for thermal-imaging of plantations to detect vole burrow systems and to observe immigration of voles. Small, lightweight, digital infrared cameras are now available at an affordable price (Gago 2002).

Sound detectors

Gnawing by voles on roots or trunks of trees creates characteristic sound waves. With a newly developed detection system, these specific sound waves can be recognised at an early stage (Schönherr et al. 2000). For this purpose, the sound detectors are fixed to selected stems of trees and the oscillation is permanently monitored. The system steadily calculates an average reference signal, which is caused by structure-borne sound waves in the environment. This reference signal is transferred to an adjustable comparator step, where the reference signal is continuously compared with the presently measured signal. If roots are gnawed by water voles, the gnawing procedure produces strong, impulse-like sound waves that significantly change the signal. The gnawing sounds predominantly occur at a frequency range around 100 Hz and they are transferred to the stem of the tree to which the sensor is fixed. If the present sound signal, caused by a gnawing vole, exceeds the average reference signal for a certain time, the detector will identify and indicate vole gnawing activity by a flashing light-emitting diode (LED). The alarm message can also be radio-transmitted to a receiving station. If more than one detector is in use, each signal will be specific to enable the identification of the infested tree and immediate control measures can be undertaken (Pelz 2002). Such a system, with detectors distributed in a strategic way to receive an alarm call as soon as voles invade a plantation and start doing damage, could greatly improve and facilitate control. The system is now about to be tested under field conditions.

Conclusion

Vole damage to cultivated plants is a complex problem with much of the ecological background still unexplored and satisfactory damage prevention not yet available. The approaches suggested at the meeting in Braunschweig on *Prevention of vole damage in organic farming* require further investigation and testing under practical conditions. They are regarded as a basis for planning research and development of projects in order to improve the situation in organic farming. As conventional agriculture and forestry too are looking for measures other than the application of pesticides for vole control, there is no doubt that they will readily adapt measures that prove efficient in organic farming. However, due to the complex nature of the problem, a single control strategy will probably remain insufficient. A successful strategy for the prevention of vole damage will have to integrate several of the approaches suggested.

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Overcoming rat infestation in Australian sugarcane crops using an integrated approach that includes new rodenticide technology

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Abstract. Two Australian native grassland rodent species cause significant, but seasonally sporadic, damage at several stages of the crop cycle in Australian sugarcane areas. These rodent infestations represent one of the most important pest problems for sugarcane growers. A series of interrelated management practices has recently been introduced to minimise the occurrence of rodent infestations and to achieve better management of those infestations that arise in the sugar crops. Components of the integrated pest management (IPM) approach include improved short- and long-term management of harbourage areas, in-crop weed control, rodent population monitoring, and baiting of emerging populations using new technology. A new rodenticide, RATTOFF® (patent pending), presents small, localised quantities of grain coated with zinc phosphide that is protected from the wet tropical environment by a biodegradable and edible cellulose membrane. This baiting approach allows the minimum effective application of chemical to control rats. Application of RATTOFF® is based on objective monitoring of emerging rodent problems and is implemented as part of (and not a replacement for) a total IPM strategy. This combined approach reduces the potential for large-scale rat plagues and reduces crop damage throughout the production cycle. An industry-wide extension program was implemented at district and regional levels to mitigate overall damage potential.

Introduction

In the 1999–2000 harvest seasons, rats in Australian cane fields destroyed approximately 825,000 tonnes of sugarcane valued at US$50 million. Rodents can potentially damage sugarcane at all stages of cane growth. In ratoon cane, rats gnaw the stems and apical meristems of young plants. As the cane grows, the rats attack the mature stalks, resulting in reduced sugar content and harvestable tonnage (Wilson and Whisson 1993). Even minor gnawing damage can predispose cane stems to infestation by insects, bacteria and fungi, and desiccation (Robertson et al. 1995). Rodent damage can cause brittle cane that shatters when harvested, or deteriorated cane quality through the fermentation of the cane juice (Rao 2001).

Rodent pest species

The main species responsible for sporadic damage in Australian sugarcane crops are the cane field or ground rat (*Rattus sordidus*) and the grassland melomys or climbing rat (*Melomys burtoni*) (Wilson and Whisson 1993). Both species are native grassland species common through the coastal tropical areas of northern Queensland. Generally the species do not pose problems for commercial crops and do not require control in grassland habitat, however they are both well suited to the introduction of sugarcane crops which provide appropriate crop habitat. Thus, these rodents have expanded their ranges to include cane fields. *R. sordidus* requires friable soil for burrow construction, and "close and substantial ground cover" (McDougall 1946), thus the soil preparation used for establishment of raised beds provides an ideal opportunity for this species to establish nest sites early in the cane-growing season, and this rat remains within the crop at all stages. Both plant cane and ratoon cane blocks are affected. *M. burtoni* is usually associated with taller native grasses that provide suitable cover, protection and support for their nests in the canopy (Redhead 1973), so this species more commonly infests cane crops from canopy closure through to harvest.

Rodent outbreaks

Populations of *R. sordidus* follow a cyclic annual pattern that is modified according to seasonal, environmental and crop conditions that regulate breeding success and mortality (McDougall 1946). Significant rodent infestations arise from a combination of factors including:

- poor in-crop weed control, leading to seeding of summer grasses that trigger the onset of rat breeding;
- abundant and uncontrolled grass cover on adjacent harbourage areas that provides habitat and food, and

thus a potential source for recolonisation of cane crops by rats;

- high spring rainfalls that facilitate summer grass and weed growth, and that lead to an early commencement of breeding;
- failure to detect and control residual or rising populations of rodents in crops that provide a breeding base for future seasons; and
- the presence of stand-over cane (after excessive wet weather that prevents harvest), providing additional harbourage for rats.

Previous management strategies for rodent control in cane fields

Control of rodents in Australian cane fields has traditionally involved large-scale baiting campaigns. Historically, these have been conducted at the time of peak rodent numbers at the end of the breeding phase in autumn. One method was based on the distribution of paper sachets containing the sulfate salt of the heavy metal thallium, coated onto grain (Wilson and Whisson 1993). Re-infestation of crops with rats from adjacent habitats occurred rapidly (Redhead and Saunders 1980) and this bait was withdrawn due to environmental residue concerns (Robertson et al. 1995).

More recently, wax blocks containing the second-generation anticoagulant brodifacoum (available commercially without restriction) were used to reduce rodent populations in cane fields (Story 1993). The blocks were often applied in reaction to very large rodent infestations late in the growing season. Often the treatments were applied long after a significant amount of early crop damage had occurred and at a time of maximum rodent infestation that required the application of large quantities of bait. Multiple applications over an extended period were sometimes used to achieve the required level of control. However, second-generation coumarin anticoagulants, such as brodifacoum, have a long biological half-life and can accumulate in the food chain (Eason et al. 1999). Also, because the action of anticoagulants is delayed, rodents can accumulate super-lethal doses of active ingredient before succumbing to the initial dose ingested. These features of potent second-generation anticoagulants have led to concerns about the potential impact on non-target species, especially birds of prey or scavenging animals that feed on the poisoned carcasses. These chemicals posed an unacceptable risk of secondary poisoning if applied in high quantities over large areas of broad-acre crops (Howald et al. 2000) and second-generation anticoagulant wax block formulations were withdrawn from the sugar industry by suppliers in 1998.

Development of an integrated pest management (IPM) strategy

The approach now adopted by the Australian sugar industry has arisen after consideration of the early work of McDougall (1946) who researched the ecology, biology and control of rodents in sugarcane crops. This work was extended by the studies of Redhead (1973) on *M. burtoni* populations. These investigations, combined with further research conducted by the Queensland University of Technology (QUT), Bureau of Sugar Experiment Stations (BSES) and the Cane Protection and Productivity Boards (CPPBs), facilitated the development of an integrated plan to control rodent pests in sugarcane (Wilson and Whisson 1993).

Traditionally, growers were accustomed to lethal control treatments applied reactively at a time of high rodent numbers and after severe cane damage was observed. In such circumstances, bait uptake was high and large numbers of rodents were killed. However, though seen as successful control by landowners, most of the crop damage had already occurred before the reactive treatment of high rodent populations (Wilson and Whisson 1993). Thus, while rodents were killed, little damage was prevented, and presumably the small proportion of survivors provided the base for the next season's rodent problems. In contrast, the present procedures of habitat manipulation, weed control and other components of the IPM program, including application of bait when rodent populations are emerging, focuses on suppression of breeding rather than killing rats *per se*, but does greatly reduce losses of crop and sugar (Robertson et al. 1995).

Since the impact of a proactive, early approach is subtle, some growers initially doubted the effectiveness of these IPM techniques compared to their previous practices. To overcome this perception, an extension program coordinated by BSES and participating CPPBs was implemented to encourage growers to adopt whole-farm management of rodent populations.

In-crop weed control

Suppression of weed and grass growth in-crop is required to restrict the available food source and habitat area for rodent breeding and development. Grass seed provides protein that is essential for rodent breeding (Wilson and Whisson 1993).

Changes in farming practices, such as green-cane harvesting and trash-blanketing, have also impacted on rodent numbers within the crop. The retention of a trash-blanket in ratoon cane improves moisture retention and reduces weed competition, and though providing a rat refuge source immediately after harvesting, reduces eventual cane damage by suppressing weed growth that leads to rat breeding (Whisson 1996). Several pre-emergent and knockdown herbicides are available as tools to reduce weed infestation at specific stages of the crop cycle, and strong extension and advisory programs are well established within the industry to maximise the effectiveness of in-crop weed control. Since weed control reduces competition within the crop and improves cane yields directly, the industry has readily accepted the collateral benefit of improved rat management in clean, weed-free crops.

Harbourage management

Non-crop habitats such as headlands, drains, river and creek banks, tram-lines and steep slopes often support weeds and other grasses, and provide refuge for rats, especially after rodent dispersal during mechanised cane-harvesting activities. Large numbers of rats can remain within these undisturbed harbourage areas until the cane canopy develops sufficiently to provide enough protection within the crop, at which time rodents return to recolonise the crop. With the development of highly effective new technology for rodent control in-crop, there is no need to use lethal control methods in the harbourage. Instead, the focus is on modifying the harbourage immediately adjacent to the crop to reduce its suitability as a reservoir for reinvasion of crops by rodents.

Where chemical and physical weed control (slashing) are impractical due to waterlogging, steepness or lack of vehicle access, the harbourage can be reduced by grazing of stock and by revegetation of difficult terrain with trees that shade out grasses. Native, fast-growing species achieve a closed canopy after only a few years (BSES 2000). Revegetation along waterways also benefits the environment by reducing erosion, stabilising banks, improving water quality and providing wildlife corridors between habitats, thus, as for weed control, a focus on rats can have collateral benefits for other aspects of responsible land management and improved crop productivity. Some growers continue to manage harbourage by burning grass during dry periods. This is a short-term solution, since the establishment of larger trees is prevented, and regrowth of weeds in the cleared areas is rapid. The present extension message therefore encourages longer-term management of difficult harbourage areas by replanting rather than seasonal burning.

Rodent population monitoring

Monitoring can be undertaken by the individual grower or at the regional level by advisory bodies. Regional programs can describe the population dynamics of the target species over a period of time and in a variety of environmental conditions. These data can be incorporated into a population model that predicts the influence of environmental conditions on future breeding intensity, juvenile recruitment, recolonisation, natural attrition, and crop damage. Feedback of regional data to growers via discussion groups and a web site are promoted by industry agencies and increase awareness well ahead of the major population rises. Thus, weed control and strategic baiting can be conducted in areas expected to incur high levels of crop damage. This early feedback is also used to alert and stimulate growers to check their own fields. Regional monitoring includes assessment of reproductive condition of female rodents. The presence of healthy females in breeding condition increases the likelihood of a rapid population increase and, therefore, the need to apply a rodenticide pre-emptively to prevent further population build-up (Robertson et al. 1995).

Development of new rodenticide technologies

In 2000, the development of RATTOFF® zinc phosphide bait sachets introduced a new option for rodent management in Australian sugarcane. The active ingredient of RATTOFF® is the acute toxin zinc phosphide. Since the 1940s, zinc phosphide has been used widely throughout the world to control rats and other rodents in crops, including sugarcane in Hawaii and the Philippines (Sugihara et al. 1995; Hoque and Sanchez 2000). Because zinc phosphide degrades once exposed to moist acidic conditions, the absorption of moisture and subsequent physical degradation of pelleted baits may reduce their acceptability to rodents in wet conditions (Sugihara et al. 1995). To overcome this problem, a more weather-resistant zinc phosphide bait presentation suitable for humid and wet conditions was developed. RATTOFF® consists of inactivated whole wheat grains coated with zinc phosphide and packaged in 10 g degradable cellulose membrane sachets, providing a localised lethal quantity for consumption by the rat. The cellulose membrane protects the bait against moisture degradation but is readily opened by the rats. Sachets are placed at 10 m intervals within the crop, which is equivalent to 100 sachets/ha, or 1 kg/ha. Only a few grains are required to kill a rat, therefore the low application rate of 1 kg/ha is sufficient to significantly reduce rodent population numbers within the crop.

In cage studies, *R. sordidus* rats typically ingest a lethal dose on first exposure to the sachet, and under field conditions often take sachets back to nests. *M. burtoni* rats appear to exhibit a more cautious initial approach, but cage-testing confirmed that they return to the sachets even after an initial sub-lethal exposure. In most instances, rats readily locate the sachets placed within the crop area and are killed within a few hours of ingesting very small quantities of RATTOFF®. Due to the high potency of the bait and the neophobic propensity of rodents, only small quantities of poison are ingested before the rodent dies, and super-dosing does not occur. In addition, zinc phosphide residues degrade quickly within the carcass (measured half-life of less than 1.5 days), resulting in a very low risk of secondary poisoning (Johnson and Fagerstone 1994). Zinc phosphide also degrades in the environment within weeks, leaving no residues, and is not readily taken up by plants (EPA 1998). This type of bait thus overcomes many of the risks associated with the use of second-generation anticoagulant baits in crops.

Strategic baiting

Robertson et al. (1995) demonstrated that where both effective weed control and strategic baiting were employed, significant reductions in damage could be achieved. Wilson and Whisson (1993) suggested that rodent management is most effective if rodenticides are applied before populations are large. Therefore, it is recommended that baiting programs be conducted during the non-breeding period from November to January, well before the maximum rodent numbers occur in March to May. In the Australian cane industry, this optimum period for bait application is during the early ratoon stage of the crop cycle, before canopy closure during the summer, and just before the wet season. At this time, the access to planted areas for both weed management and rodent control is good. From an organisational perspective, the combination of both aspects of rodent management can be achieved in the same application of labour and machinery, and this is now accepted as a more strategic time to apply lethal control methods.

Apart from RATTOFF® zinc phosphide bait, a first-generation anticoagulant, coumatetralyl, is commercially available in a wax block form and is currently registered for use in crops within bait stations. As coumatetralyl has a shorter biological half-life than the second-generation anticoagulant compounds, it is considered to pose a much lower risk of accumulation in the food chain (Mount et al. 1986). However, the short half-life also means that prolonged exposure to the bait by the rodents is required for effective rodent control. This is achieved by multiple applications or by replacing bait taken from bait stations over a period of weeks.

It is imperative that the timing of any chemical control measures be correlated with rodent population dynamics. Components of IPM such as weed control and monitoring are implemented *before* there is a resort to baiting and may overcome the need for baiting at all, even though baiting forms part of the overall IPM.

The future of rodent management in the Australian cane industry

A significant effort has been made by industry advisory bodies, chemical suppliers, farm management. and extension groups to change the reactive approach to rodent management of the past to a more proactive approach using best practice approaches. The IPM objective is to prevent the rodent problems from occurring (proactive management) rather than attempting to control rodent numbers after the population has reached an excessive level during the breeding season (reactive management). The introduction of RATTOFF® to the Australian sugar industry has satisfied the growers’ requirements of simple bait application, quick effect and high efficacy, while at the same time presenting few environmental problems.

Acknowledgments

The authors acknowledge the assistance of BSES at Tully for use of cage facilities, to BSES extension staff who assisted with training programs and to the industry body CANEGROWERS, who gave encouragement for this work. Staff of various CPPBs and several cooperating sugarcane growers in the Mackay and Herbert regions assisted with trials. An AusIndustry Research and Development Start Grant supported part of this research. A lengthened account of this work was presented at the 24th Australian Sugar Cane Technology Conference, Cairns, in October 2001.

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Review of recent advances in studies of the ecology of *Mastomys natalensis* (Smith 1834) (Rodentia: Muridae) in Tanzania, eastern Africa

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Abstract. The objective of this review is to highlight the recent advances in our knowledge of the ecology of *Mastomys natalensis.* In Tanzania in East Africa, the commonest and by far the most serious rodent pest is the multimammate or *shamba* (field) rat, *Mastomys natalensis* (Smith, 1834) (Rodentia: Muridae). Populations of *M. natalensis* sometimes erupt, reaching high densities which are favoured by ecological factors that were not well understood, but are now the subject of intensive studies in Tanzania. Recent studies have led to better understanding of the ecology of *M. natalensis.* Rainfall pattern (timing, duration and amount) is instrumental in the timing of breeding and plays an important role in regulating populations of *M. natalensis*. Spatial distribution of *M. natalensis* in both fallow and crop fields shows overlaps in home range between individuals of the same or different sexes and between habitats. Because of the variations in the suitability of habitats for colonisation, changes in them invariably affect the population dynamics of *M. natalensis*, an important consideration in developing management strategies for this pest species.

The potential for ecologically based management of *M. natalensis* lies in (i) the use of avian predators which have been shown to decrease its survival probability, and (ii) manipulation of cultivation methods and land management practices which invariably affect the population characteristics of *M. natalensis*, spatial distribution and levels of crop damage in fields. A limited and selective use of rodenticides is recommended, particularly in routine control of *M. natalensis*. A system for forecasting rodent outbreaks based on the link between unusual rainfall and population dynamics of *M. natalensis* has been developed for early preparedness of the community to control them. In plague outbreak areas, *M. natalensis* is widely distributed in peri-domestic areas, both in fallow and cultivated lands, and forms a continuum for the spread of plague between predominantly forest species and human beings in plague affected areas.

Introduction

In sub-Saharan Africa, the major rodent species causing severe damage to crops belong to the genus *Mastomys* (Muridae). In East Africa, the commonest and by far the most serious rodent pest is *Mastomys natalensis* (Smith 1834) (Fiedler 1988a,b, 1994). Certain characteristics of the species, such as high reproductive capacity and dispersal, are thought to contribute to the success of *M. natalensis* as a serious pest (Meester et al. 1979; Leirs et al. 1993). Outbreaks of populations of this species are favoured by certain ecological conditions that were previously not well understood, but are now the subject of intensive research in Tanzania.

Numerous outbreaks of *M. natalensis* have occurred in Tanzania in the past (Leirs et al. 1996b). The outbreaks are sometimes localised, but they often occur in a wide geographical area where enormous amounts of poisons would be required to control them. The idea of an ecological approach to management of *M. natalensis* has been advocated in Tanzania (Leirs et al. 1996b; Makundi et al. 1999). The major constraint in formulating ecologically-sound rodent management is lack of knowledge on the ecological processes involved in rodent outbreaks. However, in the past 10–15 years, a keen interest in the ecology of *M. natalensis* by a group of researchers in Tanzania has led to new findings which could enable the design of management strategies which are ecologically sound and appropriate. The purpose of this paper is to review the advances that have been made in understanding the ecology of rodents in Tanzania.

The ecology of *Mastomys natalensis* in Tanzania

The studies in Tanzania have been aimed at understanding: (i) the ecological processes that maintain rodent populations at low levels (and hence of no economic importance) in certain seasons or in some years, but which at times lead to eruptions of the population to proportionally high densities, and (ii) the involvement of rodents in zoonotic diseases.

Investigations carried out since 1986 addressed the following ecological aspects:

1. The environmental factors with major impact on demographic processes that affect the population dynamics of *M. natalensis.*
2. How rainfall, in particular, influences demographic parameters and rodent density.
3. The relationship between rainfall patterns and life history variations and whether such relationships could be used to forecast outbreaks.
4. Spatial patterns of distribution in the field.
5. The impact of habitat alteration on abundance and distribution.
6. Re-colonisation capacity of the species following control activity.
7. The demographic characteristics of different generations pertaining to reproduction, growth and maturation, survival and productivity.
8. The influence of people's activities (particularly agricultural practices) on population characteristics and population dynamics.
9. Management practices, including predation.
10. The relationship between rodent densities, spatial patterns and the risks of outbreaks of diseases (plague, leptospirosis etc.).

Role of rainfall

Studies of the population biology of *M. natalensis* in Tanzania have clearly indicated an association between rainfall and breeding (Telford 1989; Leirs 1992). Seasonal variations in breeding and growth have been reported (Leirs et al. 1989; Leirs 1992; Christensen 1993). These studies confirmed the previously established relationship between rainfall and reproduction of *M. natalensis* (Taylor 1968; Delany 1972; Taylor and Green 1976; Neal 1986). Further, population fluctuations, reproduction, growth and survival are strongly related to the rainfall patterns (Leirs 1992). There is evidence that the abundance of the rain early in the wet season could create conditions favourable for the occurrence of outbreaks later in the year (Mwanjabe and Leirs 1997).

Population dynamics

A range of population densities of *M. natalensis* has been reported in the field. Telford (1989), Leirs (1992) and Christensen (1996) reported densities of 1125, 900 and 384 animals/ha, respectively, in Morogoro, Tanzania. This further illustrates that wide-ranging population fluctuations between seasons and years occur. For a species whose breeding characteristics are strongly dependent on the rainfall patterns, such fluctuations are expected to be the rule rather than an exception. Further, the population dynamics of *M. natalensis* are influenced by both density-dependent and density-independent factors occurring simultaneously and these regulate population size (Leirs et al. 1997). Temporal fluctuations in the population size of *M. natalensis*, as illustrated in Figure 1, result in different levels of crop damage and losses. Makundi et al. (1991) reported losses of 15% in cereals, while Mwanjabe and Leirs (1997) estimated damage levels of 40–80% of maize seedlings, which could lead to serious losses of food at harvest.

Spatial patterns

An understanding of the spatial patterns of space use is important to develop ecological strategies for management of *M. natalensis* in Tanzania. A negative correlation between high rodent numbers and open space, and a positive correlation between high numbers and high dense grass have been reported (Leirs et al. 1996a). It has further been shown that there is a considerable overlap of home range between individuals and members of the same sex and between farms and fallow land (Leirs et al. 1996a). The home range, spatial distribution and abundance of *M. natalensis* in crop fields also appears to be influenced by activities such as methods of cultivation and cropping

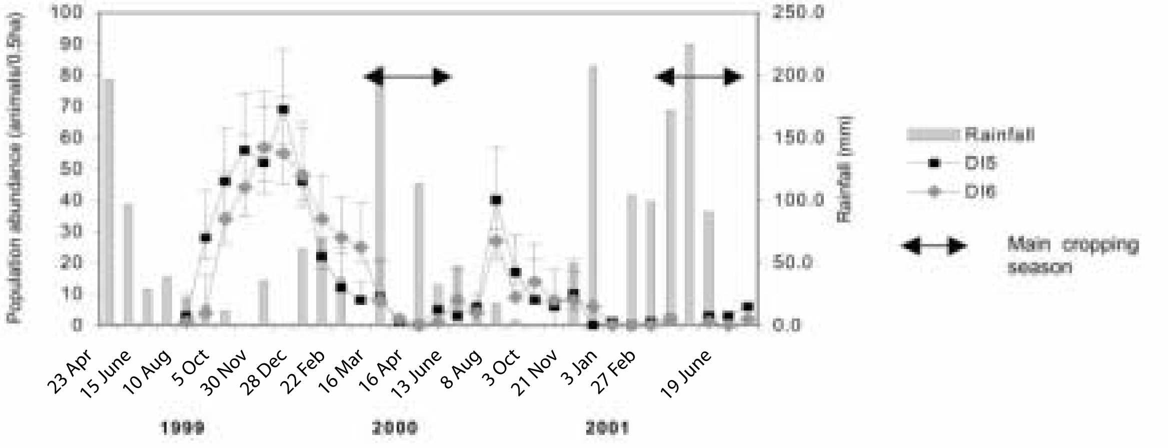

Figure 1. Rodent population fluctuations in relation to rainfall pattern in two crop fields (D15 and D16) at Morogoro, Tanzania.

systems (A.W. Massawe, unpublished data). Other studies on the home range of *M. natalensis* (Christensen 1996; Leirs et al. 1996a) have revealed that a large proportion of individuals in the population do not migrate far from their established home ranges.

Forecasting outbreaks

The idea that population eruptions of *M. natalensis* in East Africa could be predicted is not new. Harris (1937), Neal (1977) and Taylor (1968) suggested that outbreaks of *M. natalensis* were associated with wet years. The wet years, due to prolonged rainfall, appear to favour survival and breeding (Fiedler 1988a,b). Comparisons of several recorded outbreaks with the rainfall regime that preceded the outbreaks indicated that, before they occurred, there was abundant rainfall early in the season (Leirs et al. 1996b). It has been shown that, in Tanzania, abnormal (unseasonal) rainfall is correlated with population outbreaks (Leirs et al. 1996b). Outbreaks were not preceded by a long dry spell as previously thought (Fiedler 1988b) but occurred after high rainfall at the end of the previous year (Leirs et al. 1996b). The relationship between the timing of the rainfall and the population density of *M. natalensis* has been instrumental in developing a system for forecasting outbreaks of *M. natalensis* in Tanzania (Leirs et al. 1996b; Mwanjabe and Leirs 1997). A rodent forecasting model (Leirs et al. 1996b) based on the relationship between rainfall and breeding season has been developed and successfully tested to predict rodent outbreaks in Tanzania (Mwanjabe and Leirs 1997). The forecasting system will enable early preparedness of the community to carry out control activities.

Involvement of rodents in the plague cycle in north-eastern Tanzania

Among the major biological factors that have been identified to contribute to the persistence of plague in the western Usambara Mountains in north-eastern Tanzania is the existence of several species of reservoir hosts of the plague bacterium, *Yersinia pestis*. Human plague has afflicted the Lushoto District in the western Usambara Mountains for more than 20 years (Kilonzo et al. 1997). Several species of rodents are involved in the plague cycle (Figure 2) (Makundi and Kilonzo 1994; Makundi 1995). The distribution of different species of rodents in the western Usambara Mountains shows close proximity of suitable habitats and an overlapping of these habitats with human settlements. This facilitates the transfer of the disease from wild rodent reservoirs to the human population. Plague in the western Usambara Mountains occurs predominantly between October and March. To reduce the disease transmission to humans, it is recommended that case treatment, vector (fleas) control, and reservoir (rodent) management are intensified during this period (see also Makundi et al., this volume).

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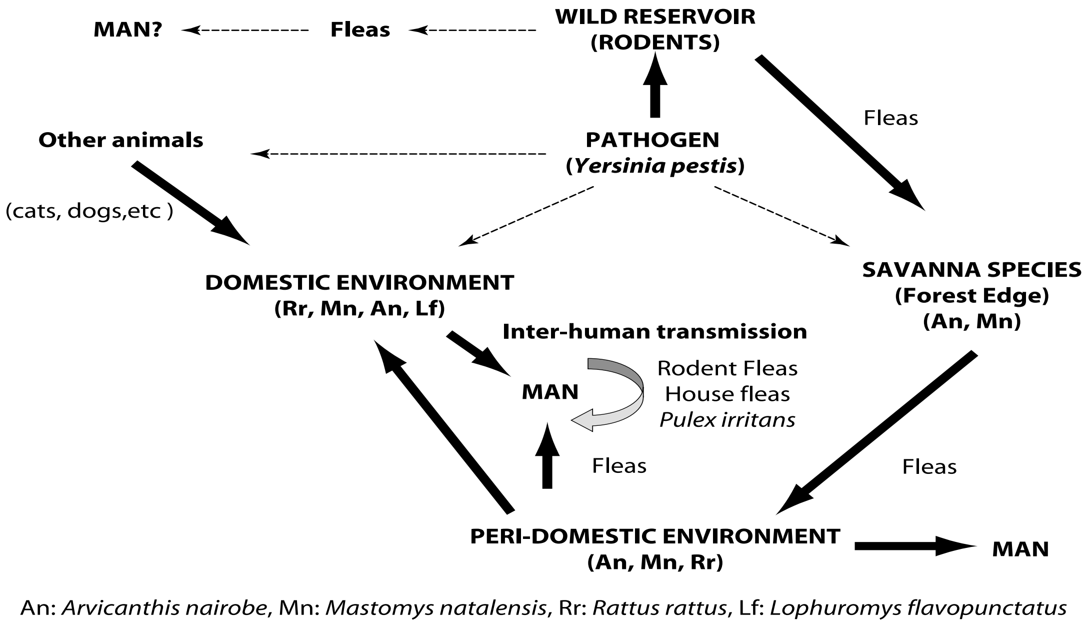

Figure 2. The plague cycle in Lushoto District, north-east Tanzania (An = *Arvicanthis nairobe,* Mn = *Mastomys natalensis*, Rr = *Rattus rattus*, Lf = *Lophuromys flavopunctatus*).

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Conservation of rodents in tropical forests of Vietnam

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Abstract. The establishment of protected areas in Vietnam has important implications for rodent conservation. However, knowledge of rodent species distribution is poor, especially in many protected areas. We examined the rodent species diversity in five protected forest areas, including sites in the poorly known Truong Son mountain range of northern Vietnam. Thirty rodent species were found in Sapa (Lao Cai province), 22 in Pu Mat (Nghe An), 18 in Huong Son (Ha Tinh), 12 in Biodup (Lam Dong) and 4 in U Minh Thuong (Kien Giang). Most squirrels (e.g. *Ratufa bicolor*, *Petaurista* spp. and *Callosciurus* spp.) were observed or captured on trees both of the understorey and the overstorey. Some squirrels (e.g. *Dremomys* spp. and *Tamiops* spp.) and some rats (e.g. *Niviventer langbianis*) and mice (e.g. *Chiropodomys gliroides* and *Typhlomys chapensis*) were captured on shrubs. Most rat species were captured on the ground. Human activities have greatly affected the distribution and species composition of rodents, especially squirrels living on trees and rats and mice of forest habitats. Our data also identify particular rodent species as characteristic of each protected area: e.g. *Petaurista elegans*, *Typhlomys chapensis*, *Eothenomys melanogaster* and *Dremomys gularis* in Sapa; *Rattus osgoodi*, *Maxomys moi*, *Menetes berdmorei*, *Vandeleuria oleracea* and *Callosciurus flavimanus* in Biodup; and *Callosciurus finlaysoni* in U Minh Thuong. The high rodent species diversity in the tropical forests of Vietnam is attributed to the combination of complex habitat structure and a biogeographical mosaic.

Introduction

In recent years, clearing of forests for cultivation and human settlements has had a major impact on forest conservation. Forests have been reduced in area and increasingly fragmented, and the habitats of many rodent species have disappeared or become insufficient for their survival. In Vietnam, forests occupy 8,630,965 ha and cover 28.1% of the land area. Deforestation is occurring at a rate of 150,000 ha annually (MSTE 1991). To protect biodiversity, the Vietnamese government established a system of protected areas; these total 2,119,500 ha and cover 5.7% of the total forest area of the country (Huynh 1997). An important step towards conserving the biodiversity of these protected areas is a systematic survey of their fauna and flora. Species composition and abundance of rodents are considered important indicators of biodiversity, but their taxonomy and distribution have not been thoroughly investigated in Vietnam. In this paper, we report on the diversity of rodent species in five protected forest areas in Vietnam: Sapa, Pu Mat, Huong Son, Biodup and U Minh Thuong (Figure 1).

Methods and study areas

The Sapa forests are located between 22°09'–22°30'N and 103°30'–104°50'E, and contain mountain peaks of 1500–3000 m in altitude. Bioclimatically, the area is unique in Vietnam. Annual temperatures range from –3.2°C to 29.7°C with a mean of 15.2°C (Moi et al. 1985). The coldest months are from November to February, and the warmest months from June to September. Mean annual precipitation is 2701 mm. Snow covers the Fasipan ridge every year. Vegetation in the area is highly varied and includes tropical montane forest, submontane forest and subalpine forest, with high species richness and diverse structure and composition (Thin 1998).

The Pu Mat forests occur between 18°46'–19°12'N and 104°24'–104°56'E, and cover an area of 91,213 ha. The area features an altitudinal range of 200 m to over 1800 m, with limestone mountains, small rivers and streams, and slopes of 25–35°. The climate of Pu Mat is characterised by a mean annual temperature of 23.5°C, with temperatures >18°C in the coolest months, and mean annual precipitation of about 1500 mm. The vegetation is classified as evergreen tropical forests (Tam and Sung 2000a,b).

The Huong Son forests are located at 18°20'N and 105°14'E and include mountains of 200–1250 m in altitude (Tam 2001).

The Biodup forests occur at 12°05'N and 108°20'E and include mountains rising to 200–1800 m in altitude.

The U Minh Thuong forests are located between 9°29'–9°42'N and 105°01'–105°09'E. This low-lying area within the Mekong River Basin supports a mosaic of *Melaleuca* forest and agricultural habitats (N.M. Tam, unpublished report).

Figure 1. Map of Southeast Asia showing location of the five study areas in Vietnam.

In each area, transects of 19–36 traps were set for six consecutive nights. Traps were set every 10 m for traps on the ground and every 20 m for traps on the trees (Adler 1996). In all, 5644 trap-nights in 22 transects were set at Sapa; 6342 trap-nights in 25 transects at Pu Mat; 3215 trap-nights in 16 transects at Huong Son; and 2050 trap-nights in 12 transects in Biodup. Trapping at U Minh Thuong was more opportunistic and the total trapping effort cannot be estimated. Three types of trap were used to sample rodents: a live-capture cage-trap, a snap-trap and a Sherman aluminum live-capture trap. These were used in the ratio of 100 live-traps for 100 snap-traps and 20–30 Sherman live-traps. All traps were baited with manioc (cassava) smeared with vegetable oil. Maize seeds, cut apple or banana were sometimes added to the bait.

Captured rodents were identified using external criteria and some individuals for each species were vouchered; these are stored at the Institute of Ecology and Biological Resources. For each captured male rodent, the testes were scored as abdominal or scrotal; for each captured female specimen, we scored vaginal perforation, lactation activity and obvious pregnancy. Maturity was also assessed on the basis of pelage characteristics.

Results and discussion

The rodent species recorded from each of the five study areas are listed in Table 1. Species recorded only from observations are distinguished from those based on actual captures.

Rodent diversity

The high diversity of rodent species in tropical rainforests of Vietnam is probably due to a combination of complex habitat structure and the interactions between two biogeographical zones (Tien 1985). Habitat diversity is promoted by the complex relief and the climatic differences across a broad latitudinal range.

In the Sapa forests, 179 individuals were captured belonging to 12 rodent species. Thirty species of rodents have been recorded in the vicinity of Sapa (N.M. Tam, unpublished report). *Niviventer fulvescens* was common and widely distributed, while *N. confucianus* was the most abundant species below 2000 m in altitude. The following rodent species are typical for the area: *Typhlomys chapensis*, *Eothenomys melanogaster*, *Dremomys gularis* and *Petaurista elegans*; all are endemic to the north-western region of Vietnam.

Of the 22 rodents known from the vicinity of Pu Mat, 17 species were caught in 1998, including representatives of seven genera of Muridae (*Rattus*, *Maxomys*, *Chiromyscus*, *Chiropodomys*, *Niviventer*, *Leopoldamys* and *Berylmys*) and four genera of Sciuridae (*Callosciurus*, *Dremomys*, *Ratufa* and *Tamiops*) (Tam and Sung 2000a,b). *Niviventer langbianis* was widely captured on trees and sometimes on the ground. *Chiropodomys gliroides* was captured only in forests mixed with bamboo. Many squirrels, including *Callosciurus erythraeus*, *C. inornatus* and *Ratufa bicolor*, were captured and observed on trees, both of the understorey and the overstorey.

At Huong Son, 18 rodent species were captured or observed. *Niviventer fulvescens* was common on the ground between 240–1240 m in altitude, while *N. langbianis* was caught predominantly on shrubs. *Chiropodomys gliroides* was captured most often on bamboo at 1–2 m above the ground. *Leopoldamys sabanus* was caught on the ground at 1250 m in altitude. There are no endemic rodent species in the North Truong Son mountain range.

At Biodup, we collected and observed 11 rodent species. One additional species, the endemic *Rattus osgoodi* (Musser and Newcomb 1985) is recorded from this area. Other rodent species typical of this forest are *Callosciurus flavimanus*, *Maxomys moi* and *Vandeleuria oleracea*.

The U Minh Thuong forests and associated agricultural habitats supported the lowest diversity of rodents (N.M. Tam, unpublished report). The only characteristic rodent species is *Callosciurus finlaysoni*; this species is otherwise widespread through Cambodia, southern Laos and Thailand.

Threats to rodents

In recent years, increased human pressure on forest areas has resulted in a great reduction in forest area and an increased level of fragmentation of surviving forests. These trends have a detrimental influence on rodent habitats. Clearing of forests for cultivation and human settlements has had a large impact on forest ecology, and has rendered many areas unsuitable for rodent survival and led to changes in species composition and abundance. These changes have threatened the survival of many species. Some rodent species have already disappeared locally, while others that are better adapted to disturbed conditions have replaced them.

In some areas, *Callosciurus* spp., *Dremomys* spp. and *Tamiops* spp. survive by utilising areas of cultivation and adjacent regrowth forest. However, in other areas, commensal rodents such as *Rattus* spp., *Mus* spp. and *Bandicota* spp. have entirely replaced the native rodents. *Rattus rattus* and *Mus* spp. are the dominant species in cultivated areas and villages in Sapa, Pu Mat and Ben En, and these rodents are regarded as serious pests in crops and grassland.

Population pressure in some areas has resulted in the exploitation of even quite remote forests. In the Sapa area, even forest on very steep slopes is cleared. After removal of some large canopy trees, all understorey trees and ground vegetation are removed. Ginger was planted alongside streams up to 2400 m in altitude on the way to Fasipan peak. This widespread disturbance of vegetation undoubtedly has deleterious impacts on the species composition and population density of rodents, especially squirrels (e.g. *Petaurista* spp., *Callosciurus* spp.) and arboreal rats (e.g. *Chiropodomys gliroides* and *Niviventer confucianus*).

Forest mammals are valued by local people as food, medicine and a source of revenue. Interviews conducted in all villages indicated that hunting and trapping contributed significantly to their consumption and cash income. Hunting pressure is most intense during the dry season when mammal activity is highest and there is less work to do in the gardens. The most common method of hunting involves the use of guns and dogs. A typical hunting group consists of two or three local people who enter the forest for several days. They generally use home-made flintlock rifles and snap-traps to capture rats and squirrels. During our survey in the Sapa forests in 2000, we encountered one party who had about 50 snap-traps in a basket, as well as eight guns and four dogs; the party had one captured bamboo rat (*Rhizomys sumatrensis*). Hunting activity was also observed in recent years in forest areas in Pu Mat (Nghe An), Huong Son (Ha Tinh), Ben En (Thanh Hoa) and Biodup (Lam Dong). Live-captured squirrels (*Callosciurus erythraeus*, *C. inornatus*, *Dremomys rufigenis* and *Tamiops* spp.), skins of flying squirrels (*Petaurista petaurista*) and quills of porcupines were often observed in villages around the margin of the forests.

Some threatened rodents

Early work on rodent taxonomy and ecology in Vietnam was conducted by Osgood (1932) and van Peenen et al. (1969, 1970). More recently, this work has been continued in Vietnam by Khoi et al. (1979), Sung (1983, 1990), Sung et al. (1980), Tien (1985), Sung and Tam (2000, unpublished report), Tam (2001), and Tam and Sung (2000a,b, 2002). Other taxonomic research involving Vietnamese material was published by Musser (e.g. Musser et al. 1979; Musser and Newcomb 1985). Research on rodent control in Vietnam was carried out by Sung et al. (1997, 1999).

Despite this prior research, knowledge of the taxonomy of Vietnamese rodents is incomplete, especially for those rodents living in forests of the Truong Son mountain range. Information on the abundance of rodent species, whether common, threatened or rare, is also essential for management and conservation. Therefore, additional research on the taxonomy, distribution and abundance of rodent species is needed urgently in order to assess their status and to develop more effective measures for their protection.

We consider the following rodent species to be under significant threat, mainly as a consequence of the continued clearance and fragmentation of their habitat:

- Giant squirrel *(Ratufa bicolor condorensis*) is a frugivore that inhabits large trees in the Con Dao forests. Deforestation is a major factor in the decline of its population.
- Giant flying squirrel (*Petaurista elegans*) is a nocturnal species that occurs in primary forests of Sapa (Lao Cai) and Xuan Nha (Son La). Its status is endangered, due to deforestation and hunting pressure.
- Porcupine (*Hystrix brachyura*) occurs in secondary and primary forests of Na Hang and Dinh Ca (Tien 1985). It lives in natural cavities in limestone hills and feeds mainly on plant roots and bulbs.
- Tree squirrel (*Callosciurus finlaysoni*) is a diurnal species that inhabits the canopy of *Melaleuca* forests in Kien Giang (N.M. Tam, unpublished reports). It is now rare in Vietnam due to the destruction of forests by burning in preparation for cultivation.
- *Dremomys gularis* is a ground-dwelling species that feeds on vegetation and insects; it is found only at elevations above 2000 m in the Sapa forests (Tam 2001). Deforestation is the major factor behind the reduction in population size of this species.
- *Typhlomys chapensis* is only found at elevations greater than 1800 m in the mixed bamboo forests of Sapa (Tam and Sung 2002). It is classified as endangered, due mainly to destruction of forest habitat.

Conclusion

The establishment of additional protected areas is clearly of the highest priority for rodent conservation in Vietnam, especially for those areas of the greatest rodent diversity and endemism. For example, the recently established Hoang Lien Son Nature Reserve of north-western Vietnam is a unique area for biodiversity conservation.

Table 1. List of rodent species recorded in five study areas (+ = present; +* = observed only).

Taxon	Sapa	Pu Mat	Huong Son	Biodup	U Minh Thuong
Hystricidae					
Atherurus macrourus	+	–	+	–	–
Hystrix brachyura	+	–	–	–	–
Rhizomyidae					
Rhizomys pruinosus	+	–	–	–	–
R. sumatrensis	+	–	–	–	–
Pteromyidae					
Petaurista elegans	+	–	–	–	–
P. petaurista	+	–	–	–	–
Sciuridae					
Callosciurus erythraeus	+	+	+	–	–
C. inornatus	+	+	–	–	–
C. finlaysoni	–	–	–	–	+
C. flavimanus	–	–	–	+	–
Dremomys gularis	+	–	–	–	–
D. rufigenis	+	+	+	+	–
Ratufa bicolor	+	+*	+*	–	–
Tamiops maritimus	+	–	–	–	–
T. rodolphei	–	+*	+*	–	–
T. swinhoei	+	–	–	–	–
Arvicolinae					
Eothenomys melanogaster	+	–	–	–	–
Platacanthomyinae					
Typhlomys chapensis	+	–	–	–	–
Murinae					
Bandicota indica	–	–	–	–	+
Berylmys bowersi	+	+	–	+	–
B. mackenziei	–	+	–	–	–
Chiromyscus chiropus	+	+	–	–	–
Chiropodomys gliroides	+	+	+	+	–
Leopoldamys edwardsi	+	+	+	+	–
L. sabanus	–	+	+	–	–
L. neilli	–	+	–	–	–
Micromys minutus	+	–	–	–	–
Maxomys moi	–	–	–	+	–
M. rajah	–	+	–	–	–
M. surifer	–	+	+	–	–
Mus caroli	–	–	–	+	–
M. musculus	+	–	+	–	–
M. pahari	+	–	+	–	–
Niviventer bukit	+	–	–	–	–
N. confucianus	+	+	–	–	–
N. fulvescens	+	+	+	+	–
N. langbianis	+	+	+	+	–
N. tenaster	+	+	+	–	–
Rattus argentiventer	–	–	–	–	+
R. nitidus	+	+	+	–	–
Rattus sp.	–	+	+	–	–
R. osgoodi	–	–	–	+	–
R. rattus	+	+	+	–	+
R. sikkimensis	+	+	+	+	–
Vandeleuria oleracea	–	–	–	+	–

The following characteristic rodents occur in this reserve: *Typhlomys chapensis*, *Petaurista petaurista*, *P. elegans*, *Eothenomys melanogaster* and *Ratufa bicolor*. The Biodup Nature Reserve supports important populations of *Rattus osgoodi*, *Vandeleuria oleracea* and *Maxomys moi*; and *Callosciurus finlaysoni* is found in the U Minh Thuong Nature Reserve within Vietnam. However, effective long-term protection of each of these significant rodent species will also depend on an improved understanding of their habitat requirements in each reserve; and on the critical and ongoing assessment of the population density for each species.

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Testing a biological control program for rodent management in a maize cropping system in Kenya

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Abstracts. Birds of prey could potentially act as control agents for rodents in some agricultural systems. However, little has been done to encourage the breeding of avian predators and subsequently to evaluate their potential as biological control agents in maize crops, an important staple food crop in eastern Africa. We set out 400 perch poles and 20 nest boxes in each of two 100 ha experimental grids in maize fields in the Kenyan Rift Valley. A capture–mark–recapture (CMR) study was set in 1 ha grids of 10 × 10 box traps in each experimental and two control sites to evaluate rodent demography. Owl abundance and diet was monitored by regular assessment of regurgitated pellets at nest boxes.

Preliminary results showed an increase in barn owl numbers and barn owl reproduction on the experimental grids. In the two experimental grids, there was over 60% occupation of the nest boxes with successful breeding taking place in 40% of the 40 boxes within a period of 12 months. During the same period, rodent catch rates dropped from a peak of 45% to 0.3% trap success in the first experimental grid, 40% to 1% in the second, and 22% to 6% in the controls. The study is in its second maize cropping season, and from these preliminary findings, avian predators appear to have promising results in control of rats. However, this will become clearer once all the demographic parameters are fully analysed.

Introduction

Rodents are recognised pests in many agricultural systems and there is a need for their control. There is a dearth of quantitative information on economic losses due to rodents in Kenya. Earlier reports (Taylor 1968) indicated 20–30% damage to maize crops, and a 34–100% loss during rodent outbreaks. Current control is symptomatic and based on the use of chemicals, some of which are proving to be ineffective due to development of resistance (Lam et al. 1982; Lee et al. 1983). Continuous use of these chemicals also has undesirable effects to the environment with risks to non-target species or domestic animals (Godfrey 1985). There is an increasing need to develop ecologically benign rodent management techniques in order to reduce the costs and risks associated with rodenticides. However, little attention has been directed to biological control as an integrated approach, partly because little information exists on predator–prey relationships. A recent, non-replicated pilot study suggested increased survival of some rodent species in predator-exclusion areas (Van Gulck et al. 1998). The barn owl and other raptors have been suggested as potent predators (Duckett 1986b; Smal 1989; Vibe-Petersen 1999). These findings have given rise to an increasing interest in understanding how predation affects rodent populations and its potential in biological control. Our ongoing study began in December 2000 to evaluate the potential of avian predators to control rodents in maize fields in eastern Africa, and here we report some preliminary results.

Study area

The study was carried out in the Kenyan Rift Valley at latitudes 35°28'–35°36'E, longitudes 0°13'–1°10'S, and altitudes of between 1822 and 1950 m above sea level. The climate in this area falls between semi-arid (annual rainfall less than 760 mm) in the lower areas and dry sub-humid (annual rainfall of 1270 mm) regions at the higher altitudes. Rainfall is bimodal with peak precipitation (70–80%) in March to May and late August to October, though great variations may occur from year to year. The maximum temperature is about 30°C, with December to March being hottest, and July being coolest at an average of 23.9°C (Nakuru District Development Plan 1997). The area is largely under maize, with a few large-scale farms growing wheat. Rodents are acknowledged as major pests in both cropping systems. There are resident and migratory raptors, as well as a resident population of barn owls in this area, making it suitable for this particular study.

Materials and methods

The study was carried out in two experimental areas (Goga and Elia) and two control areas (Beth and Kurgat), each measuring 100 ha under maize crop. In each of the two experimental areas, 400 artificial bird perches were erected at 50 m intervals to attract avian predators. Each pole had two perching points at heights of 2 m and 4 m, suitable for owls and raptors, respectively. Nest boxes were placed strategically to enhance breeding of owls. Twenty boxes were placed at 5 ha intervals in each experimental grid. The experimental grids were 15 km apart and each 5 km from controls.

In each experimental and control site, a 1 ha grid was set up for capture–mark–recapture (CMR) studies. Rodents were live-trapped using Sherman's LFA traps measuring 23 × 8 × 9 cm, from June 2001 to June 2002 in all the four grids. One trap was placed at each station during trapping. Primary trapping sessions were organised every 28 days with secondary sessions for three consecutive days and nights during each primary trapping. Traps were baited with fried coconut cubes mixed with peanut butter. Barn owl use of nest boxes was monitored monthly. Regurgitated pellets were collected from areas around the perch poles, nest boxes, and under trees.

Rodent population densities were estimated using Schnabel–Schumacher method. The monthly rate of change in *Mastomys* density was estimated by determining density differences for consecutive months for each study site. The means for the treatments and their replicates were lumped together and compared using student *t*-test.

Results and discussion

Owl activity index and diet

Twelve nest boxes were occupied between March 2001 and June 2002 at the Goga experimental site and successful breeding of barn owls took place in eight boxes. Nesting took place between June and October 2001 (Figure 1a). Thus, breeding here was noted for 5 consecutive months only in 2001. At Elia farm, 11 nest boxes were occupied with successful breeding of barn owls in seven boxes between June 2001 and March 2002 (Figure 1b). At Elia, two short breeding seasons were recorded, June–August 2001 and February–March 2002. The mean (± sem) number of eggs laid was 6.3 (± 0.4) and 6.6 (± 0.4) for Goga and Elia grids, respectively. While mean number of fledglings were 5.3 (± 0.4) and 6.1 (± 0.7), respectively. Six hundred pellets were collected from experimental grids, and preliminary analyses of 120 intact skulls recovered indicate that *Mastomys* cf. *erythroleucus* formed 80% of the predator diet. Skulls of *Crocidura* and *Tachyoryctes* species were also positively identified from the pellets. No nesting activities were recorded or pellet recovered in control areas to date.

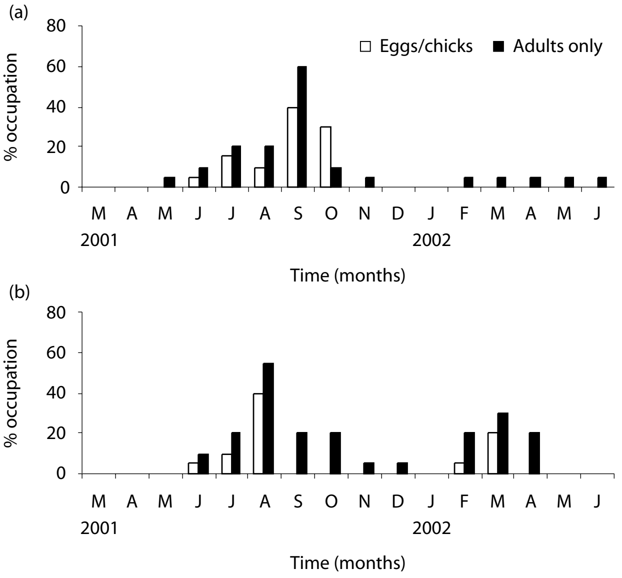

Figure 1. Occupancy rate (%) of nest boxes and breeding index by barn owls in two experimental sites in the Kenyan Rift Valley, (a) Goga and (b) Elia.

Rodent abundance

A total of 1490 rats representing six species were trapped in the four grids (Table 1). *Mastomys* cf. *erythro-*

Table 1. Species composition and number of individual rodents captured in experimental and control grids in 3600 trap nights from June 2001 to June 2002.

Species	Goga (520)	Elia (490)	Kurgat (250)	Beth (230)	Total (Proportional abundance)
Mastomys cf. *erythroleucus*	425	441	212	198	1276 (90.2%)
Arvicanthis cf. *newmanii*	10	25	21	23	79 (5.6%)
Lemniscomys striatus	5	15	2	2	24 (1.7%)
Thallomys sp.	5	0	2	4	11 (0.8%)
Mus minutoides	5	5	6	4	20 (1.4%)
Dendromus sp.	0	5	0	0	5 (0.4%)

leucus was the most common species, accounting for 90% of all captures. *Mastomys* populations declined at significantly different rates (*t* = 2.281, *P* = 0.022, *n* = 12), being higher in experimental 9.4 (± 2.0) and lower in control grids (5.1 ± 0.9). The mean monthly rate of change is shown in Figure 2.

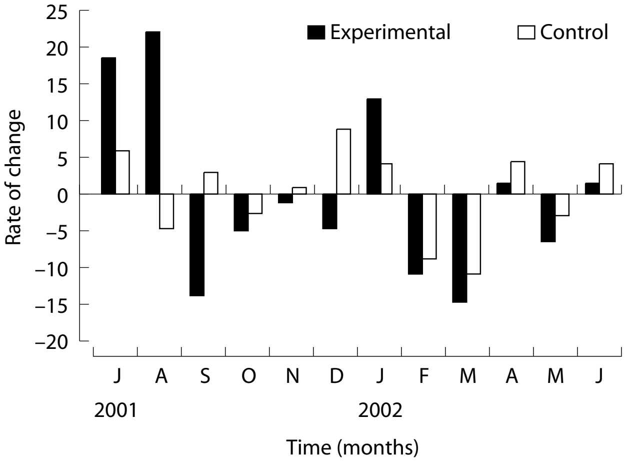

Figure 2. Rate of monthly change in *Mastomys* abundance in experimental (Goga and Elia) and control (Kurgat and Beth) grids in maize fields between June 2001 and June 2002 (data from the two replicates pooled and analysed together).

Conclusions

Our study has shown that barn owls used and successfully bred in nest boxes erected in maize fields (Figure 1). They also consumed *Mastomys,* the most common species (Table 1), in higher proportions than other species. Although *Mastomys* were more abundant on experimental grids at the beginning of the study, their rate of change in monthly numbers was higher in these grids compared to control areas (Figure 2). The higher rate of decline of *Mastomys* numbers in experimental compared with control grids may be indicative of a predation effect. However, further analysis is required before we can infer the direct effects of barn owl predation on *Mastomys* populations. This work is ongoing and will involve another season of data collection and demographic analyses of the rodent populations to provide a clearer picture of predation effects. We conclude for now that provision of nest boxes has the potential of increasing the barn owl populations in maize fields in Kenya, and this provides a potential avenue for biological control in this agricultural system.

Acknowledgments

This work was supported by grants from European Union (STAPLERAT). We thank officials from the Ministry of Agriculture of the Government of Kenya for research permission and logistic support. We are also grateful to all the farmers who gave us permission to work in their fields.

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The effects of *Tephrosia vogelii* and land preparation methods on mole rat activity in cassava fields

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Abstract. Mole rats cause considerable damage to tuber crops in eastern Africa. In experimental cassava fields in Zambia, we tested whether different land management techniques and the presence of a deep-rooted poisonous shrub, *Tephrosia vogelii*, affected mole rat activity in those fields. The bush was planted as a barrier around the field or dispersed throughout the field; cassava was planted on ridges or in mounds. Since the start of the experiment until two years later, there were significantly fewer molehills in fields with *T. vogelii* bushes and cassava planted in mounds. Future comparison of yield in the experimental fields will indicate whether this strategy offers good opportunities for the management of damage by mole rats.

Introduction

In eastern Africa, mole rats are notorious rodent pests of cassava tubers, and methods for their sustainable control are badly needed. Mole rats live and feed underground and are capable of making numerous burrows leading to granaries, latrines and feeding places. Sichilima and Zulu (1998) demonstrated that activity of mole rats in creating molehills can be associated directly with the search for food. The same study reported that some Zambian farmers claim that land preparation methods may have an effect on mole rat activity in cassava fields. In some other areas in eastern Africa, ‘fish bean’, a poisonous, deep-rooted shrub, *Tephrosia vogelii*, is reported to repel mole rats effectively from cassava fields (unpublished information from farmers). Here we report on an ongoing study to evaluate the effects of land preparation and *T. vogelii* on mole rat activity in cassava fields in Zambia.

Materials and methods

Twenty-four plots, each 50 m × 50 m, were selected in Solwezi district in Zambia. All plots had been used as crop fields (but not cassava) 1 or 2 years before and all plots had previously experienced heavy mole rat problems. The area is located at the average altitude of 1300 m above sea level with annual rainfall >1100 mm per year. The main rain season starts in mid-November and extends to mid-March and this is followed by the cold dry season from May to mid-August. The hot dry season starts from September and extends to mid-November. Main crops in the region are sweet potato and cassava.

The experiment was set up following a randomised controlled block design with two treatment levels (planting *T. vogelii*, land management) and four replications for each treatment combination. *T. vogelii* bushes were planted as three barrier rows spaced 1 m around the field edges, scattered at 3 m spacing throughout the field, or not present in controls. Cassava was planted in ridges or in mounds. The fields were set up in January 2000 and monthly data on the presence of fresh molehills were collected through until August 2002.

The data were analysed using a two-way analysis of variance with repeated measurements (STATISTICA).

Results and discussion

We found highly significant effects of both the presence of *T. vogelii* ($F = 31.45$, df = 2,18, $p < 0.001$) and land management ($F = 12.38$, df = 1,18, $p = 0.002$). Significantly more fresh molehills were counted in fields without *T. vogelii* (Newman-Keuls *a posteriori* comparison of means, $p < 0.001$) but the difference between the two types of *T. vogelii* planting was not significant ($p = 0.117$). The differences changed over time, but remained clear (see Figure 1). There was no interaction between the presence of *T. vogelii* and land management ($p = 0.608$).

Our results show that mole rat activity can be reduced when cassava is planted on mounds with the deep-rooted *T.vogelii* shrub in barriers around or scattered in fields.

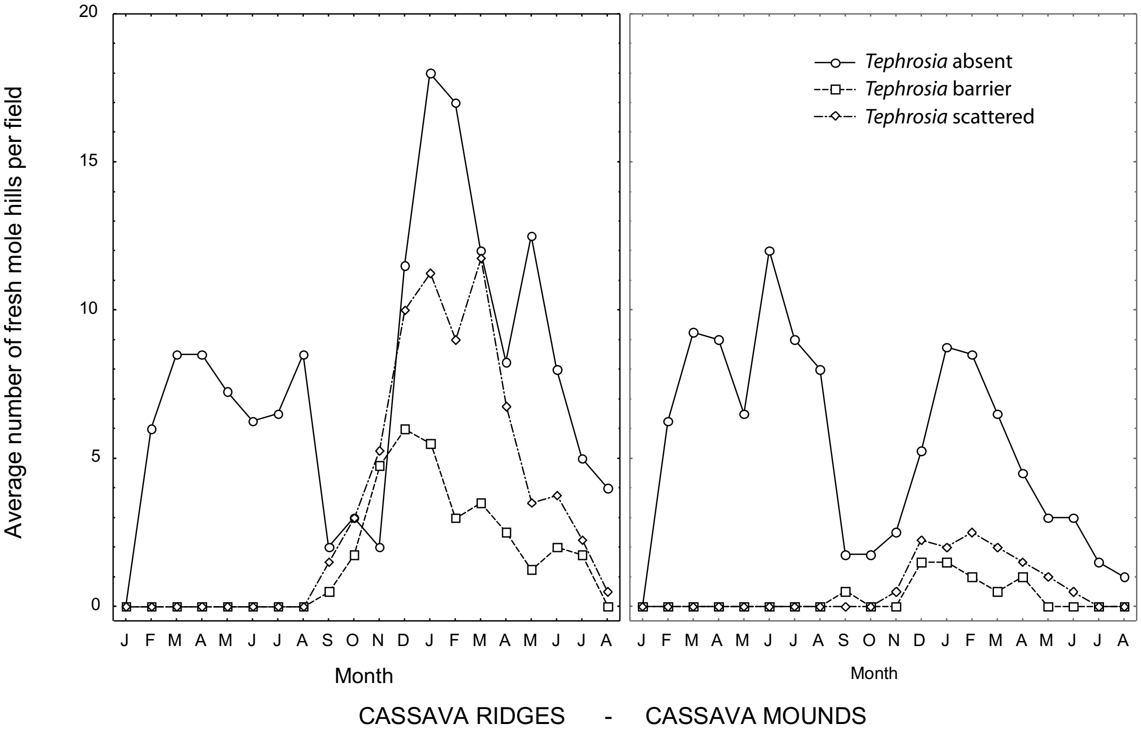

Figure 1. The mean number of fresh molehills dug by mole rats in Zambia in cassava fields with different densities of the deep-rooted shrub *Tephrosia vogelii*: molehills recorded where cassava was planted (a) along ridges; and (b) in mounds. The study was conducted from January 2000 to August 2002.

These results suggest that a simple biological method can be implemented to reduce the impact of mole rats in cassava fields in eastern Africa. This in turn will lead to reduced use of rodenticides and savings to farmers through reduced costs of rodent management. In late 2002, cassava tubers will be harvested to see how these treatments affect final yield.

T. vogelii is also used as a green manure crop and as a shade tree in young plantations (Simute 1992). Its leaves contain insecticidal products that can be prepared as an extract or powder (Karlsson 1994; McDavid and Lesseps 1994). The repellent effect on mole rats further increases its value as an agroforestry plant.

Acknowledgments

This project was funded by the European Union under the STAPLERAT project. We appreciated the help of the technical staff at Mutanda Research Station.

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Changes in community composition and population dynamics of commensal rodents in farmhouses in the Dongting Lake region of China

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Abstract. From the 1970s to 2001, there have been marked changes in the commensal rodent communities and population densities in dwellings of the countryside in the Dongting Lake plain area. The buff-breasted rat (*Rattus flavipectus*) was the dominant species in farmhouses in the 1970s and rodent population densities were low. With the excellent harvest in the early 1980s and changes in the way grains were stored in rural China, the Norway rat (*Rattus norvegicus*) became the dominant species and its population density increased quickly. In the late 1980s, the structure of farmhouses and grain storages was further improved, and a rodenticide, natrium diphacin, was used to control the pest rodents in some areas. This led to declines in the populations of *R. norvegicus* while *Mus musculus* became more dominant in the rodent community. The Norway rat and buff-breasted rat increased in numbers in the early and mid-1990s coincident with increases in livestock breeding. Following the improvement in the living standards of farmers and the farmhouse structures, people have paid greater attention to rodent pests and the methods to manage them. Subsequently, the densities of the pest rodents have declined gradually, especially the population of *R. norvegicus*, and *M. musculus* has become the dominant species in the dwellings.

Introduction

The Norway rat, *Rattus norvegicus*, house mouse, *Mus musculus*, and buff-breasted rat, *Rattus flavipectus*, are the main rodent species inhabiting farmhouses throughout China (Li et al. 1988). They consume and contaminate large quantities of human food and animal feed, as well as damaging building structures by their gnawing and burrowing. Rodents also are potential threats to both human and animal health through transmission of diseases (Wang 1996). The population structure and density of the commensal rodents are affected markedly by human activities in the environment because they live in close proximity with humans in residential premises (Langton et al. 2001). This paper describes the numbers of commensal rodents in the Dongting Lake region from the 1970s to 2001 and suggests some reasons for the observed changes.

Study site and methods

Study site

The Dongting Lake region is located in the northern part of Hunan province, China (28°13'–29°55'N and 111°11'–113°43'E). It is in a subtropical region, and shows four defined seasons. The weather is warm and humid, with a mean annual temperature of 16–17°C and a mean annual rainfall varying from 1200 to 1470 mm. It is one of the most important regions for agricultural production (grain, cotton, rapeseed, soybean, sesame, and some aquatic and husbandry products) in the Yangtze Valley of China. Each farming family owns one house, usually with five rooms, and it is one of many dwellings in local villages. In the 1970s, houses were made of clay or wooden walls and had clay floors. From the mid-1980s, houses were constructed with brick walls and concrete floors. By the end of the 1990s, more than half of the houses were made with these materials and many farmers had also built storage rooms in their homes.

Methods

A census of rodents was conducted from the early 1980s in the farmhouses in the countryside in the Dongting Lake region. Snap-traps were used throughout the census (no less than 100 traps per site). The traps were situated in each room close to a wall, behind an object or in a dark corner, with one trap in a small room (≤ 15 m^2) and two traps in larger rooms. Traps were baited with fresh sunflower seeds and placed on the ground in the afternoon. Captured animals were collected the next morning and the animals were brought back to the laboratory to be identified. Every month there was a survey in two sites in Taoyuan county. The survey in Hanshou county alternated between two villages and was carried out once every two months before 1997 and three times per year (March, July and December) from 1998 to 2001.

The survey sites in Taoyuan and Hanshou counties had similar surroundings. The rodent density was defined as the percentage of trap success per 100 traps. The data of Taoyuan county in 1970s, which were collected using snap-traps in 1975–1978, were obtained from the Health and Anti-epidemic Station of that county.

Results and discussion

The rodent community comprised *R. norvegicus*, *M. musculus* and *R. flavipectus* in farmhouses, although the most numerous species varied at different times during the period of census trapping (Table 1). Several other rodent species, *Apodemus agrarius*, *Rattus confucianus*, *Rattus losea,* and an insectivore (shrew), *Suncus murinus*, were also trapped, but in insignificant numbers. The population densities in farm buildings were low from the 1970s. Thereafter, there were two outbreaks of rodent populations—the first peak appeared in the 1980s and the second in the 1990s. According to Guo et al. (1992), no damage due to rodents was noticed until 1980 in Taoyuan, and there was only occasional harm in paddy fields in summer and houses in winter in 1981. However, there was a widespread outbreak across the county in 1983. The highest population occurred in 1986 (Table 1). The density in Taoyuan was lower than in Hanshou, due to a campaign to kill rodents using natrium diphacin across the entire county of Taoyuan in 1984. From the limited data (1992–1995) in Taoyuan and Hanshou, it was not clear in which

Table 1. Rodent density and community composition in dwellings in the Dongting Lake region.

Site	Years	No. of traps	Percentage trap success[a]				
			Rattus norvegicus	*Mus musculus*	*Rattus flavipectus*	Other	Total
Taoyuan	1975–1978	6000	1.25	1.45	1.88	0.02	4.60
			(27.17)	(31.52)	(40.87)	(0.44)	
	1982–1984	6300	6.67	1.60	0.35	0.17	8.79
			(75.81)	(18.23)	(3.97)	(1.99)	
	1986	591	8.29	9.48	0.68	0.17	18.62
			(44.55)	(50.91)	(3.64)	(0.91)	
	1987	4625	6.83	4.52	1.06	0.24	12.65
			(54.02)	(35.73)	(8.38)	(1.88)	
	1988	3657	4.87	2.93	1.45	0.03	9.27
			(52.51)	(31.56)	(15.63)	(0.29)	
	1989	3090	5.02	6.96	1.26	0.06	13.30
			(37.71)	(52.31)	(9.49)	(0.49)	
	1990	2814	3.84	7.11	0.64	0.43	12.01
			(31.95)	(59.17)	(5.33)	(3.55)	
	1991	512	3.13	10.94	1.37	0.58	16.02
			(19.51)	(68.29)	(8.54)	(3.66)	
Hanshou	1986	310	34.84	20.32	2.58	0.00	57.74
			(60.34)	(35.20)	(4.47)	(0.00)	
	1987	882	23.02	9.18	3.63	0.57	36.39
			(63.24)	(25.23)	(9.97)	(1.56)	
	1988	772	15.54	10.62	2.33	0.13	28.63
			(54.30)	(37.10)	(8.14)	(0.45)	
	1989	464	12.28	12.72	0.22	0.65	25.86
			(47.50)	(49.17)	(0.83)	(2.50)	
	1990	198	2.02	2.02	5.05	0.00	9.09
			(22.22)	(22.22)	(55.56)	(0.00)	
	1996	455	29.23	15.52	6.47	0.00	51.21
			(57.07)	(30.30)	(12.63)	(0.00)	
	1997	1091	11.55	12.07	1.75	0.10	25.48
			(45.34)	(47.37)	(6.88)	(0.40)	
	1998	853	7.32	7.71	1.57	0.39	17.00
			(43.08)	(45.38)	(9.23)	(2.31)	
	1999	968	5.14	4.46	1.35	0.00	10.95
			(46.91)	(40.74)	(12.35)	(0.00)	
	2000	489	2.30	5.75	0.86	0.29	9.20
			(25.00)	(62.50)	(9.38)	(3.13)	
	2001	317	1.26	2.84	0.95	0.00	5.05
			(25.00)	(56.25)	(18.75)	(0.00)	

[a] The numbers in parentheses are percentages of each species of the total trap success for that year, giving an indication of species composition.

year in the early 1990s the second increase in numbers of rodents began, but the highest density occurred in 1996. Thereafter, the rodent densities began to decline.

The buff-breasted rat, *R. flavipectus*, was the dominant species in farmers' houses in the 1970s (40.9%), followed by the house mouse, *M. musculus* (31.5%), then the Norway rat, *R. norvegicus* (27.2%). Each species had a low population density in 1970s relative to later years. The capture rate increased and the species composition changed in the early 1980s, with the population of Norway rats increasing and buff-breasted rats declining. The Norway rat became the dominant species, comprising more than half of the captured animals. The possible reasons for this included changes in the agricultural practices in the countryside of China in the late 1970s and early 1980s, the bumper harvest, and a change in the methods of grain storage (from collective stores to individual storage in a farmers' houses), which meant that there was abundant food that rodents, especially Norway rats, could readily obtain (Guo et al. 1992; Zhang et al. 2002a). Some investigations have shown that the building structure and materials of the farmhouse were the main factors influencing the activity of pest rodents in farmhouses (Zhang et al. 2002a). In the early 1980s, farmhouses were built of wood or clay brick, and there were no effective ways to prevent entry by pest rodents and no barns to store grains. Thus, pest rodents could obtain food grain easily when farmers put their harvest in the house.

In the 1970s and before, there was an attic in every farmhouse, and wood was the main material for walls. This benefited the buff-breasted rat until brick replaced the wood walls and attics were no longer built in the farmhouse. We conclude that this was the main factor that has limited the buff-breasted rat in recent years.

In the late 1980s, the proportion of Norway rats was decreasing, while house mice were increasing and became the dominant species. The possible reason was that most farmers had built a proper granary within the farmhouse and this could store all of their grain, making less food readily available to the Norway rat (Guo et al. 1992). Along with the improved brick housing, natrium diphacin was used regularly to kill rodents from the mid-1980s. The populations of Norway rat continued to decrease, as it is more susceptible to the anticoagulant than *M. musculus* and *R. flavipectus*. The proportions of residual individuals of *M. musculus* and *R. flavipectus* in residential premises were higher than those of *R. norvegicus* after each campaign of rodent control (Zhang et al. 2002b).

Due to the increase in livestock breeding in the early to mid-1990s, rodents again increased in this area. The Norway rat became the dominant rodent species and the population density of the rodents increased to another peak. Since the mid-1990s, the population densities of rodents in this area have been decreasing, especially populations of *R. norvegicus*. *M. musculus* has become the dominant rodent species in dwellings. Some of the reasons include an improved standard of living for the people, especially in the countryside, more fired-brick houses with concrete floors have been built, the residential premises are neat and clean, and farmers are less tolerant of rodents. By the end of 1990s, more than half the farmhouses had been changed to fired-brick structures with concrete floors. The census data show that rodent densities were very low in tidy, clean houses, and the dominant species was the house mouse rather than the Norway rat (Zhang et al. 2002a). Another reason for decreasing rodent densities is that the people have a better understanding of integrated methods of controlling rodent pests and have accepted the use of anticoagulants rather than rapid rodenticides. The dominant species in 2001 was the house mouse.

Conclusion

Commensal rodents in farm buildings experience a more stable environment and climate than field rodents. This study has shown population changes in pest rodents in dwellings of the Dongting Lake region were affected by the impact of man on the environment. The bumper harvest in the countryside in the 1980s and the growth of stockbreeding in the 1990s contributed to rodent outbreaks. The changes in house structures and the improvement in living standards have caused a decline in the rodent population and altered rodent community composition. The activity of humans was one main factor leading to the changes in the populations of commensal rodents. Thus, it is necessary to evaluate the possible effects of human economic activities on the environment and on the population dynamics of pest rodents. We forecast that the population of rodent pests in the countryside of the Dongting Lake region will continue to decease with continued improvements in living standards.

Acknowledgments

We are grateful to Professor Guo, C. of Sichuan University, to Chen, A.G., Li, S.B. and Hu, Z.J. of Changsha Institute of Agricultural Modernization, the Chinese Academy of Sciences, for their help with the field work. The Chinese Academy of Sciences (KSCX2-SW-103) supported the study.

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Evaluation of thiram and cinnamamide as potential repellents against maize-seed depredation by the multimammate rat, *Mastomys natalensis*, in Tanzania

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Abstract. In maize fields in Tanzania, rodents are responsible for high levels of seed depredation at sowing and cutting of the seedlings at emergence. We evaluated the potential of two seed-dressing compounds, thiram and cinnamamide, as rodent repellents to protect maize against damage by multimammate rats, *Mastomys natalensis*. The two compounds were evaluated in the laboratory using choice and no-choice tests. In the choice experiment (single cages), <10% and <2% of cinnamamide- and thiram-treated seeds, respectively, were damaged compared to 20–50% damage in untreated seeds. In the no-choice experiment (room), only a few seeds were damaged (0–6 seeds for cinnamamide and 1–5 seeds for thiram in 4 days, out of about 70 seeds provided), although the animals had no alternative food. These experiments clearly indicate the potential for thiram and cinnamamide to protect seeds from depredation by rodents. Further evaluation of these compounds will be carried out to establish efficacy in the field.

Introduction

Maize is most susceptible to rodent damage at planting and during the seedling stage (see Mulungu, Makundi, Leirs et al., this volume, for review). This period spans 2 weeks and is the most critical period for damage throughout the growth stages of the maize crop. Farmers will likely avoid crop losses (seed loss, replanting, extra labour etc.) if an appropriate seed dressing, capable of repelling depredation of seed at the susceptible planting stage, could be used. This paper reports on two seed-dressing compounds, cinnamamide and thiram, for repellence against the multimammate rat, *Mastomys natalensis*, a major pest species in Tanzania. Germination tests indicated no phytotoxic effects of these compounds on the seeds.

Materials and methods

Tests were carried out in the laboratory with wild-captured animals, after an acclimatisation period of 4 days. The seeds were dressed with the candidate repellent 24 hours before supplying them to the experimental animals. In a choice experiment with 10 singly caged animals, treated (20 g) and untreated (20 g) seeds were supplied in two crucibles in each cage. The number of seeds in each 20 g lot was counted before placement in the cage. The positions of the crucibles were changed daily to prevent location preferences. The number of seeds consumed or damaged was counted every morning and the crucibles were replenished with fresh treated and untreated seeds. The evaluation was carried out over 4 days with the same animals in each cage.

In a no-choice test in a room (222 × 278 × 122 cm), a group of 10 animals was supplied with 20 g of treated seeds in crucibles. The seeds were inspected for rodent damage/consumption for 4 days as in the choice experiment and were replenished every day for a period of 4 days. Drinking water was provided *ad libitum* to animals. Nesting boxes were provided in the experimental room.

Results and discussion

The choice tests clearly showed that cinnamamide- and thiram-treated seeds were less preferred by *M. natalensis* compared to untreated seeds (Figure 1). Consumption of seeds generally was lower in the test with thiram-treated seeds in the cage, perhaps due to the repellent effect of the strong smell of thiram. In the no-choice tests, there was also a strong repellence to *M. natalensis* by the two products (Table 1). Only a few seeds were damaged or consumed, and the repellent effect persisted for at least 4 days, although the animals had no alternative food available. This suggests that the seeds were also unpalatable due to treatment. Most mammals, including rodents, have developed a behavioural mechanism to cope with toxic substances in their food, including avoidance (Bull 1972). In the current investigation, we did not expect 100% protection of the seeds. This is clearly shown by the low levels of damage that occurred in the treated seeds.

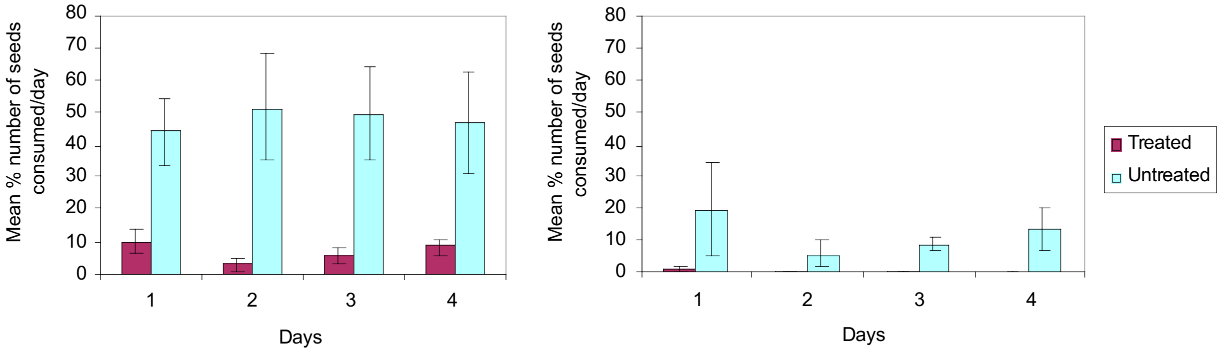

Figure 1. Mean daily percentage (± se) consumption of untreated and repellent-treated maize seeds by singly caged animals. Left: treatment with cinnamamide; right: treatment with thiram.

Table 1. Consumption of seeds treated with either cinnamamide or thiram in the no-choice room experiment.

Days	Cinnamamide		Thiram	
	Mean no. (± se) of seeds supplied	Mean no. (± se) of seeds consumed or damaged	Mean no. (± se) of seeds supplied	Mean no. (± se) of seeds consumed or damaged
1	70.5 ± 1.19	6.0 ± 1.3	68.3 ± 0.63	5.0 ± 2.9
2	70.3 ± 1.60	0.3 ± 0.3	68.3 ± 0.85	1.0 ± 0.7
3	70.3 ± 1.60	0.3 ± 0.3	68.3 ± 1.11	1.5 ± 0.9
4	70.0 ± 1.47	0.5 ± 0.5	68.3 ± 1.22	3.8 ± 3.4

Thiram has been found to repel not only rodents but also a number of birds (Young and Zevallos 1960; Sandhu et al. 1987). Other studies showed that thiram repelled ground squirrels causing damage to corn seeds (Zucher et al. 1983). Cinnamamide, a non-lethal bird repellent, has been evaluated against house mice and wood mice, and was found to have greater potential for control of house mice (Gurney et al. 1996). Repellency of cinnamamide against *Rattus norvegicus* also indicated its potential for prevention of damage in crops (Crocker et al. 1993).

The preliminary laboratory results in the current study suggest that dressing maize seeds with thiram and cinnamamide can reduce damage to seeds by *M. natalensis*. Further testing will be conducted to establish the efficacy of the two compounds to repel *M. natalensis* in fields planted with maize seeds.

Acknowledgments

This work was carried out under the European Union-funded project, STAPLERAT. We appreciate the help from the technical staff at the Rodent Control Centre and Sokoine University of Agriculture.

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Composition of rodents and damage estimates on maize farms at Ziway, Ethiopia

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Abstract. Rodent composition and estimates of rodent damage were investigated in maize fields of central Ethiopia. The most common species caught were *Arvicanthis dembeensis*, *Mastomys erythroleucus*, *Mus mohamet*, *Tatera robusta* and *Graphiurus murinus*. Both live-trapping and snap-trapping of rodents were conducted at different stages of maize development. The snap-trapping yielded 277 small mammals from 2400 trap-nights. The live-trapping yielded 591 small mammals from 3000 trap-nights. The population abundance of each species varied with season and with vegetation cover and type. Maize seeds sown in both fenced and unfenced plots differed as a result of variation in the distances between planting holes. Percentages of seedlings missing in the fenced and unfenced plots were 9.6 and 12.6, respectively. Yield loss at the harvesting stage of maize where rodents were admitted was 26.4%.

Introduction

The diverse topographical features of Ethiopia, coupled with variations in temperature, have resulted in diversification of the mammalian fauna (Yalden and Largen 1992; Yalden et al. 1996). Out of a total of 277 mammalian species that are recognised in the country, 84 are rodent species. About a dozen of these rodent species are significant agricultural pests. *Arvicanthis* sp. and *Mastomys* sp. are the major pests in maize, bean and tomato plantations. Both species have a wide distribution in many parts of Ethiopia (Afework Bekele et al. 1993; Lavrenchenko et al. 1998). In Ethiopia, comprehensive studies on the effect of rodent damage to agricultural crops are lacking. Afework Bekele and Leirs (1997) described the population ecology of two common species of rodents in grasslands, but there are no quantified estimates of the crop yield that is lost to rodents. In this paper, we present preliminary data about the rodent species composition, and the damage rodents cause in maize plantations in central Ethiopia.

Materials and methods

The study was conducted at Ziway agricultural station, 160 km south of Addis Ababa, from March to November 2001. Removal and live-trapping grids of 50 traps each were located within the maize fields, with 5 additional lines of 20 traps each set at different distances from the edge of the target crop. Trapping sessions (three trapping nights) were conducted before and after planting, during the different growth stages of maize, and after harvesting of the crop. All rodents were identified to species.

In order to estimate the damage and yield loss caused by rodents in maize fields, five control and five rodent-proof, fenced experimental plots, each 10 × 10 m, were used to estimate damage at the seedling stage and at harvest. In both fenced and unfenced plots, seeds sown varied from grid to grid since the distance between holes was not proportional. The distance between holes ranged from 15 to 30 cm. Only one seed per hole was used.

Results and discussion

Species composition and abundance

Removal-trapping yielded 277 small mammals in 2400 trap-nights with a trap success of 11.5%. The species composition was: *Mastomys erythroleucus*, 128 (46.2%); *Arvicanthis dembeensis*, 98 (35.4%); *Tatera robusta*, 25 (9.0%); *Graphiurus murinus*, 12 (4.3); and *Mus mohamet*, 11 (4.0%). *Mastomys* and *Arvicanthis* are recognised as the major pest species, while *Tatera* and *Mus* are minor pests. Density estimation of rodent populations using Sherman live-traps was conducted also before sowing, and at the seedling, vegetative, harvesting and post-harvesting stages of maize. A total of 591 small mammals in 3000 trap-nights were live-trapped. *M. mohamet* comprised 210 (35.5%), *M. erythroleucus* 184 (31.1%), *T. robusta* 135 (22.8%) and *A. dembeensis* 61 (10.3%) of those captured. *A.*

dembeensis and *M. erythroleucus* made up 81.6% of those rodents caught in snap-traps, however this decreased to just 41.4% of rodents caught in live-traps. The decline in the capture of *A. dembeensis* was highly pronounced. There were differences in ground cover on the snap-trap and live-trap grids. Therefore the differences in trap success may be due to effects of habitat preference and selection, especially where ground cover at the maize farm was devoid of vegetation. Delany and Roberts (1978) have observed similar changes in densities of rodent populations between scrub and grassland vegetation, the scrub serving as a refuge habitat during adverse periods. The higher density of *M. mohamet* in the live-trapping grid (35.5%) compared to the snap-trapping grid (4.0%) may suggest better habitat for rodents that are good climbers. The population abundance of the respective species fluctuated across the seasons; further studies are required to ascertain the key factors influencing these fluctuations.

Table 1. Number of maize seeds sown and missing seedlings in fenced (to reduce access by rodents) and unfenced grids.

Grid	Seeds sown		Missing seedlings	
	Fenced	Unfenced	Fenced	Unfenced
1	1221	1554	120	180
2	1200	1440	85	170
3	1332	1443	95	190
4	1116	1680	105	135
5	1332	1170	190	240
Total	6201	7287	595	915

Table 2. Actual (kg maize) and proportionate yield (kg maize per planted seed) on different grids.

Grids	Actual weight		Proportionate weight	
	Fenced	Unfenced	Fenced	Unfenced
1	87.91	54.74	0.072	0.035
2	61.95	48.67	0.052	0.034
3	77.82	67.52	0.058	0.047
4	40.00	55.06	0.036	0.033
5	63.66	51.05	0.048	0.044
	Total: 331.34	Total: 277.04	Mean ± sd: 0.053 ± 0.012	Mean ± sd: 0.039 ± 0.006

Rodent damage to maize

A total of 6201 and 7287 maize seeds were sown in both experimental and control plots, respectively (Table 1). There were 595 seeds missing in the experimental and 915 in the control plot. Damage by rodents at the seedling stage in the unfenced plot was 12.6%, whilst in the fenced plot it was 9.6%. By comparing the obtained yield per planted seed (proportionate weight), the final yield loss was estimated to be 26.4% in the unfenced fields (Table 2). This suggests that an important part of the damage occurred after the seedling stage. These are preliminary results, with further work planned for another 12 months.

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MOUSER (Version 1.0): an interactive CD-ROM for managing the impact of house mice in Australia

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Abstract. *MOUSER* is an interactive training and resource package that provides decision support for the management of house mouse plagues. This knowledge management software has been developed to run from a CD-ROM on personal computers. The number of farmers who have computers is increasing: in 1999, nearly half of Australia's rural properties had computers. *MOUSER* is designed for use by growers, grower groups and State Government departments. This new version of *MOUSER* has been written using web-based software so that users can link directly to web pages for updates and for further information. It contains the most recent information available for managing house mice and includes an expanded decision key, more information and new videos. Another feature is an economics model (*EcoNoMice*), which can be used to compare the relative costs and benefits of different control techniques. The model is based on a gross margin for wheat for the mallee region of north-western Victoria. This technology can be applied to a wide range of rodent problems and can include identification keys, simple economic and population models, videos and training modules.

Introduction

MOUSER VERSION 1.0 is a CD-ROM for the management of house mouse plagues in south-eastern Australia. The concept of developing *MOUSER* came from Geoff Norton's keynote address at the 10th Australian Vertebrate Pest Conference in Hobart (Norton 1995). From this, a prototype version of *MOUSER* was developed in collaboration between the Cooperative Research Centre (CRC) for Tropical Pest Management and the Commonwealth Scientific and Industrial Research Organisation (CSIRO). This was completed in 1998 and was presented at the 11th Australian Vertebrate Pest Conference in Bunbury (Brown et al. 1998b). Funding was obtained from the Natural Heritage Trust (through the Bureau of Rural Sciences) to further develop the prototype software, to build an economics module, and to update the software. *MOUSER VERSION 1.0* was released in 2001. This type of software could be useful for managers of rodents and other pests in many countries around the world.

Features of *MOUSER*

MOUSER VERSION 1.0 contains a number of sections that provide a wide range of information to assist with the management of mouse plagues. The topics listed on the main screen of *MOUSER VERSION 1.0* are:

- *Contents*—allows users to access information directly on any topic.
- *Biology of mice*—information about the biology and ecology of the house mouse (*Mus domesticus*) in Australia such as breeding, food and nesting requirements, home range size, movements, behaviour, and population dynamics.
- *Mouse control*—information about types of control methods for house mice such as where, when, and what type of control methods should be used and includes information about chemical or non-chemical control techniques.
- *Mouse plagues*—information on the impact of mouse plagues, why they occur and the type of damage caused.
- *Monitoring*—information about various methods for monitoring the abundance of mice, both directly (e.g. trapping, census cards) and indirectly (e.g. faecal pellets, number of active burrows found per unit of area).
- *Damage assessment*—contains information about the type of damage and how to assess damage caused by mice to various crops and in buildings (e.g. damage to electrical wires, gnawing).
- *Decision key*—steps the user through a series of questions to provide possible management options. Information is provided for the central mallee region of Victoria and for the Murrumbidgee Irrigation Area of

southern New South Wales, two areas significantly affected by mouse plagues.

- *Common questions/myths*—answers some of the frequently asked questions about mouse plagues and exposes some of the myths.
- *Economic model (mouse control simulator)*—see below for more information.
- *Further information*—provides additional resources and information such as a list of references, a direct link to related web site addresses (using the browser contained on the CD-ROM), some brochures, acknowledgments, and a link to email support (<Mouser-Support@cse.csiro.au>).

Other features of *MOUSER VERSION 1.0* are:

- *Video*—showing some of the control practices, monitoring methods and behaviour of mice.
- *Graphs and pictures*—to help explain information.
- *Hotlinks to other sections*—to give more detail on a topic or see information about a related topic.
- *Audio*—listen to experts explaining good practice and hear the sound of a mouse squeak!
- *Active glossary*—click on technical words to find their meaning.
- *Print pages*—print off information.
- *Keyword search*—perform a search of the CD-ROM to find related information.

Economics module (mouse control simulator)

A review of current literature and existing knowledge was conducted to provide the best available information for inclusion into building the economics module (see Brown and Singleton 2002 for details). The main sources of information came from two projects conducted to assess the effects of farm management practices on mouse populations in different farming systems (Brown et al. 1997; Brown, Davies, Croft and Singleton, this volume). Additional information came from Brown et al. (1998a, 2002).

Options for managing mouse populations were split into two categories: routine actions; and preventative actions implemented only when mouse numbers were increasing. A list of mouse control actions was compiled and information was sought on the cost per hectare or kilometre for each mouse control action, the effectiveness (percentage reduction) of each action and the effect on the available food supply (e.g. grain remaining on the ground after harvest).

The basic population model underlying the economics module was modified from the mouse population model developed by CSIRO (used to predict mouse outbreaks in the Victorian mallee region). The population model was derived using the numerical response of mice over a 15-year period in the Victorian mallee region (Pech et al. 1999). Abundance of mice was related to estimates of food availability from cereal crops and grazed pasture and a density-dependent factor representing the effects of predation, disease and intrinsic regulatory processes. The Centre for Agricultural and Regional Economics (CARE) built the economics model using Excel with input from CSIRO. The model was converted into a stand-alone executable file in Delphi.

Results of the simulations provide a comparison of 'control' with 'no control' over a 12-month period. Graphs are used to show the effect on the response of the mouse population, gross margins, cost of control, and wheat yields. Much of the data used to generate the economics model have come from the Victorian mallee, and so caution must be made when using the model in other agro-ecosystems.

MOUSER software

The Centre for Pest Information Technology and Transfer (CPITT) at the University of Queensland reprogrammed the prototype version of *MOUSER* using an in-house web-based software package (WebGIST). WebGIST utilises Internet Explorer 5, which can be installed as part of the package if the user does not already have it installed. WebGIST provides a number of advantages over the prototype software, including supporting HTML, providing easier navigation around the CD (especially the decision key), providing 'seamless' links to remote web sites, and comes with a built-in search facility. WebGIST also supports executables, such as the economics package developed by CARE. Another advantage is that the HTML content of the CD version of *MOUSER* could easily be transferred to a server for web delivery.

The information contained in *MOUSER* was updated. New images and text were added directly to *MOUSER* and the Decision Key was updated and modified to incorporate the recommendations from the recently-completed Bureau of Rural Sciences-funded project on farm management practices for mouse control in southern New South Wales (Brown, Davies, Croft and Singleton, this volume). Also, new video footage showing farm management practices and footage of wild mice was digitised.

How to obtain a copy

If you would like to obtain a copy of *MOUSER VERSION 1.0*, see the demonstration at the Conference and add your name to the list provided, or contact Peter Brown (contact details given above). *MOUSER VERSION 1.0* costs A$19.95 plus $10.00 postage and handling (GST included).

Applicability of software for management of other rodent species

The software described here could be modified to assist with the management of other rodent species, providing there is a good understanding of the ecology and biology of the pest species. A valuable addition would be to include an interactive identification key, such as Lucid (Centre for Pest Information Technology and Transfer 2001). Lucid has been developed as an interactive key for a wide range of insects, fungi and plants. A key for the rodent species of Southeast Asia is currently being developed using Lucid, and would include diagnostic characteristics, detailed photos to aid identification, and a description of the species biology and ecology.

Another example of a CD-ROM for the management of pests is RiceIPM (Centre for Pest Information Technology and Transfer 2002). RiceIPM is an interactive training and resource package on CD-ROM for those who want to learn more about integrated pest management (IPM) for tropical rice crops. It contains a wealth of information that can be accessed in a variety of ways, including the use of Lucid keys, and should be of interest to rice-growers, advisors, researchers, students and anyone interested in learning more about IPM in tropical rice. It contains some basic information about the management of rice rats in tropical rice crops.

If developing software for pest management, it is important to build the software from readily available programs, such as Internet Explorer, and to allow the program to be upgraded easily. Now that the Internet is becoming more accessible in many countries, it would be useful to include Internet links with any software for updates, provide links to web pages, and for new information. Finally, it is desirable to collaborate with people who know how to design, build and test software to ensure a high-quality product.

Acknowledgments

We thank Greg Hood (CRC for Pest Animal Control) for assistance with the development of the mouse control simulator, and Sue McGrath and Matthew Taylor (CPITT, University of Queensland) for programming.

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Observations of bamboo flowering and associated increases in rodent populations in the north-eastern region of India

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Abstract. The phenomenon of an outbreak of a rodent population synchronous with flowering of bamboo was investigated in the north-eastern region of India. In order to study the activities of rats and their association with different types of vegetation, the rodent-infested and bamboo-flowering areas were extensively surveyed. Various species of bamboo flowered during the study. During the period of flowering of *Bambusa tulda* (1976–79), five major species of wild rats and mice occurred in the study area. *Rattus rattus brunneusculus* was the most common rat in Mizoram and *Rattus nitidus* in Manipur and Nagaland. The populations of these rats were high in crop fields and caused extensive damage to paddy crops. The population density of *R. r. brunneusculus* and *R. nitidus* in abandoned crop fields was highest in January, whereas in freshly cultivated areas, the populations peaked in November and December. The flowering of the bamboo had no measurable effect on rodent population dynamics.

Introduction

A peculiar phenomenon observed in the north-eastern, hilly areas of India, namely, Mizoram, parts of Meghalaya, Arunachal Pradesh, Nagaland and Manipur, is the periodic mass-flowering and seeding of certain bamboo species which is accompanied by a tremendous increase in populations of certain rodent species. Enormous increases in the populations of species of *Nesokia*, *Mus*, *Rattus*, *Golunda* and *Rhizomys*, coinciding with bamboo flowering, have been reported in various parts of India (Win 1951; Kermode 1952; Chatterjee 1960; Santapau 1962; Nath 1968; Rao et al. 1995). The occurrence of similar phenomena has been reported from many other parts of the world, such as Madagascar, Burma, Japan, Brazil, southern Chile and Argentina (Janzen 1976; Jaksic and Lima 2002).

This biological phenomenon results in severe famine conditions due to rodent damage to agricultural crops. A study was conducted in the north-eastern region during 1976–79, the period of flowering of the bamboo *Bambusa tulda*. In this region, following the flowering of bamboo, there is a sudden increase in the number of rats, which causes damage to such an extent that it results in almost famine-like conditions. This was first reported by Elles (1881) in his military report on the Chin-Lushai Hill county. As a great famine is expected sometime during 2003–2005, there is an urgent need for a detailed study on bamboo flowering and ecology and behaviour of rodent species in this region. This paper reports on a population study of the rodent community conducted in the north-eastern region from 1977 to 1979.

Materials and methods

Study area

The north-eastern region of India comprises of Mizoram, Nagaland, Manipur and Meghalaya union territories and is situated on the eastern border of India. The land is between Chin Hills (Burma) in the east and south, and Chittagong hill tracts (Bangladesh and Tripura) in the west.

The climate and soil of the north-eastern region is suitable for growing many kinds of tropical crops. The principal crop is paddy rice (*Oryza sativa*), with other crops including maize (*Zea mays*), ginger (*Zingiber officinalis*), sweet potato (*Ipomoea batatas*), turmeric (*Curcuma longa*), chilli (*Capsicum* sp.), tobacco (*Nicotiana tabacum*), orange (*Citrus* sp.) and certain vegetables. One-fifth of the area is covered with tropical forest. Thick bamboo forests are in abundance on the low-lying hills and valleys. Shifting cultivation (*jhum*) is widely practised and results in the serious destruction of forests. Terrace and wetland farming has recently begun.

In Mizoram, the famines associated with the flowering of *Melocanna bambusoides* (local name, ‘Mautak’) and *Bambusa tulda* (local name, ‘Rawthing’) are locally known as ‘Mautam’ and ‘Thingtam’, respectively. These famines occurred in 1880–81, 1927–29, 1976–78 (associated with

'Thingtam') and 1910–12, 1956–59 (associated with 'Mautam'). 'Mautam' flowering is expected in 2005. Other minor bamboo species found to be associated with 'Mautam' are *Dendrocalamus longispathus* (Rawnal), *Melocalamus campactiflorus* (Sairil) and *Dendrocalamus sikkimensis* (Rawmi) (Parry 1928) and with 'Thingtam' are *Melocalamus campactiflorus* (Sairil), *Dendrocalamus sikkimensis* (Rawnal), *Dendrocalamus longispathus* (Rawmi), *Bambusa spinosa* (Phar) and *Pseudostachyum polymorphum* (Chal) (Mohan Ram and Hari Gopal 1981). 'Thingtam' is associated with a famine of lesser magnitude than 'Mautam' and occurs at an interval of approximately 48 years; 18 years after the occurrence of 'Mautam'.

The bamboo-flowering areas and rodent species were studied by undertaking extensive field surveys of crop fields (*jhum* and wetland cultivation areas), bamboo forest, other adjoining forests and tribal settlements in Mizoram, Meghalaya, part of Manipur and Nagaland. Rats and mice were regularly collected from crop fields, bamboo forest and tribal settlements of Mizoram by extensive digging of burrows or trapping. Collection sites were periodically changed to provide adequate sampling of an entire area.

The rodent-infested and bamboo-flowering areas, village sites and forests were extensively surveyed in order to study the activities of rats and their association with different types of vegetation. Simultaneously, bamboo seeds and fruits were collected for the purpose of using them in 'feeding experiments'.

The relative density of rat populations was estimated by counting live burrows and capturing rats through excavation of their burrows. Population estimates were conducted 2–8 times a month in fallow and freshly cultivated crop fields from January to December 1978 and May 1978 to March 1979, respectively.

Results and discussion

In the total collection of about 2500 rats and mice, 8 species were identified. In Mizoram, *Rattus rattus brunneusculus* constituted the major part of the collection (92.5%). In Manipur and Nagaland, the Himalayan rat, *Rattus nitidus*, was the predominant species. Other species collected in low numbers were *Rattus bowersi mackenziei*, *Bandicota* sp., *Cannomys badius*, *Rattus rattus* and *Mus musculus*. The first three species occurred in the cultivated areas whereas the latter species occurred mainly in tribal settlements and granaries.

R. r. brunneusculus and *R. nitidus* were both collected from paddy fields. They make simple to complex burrows, which contained stored paddy grains and vegetable matter. After harvest, the grain stores of burrows were slowly depleted, but paddy husk, chilli, ginger, brinjal, tomato etc. could still be seen. These observations suggest that although the main food of these rodent species is rice, when it is not available they feed on other vegetable matter and tender shoots. *R. b. mackenziei* rats make complex, deep burrow systems mainly in the paddy fields. They feed on the tender shoots of various crop plants and underground vegetables. Rats of *Bandicota* sp. are fossorial in nature. They are normally found in low-lying areas cultivated for wetland rice and near marshy stretches. They have complex but shallow burrow systems. Although the population of these rats was not as high as it was during 'Mautam' flowering time (as reported by local people), the damage caused by them to paddy crops often was quite extensive. Bamboo rats, *C. badius*, usually occurred in sugarcane, arabi (*Colocasia* sp.), ginger and sweet potato fields. They were found also in grassy areas near bamboo thickets, bushes and trees. They make complex burrow systems which usually contained ginger and sugarcane pieces. At times, nearly 5–6 kg of these food materials were collected from a single burrow. They also feed on other plants, grasses, seeds and fruits. *Vandeleuria oleracea dumeticola* occurs in bushes, trees and bamboo thickets and feeds on fruits, buds, rice grains etc. Their nests were usually found in tree cavities or between the branches.

During the flowering period of *Bambusa tulda*, large numbers of *R. r. brunneusculus* and *R. nitidus* were found in paddy fields. They caused extensive damage to the paddy crop. Due to deforestation in preparation for cultivation or after harvesting of crops, perhaps these rats disperse to bamboo forests and later recolonise freshly cultivated land. The presence of live burrows, paddy husks, damaged panicles, cut leaves and faecal matter on their runways were signs of their increasing population and activities.

In abandoned crop fields, the numbers of live burrows and rats captured per hectare during 1978–1979 were significantly correlated ($Y = 2 + 0.4x$, $r = 0.935$) (Table 1). In January, a peak population level was observed (live burrows/ha: 36 ± 1.71, rats captured/ha: 15 ± 1.27), which later declined and remained low from April to December. The lowest number of live burrows was in July (3 ± 1.53) and lowest rat captures were in June (2 ± 0.50). In the freshly cultivated land, the population estimates based on the number of live burrows per hectare and the number of rats captured were not correlated ($Y = 10 \pm 0.46x$, $r = 0.447$, $P > 0.1$). The number of live burrows revealed peak population levels in May (30 ± 1.4). The number of rats caught from burrows was also relatively high in May (21 ± 0.70), then decreased in the following few months, but started increasing after July and attained a peak in November (36 ± 1.40). Thereafter, the population again showed a gradual decrease and reached a low level in March (12 ± 0.70).

In this study, counting of live burrows and rats captured from them were found to be the most practical methods for estimating the relative density of *R. r. brunneuculus* and *R. nitidus* inhabiting the north-eastern hilly areas. These population indices showed marked monthly changes for both species, both in abandoned and freshly cultivated fields during 1978–79. The factors governing these fluctuations may be both biotic and abiotic. Monthly fluctuations in the relative density of the rats have been discussed mainly in relation to biotic factors such as seasonal periodicity in breeding activity and food availability. These biotic factors have been found to be of considerable importance in the regulation of population density of many rodent species (e.g. Bindra and Sagar 1968; Prakash 1981; Taitt and Krebs 1981).

In the abandoned crop fields, the maximum population is observed in January (post-harvest period) following high breeding activity from July to October during the crop of the preceding year. Marked decline in the population thereafter (January to April) may be mainly due to the cessation of breeding activity and a progressive decrease in the amounts of available food, which probably enables a majority of animals to move out to areas where they can obtain sufficient food and shelter. Declines in other rodent populations have been also reported to be due to food shortage and/or termination of breeding activity (e.g. Pearson 1963; Desy and Thompson 1983). If there is no migration of the rats from the abandoned crop fields, then the reduction in the population may also be due to starvation. Increased intra- and interspecific competition, through greater incidence of cannibalism and fighting behaviour, possibly due to scarcity of food, may also be responsible for the decline in population. No direct evidence for their emigration and mortality was obtained, so further studies are required to test the importance of these factors on population decline.

The population density remained low from April to December even though this period coincided with the breeding season of these rats. Therefore, the scarcity of food might have led to increase pre-natal and infant mortality and decreased fecundity, which ultimately reduced the population to low levels. The food available at that time included only a few vegetables and wild plants, which might be just sufficient to maintain a small population of the rats.

In freshly cultivated areas, the significant rise in populations of rats in July, before the onset of breeding, is likely to be due to the immigration of large numbers of rats from surrounding areas in search of sown paddy grains. Later, with the exhaustion of paddy grains, either due to consumption by the rats or their germination into seedlings, the population temporarily disperses to surrounding areas in search of alternative food. In the ensuing months, the population shows an increasing trend coinciding with the growth of the paddy crop, especially the development of rice panicles, which are their favourite food, and many vegetables. The onset of rainfall could possibly be an indirect factor regulating the population by causing vegetation growth, and thus an increase in food supply. Growth and maturation of paddy panicles also probably attract rats from surrounding areas, which—along with intense breeding—results in further population increases. The population was highest during November–December, the period when paddy was harvested.

The common bamboo rat, *C. badius*, that is believed to be the only species that causes sufficiently extensive damage to paddy crops to result in famine, was not found to be of much significance. These rats were uncommon in the paddy fields, inhabiting mainly the sugarcane, arabi, ginger, sweet potato fields and grassy areas near the bamboo forest.

Table 1. Monthly variation in the relative density of *Rattus rattus brunneusculus* based on the number of live burrows and rats captured in abandoned and fresh crop fields during 1978–79.

Year	Month	Abandoned crop fields		Freshly cultivated fields	
		Number of live burrows/ha (mean ± se)	Number of rats captured from burrows/ha (mean ± se)	Number of live burrows/ha (mean ± se)	Number of rats captured from burrows/ha (mean ± se)
1978	January	36 ± 1.71	15 ± 1.27	–	–
	February	22 ± 1.27	13 ± 1.10	–	–
	March	14 ± 1.22	8 ± 0.50	–	–
	April	9 ± 0.55	7 ± 0.58	–	–
	May	8 ± 0.58	4 ± 0.28	30 ± 1.40	21 ± 0.70
	June	6 ± 0.33	2 ± 0.50	25 ± 1.00	16 ± 0.58
	July	3 ± 1.53	3 ± 0.70	13 ± 2.20	12 ± 2.20
	August	6 ± 0.36	4 ± 0.58	18 ± 3.00	15 ± 1.00
	September	6 ± 0.42	6 ± 0.33	19 ± 1.40	16 ± 1.15
	October	8 ± 0.58	4 ± 1.22	20 ± 0.52	19 ± 3.00
	November	8 ± 0.58	6 ± 0.70	25 ± 0.70	36 ± 1.40
	December	9 ± 0.71	6 ± 0.55	18 ± 0.96	24 ± 0.82
1979	January	–	–	9 ± 1.40	19 ± 2.20
	February	–	–	11 ± 3.40	18 ± 1.00
	March	–	–	13 ± 1.92	12 ± 0.70

The flowering of bamboo results in abundant food supply in the form of bamboo seeds and fruits. These bamboo seeds and fruits are not only palatable but are preferred by some rodent species, attracting them to flowering areas (Janzen 1976). Despite a constant vigil, no sign of rat migration from *jhum* to bamboo forest or vice versa was observed in Mizoram during flowering of *B. tulda*. The rats mainly inhabited paddy fields, and showed variation in their numbers in relation to the crop cycle during the flowering of *B. tulda*. Only a few rats were noticed in the forests during this period. This suggests that the extent of bamboo flowering and seed production during these years may not be sufficient enough to attract the rat population. Only in a very few places in the north-eastern region did the bamboo flowering result in seed formation. Most of the flowers were destroyed by heavy rain and high-velocity winds. Therefore, ultimately the food available in the form of bamboo seeds and fruits in these areas was negligible and insufficient to generate an explosion of rodent populations. The effect of bamboo seeds and fruits on the reproduction of rats and the rate of growth of their populations need to be investigated further.

Acknowledgments

We sincerely thank the government of Mizoram, Meghalaya, Arunachal Pradesh, Nagaland and Manipur and the local people, especially the farmers, for their cooperation and providing necessary facilities for carrying out this work in different areas. The work was supported by a grant for a research assignment from the Indian Council of Agricultural Research, New Delhi, that is gratefully acknowledged.

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Rodent removal with trap–barrier systems in a direct-seeded rice community in the Philippines

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Abstract. The rat population in a rice-based agro-ecosystem was monitored with four trap–barrier system plus trap crop (TBS+TC) set-ups, each measuring approximately 7 m × 20 m, during the 2002 dry-season rice crop in Maragol, Muñoz Science City, Philippines. The highest number of rats caught coincided with the period of field operations (preparation and planting of the surrounding rice crops). This period of disturbance may have forced the rats to disperse, resulting in high numbers of trapped rats. During the growing period of the rice plants, more rats were trapped at the seeding to maximum tillering stages than from the panicle initiation–booting stage through until the milking stage of the rice plants. No rat was trapped during the dough stage through until harvest. More females than males were trapped during the field operations' period and until the maximum tillering stage of the rice. Thereafter, more males than females were trapped. More females were trapped during the entire study period, suggesting that use of TBS+TCs may decrease the reproductive performance of rat populations. Although the initial cost of each TBS+TC is US$54.50, about 10% is recovered with the sale of paddy rice harvested from the trap crop. The capture of 368 rats indicated that this system has potential, if used together with a rat campaign of 1–2 weeks immediately after the crop has been sown. This study continues to obtain more data on the population dynamics and demography of rats that will provide baseline information for the implementation of rat control strategies in the area.

Introduction

Rats have been causing immeasurable damage to crops for thousands of years. Although some progress in rodent management has been reported in the past decades (Singleton et al. 1999a), rodents still cause serious economic damage and pose health risks worldwide. In the Philippines, rats cause substantial yield loss to rice crops (Ahmed et al. 1987). In a 1998/99 survey, farmers considered rats as one of the major pests of rice, causing serious damage to the crop in irrigated and rainfed rice fields in all regions of the Philippines (R.B. Malasa, pers. comm.). The use of rodenticides, in the form of poison bait, is the most common means of rat control in the Philippines (Sumangil 1990). However, anticoagulant resistance and bait shyness (Buckle 1999), potential hazards of rodenticides to non-target organisms, and the pollution of the environment are risks posed by constant and indiscriminate use of rodenticides. Knowledge of the population dynamics of pest rodents is important in the proper application of control strategies. In this study, we tested the performance of the trap–barrier system plus trap crop (TBS+TC) (see Singleton et al. 1999b) in a rice agro-ecosystem to gain knowledge about population dynamics of pest rodents and to determine the best time to implement rat control strategies.

Materials and methods

Study site

We selected a 40 ha contiguous rice-growing area in Maragol, Muñoz Science City, Nueva Ecija, Philippines as a study site. A high level of rat infestation was reported in the previous crop (wet season 2001) where about 45% of the fields were planted with the popular, high-yielding rice variety IR64. PSB Rc28 and PSB Rc82 were the other major varieties planted. The location of the paddy-field parcels was mapped with a global positioning system to determine their distance from the TBS. The size and ownership of the farms was also checked with the local cadastral maps and records. Data on farm inputs of fertiliser and pesticide usage and other farm information, such as variety planted and time of planting, was collected in interviews with the farmers. During the 2002 dry season, 73% of the fields in the study site were directly wet-seeded and the rest was transplanted. Most of the fields were planted with IR64 (52%) and PSB Rc82 (33%).

TBS+TC establishment

Four TBS+TCs were established in the study site near the irrigation embankments. Generally, each TBS+TC measured 7 m × 20 m. Dimensions did vary slightly, depending on the dimension of the paddy field. The TBS+TCs were erected about a month before the general planting time in the area. A polyethylene sheet about 0.5 m from ground level was fastened with staple wires on the outer side of bamboo sticks to serve as protection for the rice plants growing inside the barrier system. To attract the field rats, an aromatic rice variety, MS8, was used as trap crop. The small size of the TBS allowed for manual land preparation and broadcasting of pre-germinated rice seeds inside the TBS.

Traps

The multiple-capture rat traps used in this study were made of metal wire mesh and measured 50 × 20 × 20 cm. The entrance tunnel was cone-shaped, narrowing to the end with bent metal wires to prevent the captured rat from escaping. One trap was installed in the centre of each side of the TBS+TC, with its entrance facing an opening at the base of the polyethylene sheet.

Data gathering

Daily counts of rats began a day after TBS+TC establishment. The rats trapped were removed and killed, and their sex and the growth stage of the rice crop were recorded.

Results and discussion

Rats were trapped as soon as the TBS+TC was established but at a low rate. An abrupt increase in the level of rat catches occurred a week after the start of field operations in the study site. This may be due to the flooding and destruction of the rats' burrows in the levees of the rice field. This indicates there is a time window to conduct community-wide physical rat control to reduce the initial population in the field present at the beginning of the cropping season. However, there was a gradual decline in the number of trapped rats at the time when most fields were established. This was possibly caused by the presence of abundant food in the fields decreasing the rats' motivation to enter traps. The catches during the early growing stage of the rice were lower than at field operations' period and gradually declined up to the maximum tillering stage of the rice plants. Most rats were trapped during the seeding to maximum tillering stages (Figure 1). A similar trend in rat captures in a TBS+TC was recorded in Indonesia and Vietnam (Singleton et al. 1999b). A reduced level of rat catches occurred at mid-rice growth stage but this slightly increased at the booting to milking stages of the rice plants in the surrounding area (Figure 1). No formal identification of rat species was conducted during the study period. However, all rats trapped have longer tail length than head–body length.

Before the trap crop emerged, only four male rats were trapped. However, during the field operations period, 70% of the trapped rats were females. This indicates the potential for a high rate of increase in population size after the establishment of food sources and commencement of breeding. The first pregnant rat trapped was recorded within a month after crop establishment. Of the 32 female rats caught from 13 February to 30 March 2002 (tillering stage), nine were pregnant. They were dissected and yielded a total of 74 foetuses. Although the proportion of female rats declined during seeding to the maximum tillering stage, there were still more females (58%) than males (42%). Thereafter, more males than females were trapped (Figure 1).

In this study, the cost of establishing one TBS+TC with an area of 140 m^2 was about US$54.50. This is slightly higher than the cost of a TBS+TC in Indonesia but

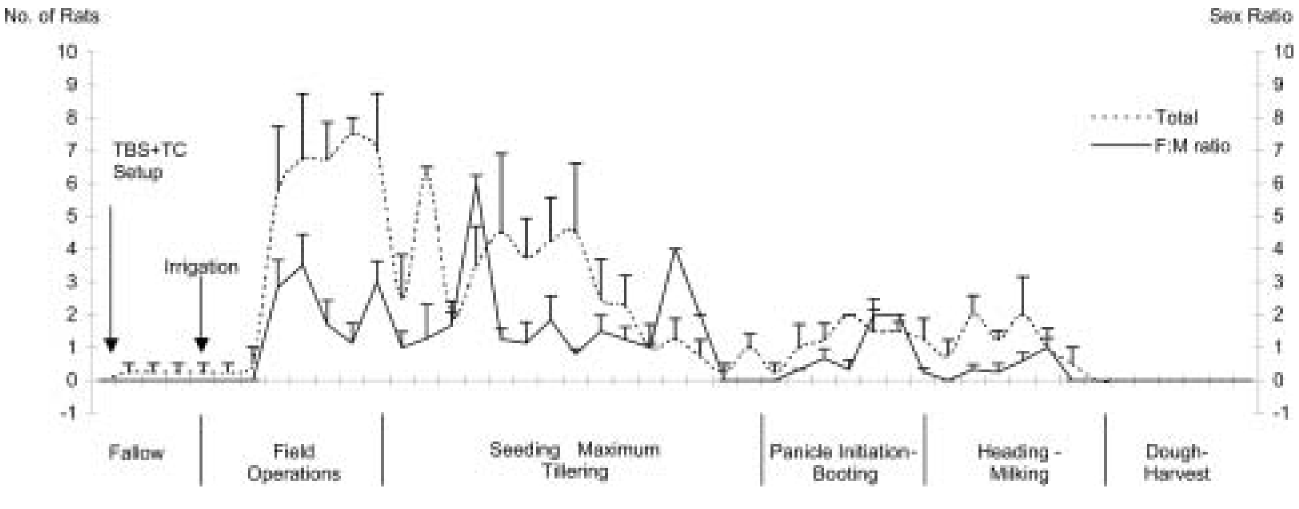

Figure 1. Average number of field rats and sex ratio (female/male rats) trapped at 3-day intervals in four strategically installed trap–barrier system plus trap crop (TBS+TC) set-ups before and during the rice-growing period (+1 se), Nueva Ecija, Philippines, dry season 2002.

lower than in Malaysia and Vietnam (Singleton et al. 1999b). The polyethylene sheet accounts for about 37% of the total cost; followed by the labour cost in land preparation and installing the system (35%). The other expenses were minimal, but the cost of four traps was about 18% of the total cost. However, the farmers harvested about 75 kg of paddy rice from each trap crop, resulting in a US$15.00 return. In effect, the cost of each TBS+TC was about US$39.50. The cost would be reduced further because the polyethylene sheet and traps are re-used in the following cropping season. In addition, the farmers can consume the trapped rats because poison baits are absent during the fallow period and the time that the TBS+TC is in operation.

Conclusion

The population dynamics of the field rat caught in the TBS between the start of irrigation-water delivery to the farm and subsequent field operations suggested that this was a strategic time for rat management. The capture of 368 rats, most before the onset of breeding that occurs at maximum tillering, indicates that TBS+TC holds potential for rodent management in the Philippines. Detailed knowledge about population dynamics and the activity of pest rodents is useful for the development of a strategic rat management system for rice-based agro-ecosystems in the Philippines. The study continues and alternative materials for the TBS that are cheaper and locally available to the farmers are being tested. The crop damage will also be assessed in relation to the distance from the TBS+TC.

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The use of the barn owl, *Tylo alba*, to suppress rat damage in rice fields in Malaysia

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Abstract. We investigated the damage caused by rice-field rats to rice crops in Malaysia in areas where barn owls were provided with nest boxes. We measured damage from February to May 2002 (first planting season), and assessment was made for three rice growth stages: tillering, booting and harvesting. Three plots with five nest boxes were set up to provide a nest box density of 1 box per 5 ha (plot A), 1 box per 10 ha (plot B) and 1 box per 20 ha (plot C). Rice damage assessment involved sampling of damaged tillers and hills using 0.5 × 0.5 m quadrats every 5 m along ten parallel, linear rows of paddy. Damage on all plots for all three paddy growth stages was less than 2%. In areas where there were no nest boxes, damage by rat activities was as high as 12%. The average damage levels for plots A, B and C were 0.63%, 0.68% and 1.58%, respectively. The difference in damage levels between A and B was not significant ($p >$ 0.05) but differences between A and C ($p = 0.003$) and between B and C ($p = 0.029$) were both significant. At the tillering stage, damage levels were lower by a factor of 3 in plot A and 7 in plot B; at the booting stage, by a factor of 2 in A and B; and at the harvesting stage, by a factor of 2 in A and B compared with the low owl density plot C. While the results suggest that an owl nest box in every 10 ha may be sufficient for the effective control of rats in rice fields in Malaysia, a properly replicated experiment is required with more levels of treatment before an effective threshold density of nest boxes can be defined.

Introduction

Rats are important pests in Malaysian rice fields. They attack all stages of paddy, from seedling until harvest, as well as the stored grain (Lam 1982; Shamsiah and Goh 1991) The rice-field rat, *Rattus argentiventer,* is the most common rat species attacking paddy, although other species have been occasionally recorded—*Rattus tiomanicus, R. exulans, R. rattus diardii, R. norvegicus* and *Bandicota indica* (Lam 1982).

The average rice crop loss due to rat activities in Peninsular Malaysia varies from 5% (Lam and Abdullah 1975) to 18% or even higher in some years and some areas (Department of Agriculture, cited in Hafidzi et al. 1999). Chemical control using various formulations and classes of rodenticides has been the normal practice in dealing with rat infestations. Rodenticides have a number of undesirable side effects, including secondary toxicity to non-target animals and the prospect of rats developing resistance to rodenticides. The natural propagation of barn owls, *Tyto alba,* in the oil palm sector (Duckett 1976; Lenton 1980; Smal 1988) has opened the way for similar efforts in rice fields, starting in 1988. The barn owl program in rice fields has successfully reduced crop loss from as much as 12% to less than 2% within a year of its implementation (Hafidzi et al. 1999).

There have been several suggestions as to the optimal nest box density for barn owls to produce stable and effective rat control in oil palm. Smal (1988) placed boxes at approximately one box per 2 ha in new areas to encourage *T. alba* breeding. Ali et al. (1995) suggested one box per 10–15 ha in newly established oil palm areas and to increase nest box density to one box every 10 ha once the owl population is established. Lim et al. (1993) estimated the occupancy rate was 72% from a census in an oil palm plantation in Johore, Malaysia, where the nest box density was one box per 10.9 ha. Smal et al. (1990) constructed a model to predict the behaviour of rat populations subject to barn owl predation and suggested that theoretically *T. alba* can control rats effectively (without poison baiting) at a density of one box every 6–8 ha. However, Chia et al. (1995) argued that, at high rat infestations, a nest box density of one box every 3–4 ha is more effective and can give rise to sustainable control, i.e. sustain a viable population of *T. alba.*

In rice-field areas of Malaysia, the Department of Agriculture recommends a nest box density of one box for every 20 to 40 ha (Anon. 1997). In practice, however, this is rarely conformed to because farmers normally put up nest boxes on their own initiative, leading to a higher nest box density than recommended. The objective of this study was to determine the effect of intraspecific competition between barn owls as a consequence of varying nest box density and how this affects rat control indirectly through damage assessment.

Materials and methods

The area selected for the study was at Sawah Sempadan in Tj Karang, Selangor, where rice is planted using direct seeding. There are two planting seasons per year: the dry season (first planting season) and the wet season (second planting season). Rice varieties planted are the MR 102, MR 129 and MR 185, which can be harvested after 110 days.

Fifteen nest boxes were set up in December 2001 in a designated area where there were no boxes previously. The nearest nest box to the study site was more than 1 km away to reduce any residual effect from neighbouring nest boxes. This distance was thought to be sufficient, as the foraging area of female owls as determined from radio telemetry, is relatively small, ranging from 0.6–2.8 ha (Hafidzi et al. 2000). The boxes were arranged in three clusters of five boxes (plots A, B and C), each according to the plan shown in Figure 1. Four nest boxes constitute the corners of a square plot with a central box. In this study, *T. alba* is assumed to hunt over a circular area and maintain an exclusive home range with respect to the outlying boxes, giving a coverage of 4.9 ha (r_a = 126 m) (r = radius from the nest box to the perimeter of the circle), 9.95 ha (r_b = 178 m) and 19.95 ha (r_c = 252 m) for plots A, B and C, respectively. The linear distances between plots A and B of 356 m ($2 \times r_b$) and between B and C of 504 m ($2 \times r_c$), were judged to be sufficient to eliminate any impact of one plot on the adjacent plot, since breeding females seem to maintain an exclusive home range (Hafidzi et al. 2000).

Rat damage assessment was divided into three paddy growth stages: tillering (4 weeks after seeding) in the third week of February 2002; booting (9 weeks after seeding) in the fourth week of April; and harvesting (2 weeks before harvesting) in the second week of May. The method involved sampling along ten parallel, linear rows of paddy chosen at random within each plot. Ten quadrats of 0.5 × 0.5 m, 5 m apart, were sampled along each row for a total of 100 quadrats. Damage was calculated as follows:

$$\% \text{ damage} = (a \times c)/(b + c) \qquad (1)$$

where a is number of damaged hills out of 100 sampled; b is the number of undamaged tillers in the hills with damage; and c is the number of damaged tillers in the hills with damage (Buckle 1994, p. 223).

Damage estimates were combined for all stages of plant growth by taking the average for the percentage damage during tillering, booting and before harvesting for each plot.

Results and discussion

All boxes put out in December 2001 were occupied by January 2002. We made no attempt to inspect the breeding status of barn owls using the boxes to avoid disturbance of the newly arrived birds. There was an inverse relationship between damage and nest box density, i.e. there was lower damage in plots with higher nest box density (Figure 2). Damage on all plots for all three stages was less than 2%, which is the level of damage recorded in most areas in Tanjung Karang where the barn owl program has been implemented (Hafidzi et al. 1999). More importantly, the damage levels in the one box per 5 ha plot (A) and the 10 ha plot (B) were lower than damage levels in the one box per 20 ha plot (C) which represents the normal nest box density at Tanjung Karang. The average damage was 0.63%, 0.68% and 1.58% for plots A, B and C, respectively. The difference in damage levels between plots A and B was not significant ($p > 0.05$) but differences between plots A and C ($p = 0.003$) and between plots B and C ($p = 0.029$) were significant.

At the tillering stage, the number of rats is low and *T. alba* may have to forage over a larger area to fulfill its daily food requirements. When the rice crop reaches the booting stage, rats start to produce their first litters (Leung et al. 1999) and the number of rats increases rapidly in the field, producing higher crop damage. The second litter of rats is usually born during the ripening stage, which leads to still higher damage as is apparent in this study, and third litter arrives shortly after harvest (Leung and Sudarmaji, cited in Leung et al. 1999).

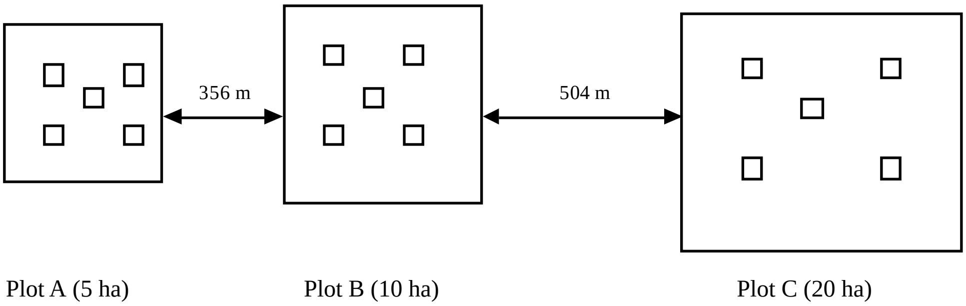

Figure 1. Arrangement of nest boxes.

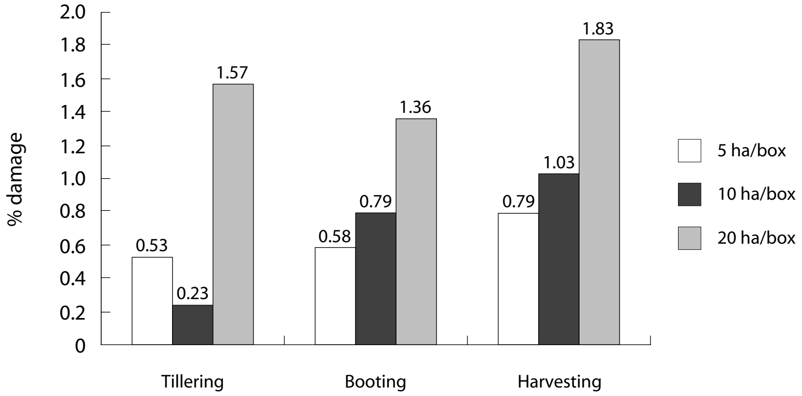

Figure 2. Rat damage in rice fields with different barn owl nest box densities. Data from the first planting season of 2002.

The current study suggests that at five nest boxes per ha and 10 nest boxes per ha, barn owls may be able to control rat numbers and thereby reduce crop damage at all stages of paddy growth. If we compare the 5 and 10 nest box treatments relative to the 20 nest box treatment, at the tillering stage, damage levels were lower by a factor of 3 and 7; at the booting stage, by a factor of 2.3 and 1.7; and at the harvesting stage by a factor of 2.3 and 1.8, respectively.

Conclusion

This study suggests that a density of one nest box per 10 ha may be sufficient to permit barn owls to reduce crop damage in rice fields in Malaysia. However, the results of this study are only suggestive because we need more replicates and simultaneous controls with no nest boxes provided. This study needs to be carried out over a larger area with more nest boxes to provide at least three replicates for each nest box density before definitive conclusions can be reached. The second planting season starts in late July 2002 and forthcoming data at the time of print would substantiate these findings.

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Pre- and post-harvest movements of female rice-field rats in West Javanese rice fields

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Abstract. This study examined changes in the spatial behaviour of rice-field rats (*Rattus argentiventer*) associated with the harvest of lowland irrigated rice. Radio-collared female rice-field rats were tracked before and after harvest in rice fields in West Java, Indonesia. The rice-field rats clearly reacted to the changes in habitat structure caused by the harvest by relocating their home ranges on average 300–400 m to piles of rice straw left on the fields and to unharvested areas. Post-harvest, there was a decrease in home-range size of 67% (0.6 ha pre-harvest; 0.2 ha post-harvest) and a decrease in range span of 35% (139 m pre-harvest; 90 m post-harvest), which may indicate an immediate response to predation risk. Most rats remained in the rice fields for 2–3 weeks post-harvest. This contrasts to their pre-harvest preference for refuge habitats near the margins of crops.

Introduction

Small mammals are a common feature of agricultural landscapes but for many rodent species very little is known about the impact of farming practices on spatial behaviour. Exceptions include wood mice, *Apodemus sylvaticus*, which relocate to adjacent refuges from areas disturbed by harvest (Tew and Macdonald 1993) and common voles, *Microtus arvalis*, which considerably reduce spatial activity after the harvest of grain (Jacob and Hempel 2002).

Home-range size of small mammals can vary due to intrinsic factors including breeding activity (McShea 1989; Krebs et al. 1995) and population density (Erlinge et al. 1990), as well as extrinsic factors including food availability (Ostfeld 1986) and vegetation height (Tew and McDonald 1993; Jacob and Hempel 2002). The removal of vegetation by mowing of verges and grazing stubble is often used as a management tool to minimise food and shelter. This can also expose pest rodents to predators thereby reducing pest rodent density (White et al. 1998). However, exposed prey may adapt behaviourally and decrease spatial activity as a counter-strategy to minimise predation risk.

Rice-field rats (*Rattus argentiventer* Robinson and Kloss 1916) are the most important pre-harvest pests in lowland flood-irrigated rice systems of Java, Indonesia (Singleton and Petch 1994). They and other species including black rats (*R. rattus*) and Norway rats (*R. norvegicus*) also invade facilities for processing and storing rice.

We used radio-telemetry to estimate the home-range size of female rice-field rats from about 3 weeks before harvest until about 3 weeks after harvest in lowland rice fields of West Java, Indonesia. We hypothesised that there would be (1) a decrease in spatial activity post-harvest leading to smaller home-range size and smaller range span and (2) a change in habitat use due to preference by the rats for refuge areas post-harvest.

Material and methods

The study was conducted between Sengon and Sukamandi (06°20'14"S, 07°39'24"E) Subang district, West Java, Indonesia. The climate in the region is tropical with small variations in annual average temperature (28°C). About 75% of the annual rainfall (1450 mm) occurs during the wet season (November–April) but rain is also frequent during the dry season (May–October).

The West Javanese agro-ecosystem is characterised by lowland irrigated rice fields, which are partitioned by many dikes, dams and irrigation channels. Individual farmers typically manage 1–2 ha of rice. Usually, one rice crop is grown in each of the seasons. Rice is sown in nurseries and after 2–3 weeks transplanted by hand into the fields. The main crop stages are tillering (55 days after sowing), booting (75 days) and ripening (95 days). Rice is harvested by hand about 120 days after sowing. Rice-field rats usually breed from about 2 weeks before maximum tillering until a few weeks after harvest (Leung et al. 1999).

We used a contiguous rice-growing area of about 400 ha for the study. Harvesting (rice variety 'Ciherang') was conducted from 25 July to 31 July 2001. Rice-field rats ($n = 14$) were trapped with multiple-capture wire-cage live-traps set along a drift fence in early June and fitted with 4.8 g single-stage radio transmitters (Sirtrack, New Zealand). For this study, we tracked the rats from 10 July (generative stage of rice crop) until harvest. Four of these rats were also followed for about three weeks post-harvest. Seven additional rats trapped and radio-collared in mid-July were tracked until the end of August. Radio locations (fixes) were obtained once a day and twice a night. Incremental area analysis (Kenward and Hodder 1996) revealed that 20 locations were sufficient to determine 80% of the 95% minimum convex polygon (MCP) home ranges of the rats. Therefore, only rats with ≥20 radio locations pre- or post-harvest were included in the analyses of home-range size and range span (pre-harvest, only $n = 10$; post-harvest, only $n = 3$; pre- and post-harvest $n = 4$). For seven individuals radio-tracked before and after harvest we calculated centres of activity using the recalculated arithmetic mean (Kenward and Hodder 1996) to detect shifts in the position of home ranges during harvest.

Rats were radio-tracked in five plots of about 2–23 ha within the study area. The distance between plots was at least 400 m. For each of the plots, habitat was classified as rice field, refuge (channel banks, gardens, roadsides) and village. Vegetation height of the ripe rice plants was about 0.9 m and the height of the stubble after harvesting was about 0.25 m.

We compared ln-transformed data of 95% MCP home ranges and range spans of rats pre- and post-harvest using general linear regression. We calculated the Jacobs' index (Jacobs 1974) as a measure of habitat use relative to habitat availability for all rats that were located in >1 habitat. The index results in values between 1 (complete preference) and –1 (complete aversion). The proportion of the rat population that did not move outside rice fields was compared pre- and post-harvest with generalised linear regression for binomially-distributed data (radio locations in rice field only yes/no) using a regression model including time (pre- and post-harvest) and plot. Range measurements were calculated in Ranges V (Kenward and Hodder 1996).

Results and discussion

Home range and range span

A total of 672 radio-locations were used for analyses. Home ranges pre-harvest of 0.59 ha (se = 0.12 ha) were about 67% larger than home ranges post-harvest ($F = 20.99$, df = 1,18, $p < 0.001$) (Figure 1a). Similarly, range spans pre-harvest of 139 m (se = 13 m) were about 35% larger than post-harvest range spans ($F = 9.75$, df = 1,18, $p = 0.006$) (Figure 1b). This was in agreement with hypothesis 1. Pre-harvest home ranges were similar to the home ranges of rice-field rats during the vegetative stage of the rice crop (Brown et al. 2001). However, post-harvest home ranges were much smaller, indicating a considerable decrease in spatial activity shortly after harvesting.

Vegetation height was considerably shorter after harvest and consequently the shelter available to rice-field rats decreased. The reduction of shelter exposes small mammals to increased predation risk (Sheffield et al. 2001) and can lead to changes in spatial behaviour (Jacob and Hempel 2002). We believe the changes in home-range size found post-harvest were due to decreased vegetation height and not a result of a potential decrease in food availability. A decrease in food availability should have caused an increase in home-range size but home range size decreased. An effect of breeding on home range size seems also unlikely because breeding in rice-field rats continued for 2–3 weeks post-harvest when the study was completed. Given high activity by farmers in conducting rat control measures, 'predation by humans' could have

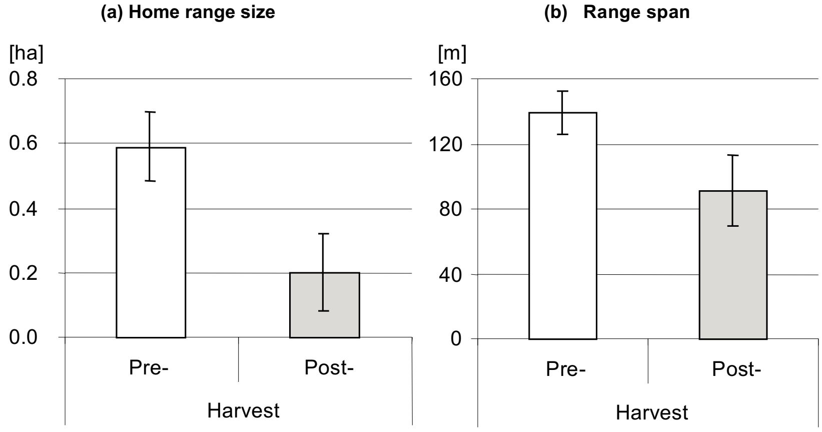

Figure 1. 95% minimum convex polygon home ranges (a) and range span (b) for female rice-field rats pre- and post-harvest. Rats were radio-tracked on three plots (13 rats pre-harvest, 7 rats post-harvest). Error bars are standard errors.

been a major factor in determining the rice-field rats' home-range size.

Centres of activity

For the seven rice-field rats we were able to track pre- and post-harvest, we found a relocation of the centres of activity by an average of 367 m (se = 130 m) during harvesting. This is a distance more than three times longer than the average range span before and after harvest (115 m). Other species of small mammals, such as common voles, do not shift home ranges when grain fields are harvested (Jacob and Hempel 2002). Harvesting of the rice continued for about one week and unharvested patches as well as piles of rice straw left on the fields provided shelter during that time. Two of the radio-tracked rice-field rats moved >700 m to reach unharvested patches of rice field. The rats left their pre-harvest home range, which resulted in a shift of their centres of activity. The pre- and post-harvest home ranges overlapped for only one rat. The concentration of the activity of the rice-field rats in unharvested patches may have led to high rat densities there. This may have resulted in smaller home ranges post-harvest because high density is correlated to small home ranges in small mammals (e.g. Erlinge et al. 1990). The aggregation of rats in unharvested areas could have led to pronounced damage in areas harvested late.

Habitat use

The mean availability of the different habitat types in the five plots were: 94% (±3%) rice field, 8% (±4%) refuge and 1% (±0.2%) village. Pre-harvest, rats tended to not prefer rice fields (Jacobs' index = –0.50, $n = 7$) and to prefer refuge habitats (Jacobs' index = 0.38, $n = 7$). There was a difference in habitat use pre- and post-harvest. Pre-harvest, 74% (±14%) of the rats did not leave the rice fields, while post-harvest, all of the rats stayed in rice fields only ($F = 5.69$, df = 1,23, $p = 0.017$). The avoidance of refuge habitats post-harvest was unexpected (hypothesis 2). The rats may have stayed in the rice fields because this habitat became suitable for nesting after the water was drained from the rice fields shortly before harvest. The piles of rice straw left on the fields post-harvest may also have provided shelter. In addition, nesting in the fields may have provided the rats with the opportunity to avoid rat control by farmers who focus fumigation and digging on refuge habitats (channel banks, dikes). The pre-harvest strategy to travel between refuge habitats and rice fields may have become more risky post-harvest because it would have resulted in moving through unharvested sections of the crop. It is possible that the rats tried to avoid exposure to predators in unharvested sections by remaining in the rice fields.

Conclusions

The behavioural response of rice-field rats to harvesting of rice may have general relevance for population trends and management of rice-field rats in rice-based agro-ecosystems. The relocation of rice-field rats from harvested to unharvested patches may lead to higher rat damage in the fields harvested last. Targeting these areas for rat management may help the owner of these fields to minimise damage there. A carry-over effect of such management to the next growing season would only occur if there were a short fallow period. This is normally not the case after a dry season crop, when the fallow period lasts for 2–3 months before the wet season crop is planted.

Our findings emphasise the importance of synchronous harvesting because removal of shelter and food within a short period of time will maximise the length of the fallow period and minimise the risk of sustaining populations of rice-field rats during the fallow period. Grazing stubble as well as the removal or burning of rice straw will minimise shelter for rice-field rats after harvest. Prey perceive tall vegetation as good protection (Tchabovsky et al. 2001) and removal of shelter leads to higher direct and indirect risk of predation. However, low vegetation post-harvest restricted spatial activity that may in turn lessen the direct impact of predation. Therefore, the success of pest rodent management relying only on the decrease of vegetation height may be compromised.

Our study showed that rats persist in rice fields until 2–3 weeks post-harvest. From a management perspective, it would be beneficial to know when the rats leave harvested rice fields and to where they move.

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Comparison of different baits to attract rats to traps in rice fields in Bangladesh

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Abstract. Rats are a chronic problem for Bangladeshi agriculture. The use of rodenticides and traps are the common tactics adopted for rat control by Bangladesh farmers. They use different kinds of bait materials for trapping rats. We tested the response of rats to four types of common baits—paddy grains, dry fish, coconut meat, and snail flesh—in both the *boro* (dry season) and *aman* (monsoon) rice-growing seasons. Tests were conducted during the reproductive phase of the rice crops on an experimental farm at Gazipur in 2001 and 2002. About 94% of the trapped rats were *Rattus rattus* and only 6% *Bandicota bengalensis*. Some predators such as gray mongoose and snakes were caught as well. In both seasons, paddy grains were the bait most preferred by rats, while snail flesh was the least preferred. Preference for dry fish and coconut meat was similar and moderate compared to paddy grains. Considering preference, cost and availability, it is recommended that paddy grains be used as bait for trapping *R. rattus*.

Introduction

Rats are serious pests of rice in Bangladesh. They damage the standing crops and also grains in stores. Rodent droppings and urine spoil stored grains and make them unfit for human consumption. Some rodents damage irrigation systems through their burrowing activity, thus causing loss of irrigation water and plant nutrients. In a recent integrated pest management (IPM) needs assessment survey, it was emphasised that rodents are important pests during pre- and post-harvest periods in areas of both low and high crop diversity. It was stressed in a national IPM workshop in November 2000 that more effort is required to develop IPM strategies for rodent pests. This is consistent with recent research elsewhere in Asia, Australia and Africa that focuses upon ecologically based rodent management strategies (Singleton et al. 1999).

In Bangladesh, control strategies for rodents have been traditionally based upon the use of poison baits (rodenticides) and traps. Zinc phosphide baits, and snap- and live-traps are most commonly used in rat control. A bait is necessary to attract rats to the trap and the preference of the rat for particular baits will influence trapping success. The preference for baits may vary between rodent species. So far, information on bait preference of different rat species is scanty. Islam and Karim (1995) reported that in a deepwater rice environment, bandicoot rats preferred snail flesh, paddy grains and dry fish rather than coconut meat and banana. Environmental conditions influence rat species composition and abundance. In the annually flooded environment, bandicoot rats are the most abundant, while in the non-flooded situations, *Rattus* sp. is more abundant. Therefore, the bait preference of rats in the non-flooded environment could be different from that of bandicoot rats in the flooded environment. In this study, we evaluated bait preference of field rats in a non-flooded rice environment of Bangladesh.

Materials and methods

Preference of four bait materials—dried coconut meat, snail flesh, dry fish, and paddy grains—were evaluated at the experimental farm of the Bangladesh Rice Research Institute in Gazipur. Tests were conducted at the reproductive phase of rice crops in the *boro* (dry) and *aman* (monsoon) seasons. Single-capture live-traps were used. Trapping was done on 68 consecutive nights in the 2001 *aman* season (19 September to 26 November) and 46 nights in the 2002 *boro* season (25 March to 10 May). Three traps were used with each type of bait. Average weight of each type of bait was 3.98, 4.64, 2.36, and 3.37 g for dried coconut meat, snail flesh, dry fish, and paddy grains, respectively. Paddy grains were wrapped in a piece of white nylon net. Traps were placed at random near active rat burrows in paddy fields. Traps were set in the field in the evening and checked the next morning. Each trapped animal was examined and identified to species.

Results and discussion

Rodent species composition

During the *aman* season, 50 (89.3%) of the 56 trapped animals were rats, four were shrews (7.1%) and two were gray mongoose (3.6%) (Table 1). Of the rats, 48 (96.0%) were *Rattus rattus* and only two (4.0%) *Bandicota bengalensis*. In the *boro* season, 18 animals were trapped of which 17 (94.4%) were rats and one (5.6%) was a snake. Similar to the *aman* season, 15 (88.2%) out of 17 rats trapped in the *boro* season were *R. rattus* and only two (11.8%) were *B. bengalensis.* In these non-flooded rice environments, *R. rattus* was the dominant rat species and *B. bengalensis* was present at low population densities. The latter is the dominant species in the annually flooded rice environments (Islam and Karim 1995; Catling and Islam 1999). Predators such as the gray mongoose and snakes were active in the non-flooded prone rice environment. There was higher rat activity (populations) in the *aman* than the *boro* season, which is consistent with farmers' perception of higher rat damage to the *aman* than to the *boro* rice crops.

Bait preference

In the *boro* season 47, 29, 18, and 6% of trapped rats were caught in traps that had paddy grains, dry fish, coconut meat, and snail flesh as bait, respectively. In the *aman* season, 44, 26, 24, and 6% of rats were caught with paddy grains, dry fish, coconut flesh, and snail flesh, respectively. Over the two seasons, 44.8%, 26.9, 22.4, and 6.0% of rats were caught in traps with paddy grains, dry fish, coconut flesh, and snail flesh, respectively. In the *aman* season, the number of rats caught in the trap with paddy grains was significantly higher ($P < 0.05$) than the number caught in traps with snail flesh (Table 2).

These findings for *R. rattus* contrast with a study of five tested baits which concluded that snail flesh was the most preferred and coconut flesh least preferred by bandicoot rats in a flood-prone environment (Islam and Karim 1995). The bandicoot rats had a moderate to high preference for paddy grains and dry fish. Considering the preference, availability and cost, this study recommended snail flesh and paddy grains for trapping bandicoot rats in flood-prone areas of Bangladesh.

Conclusion

In Bangladesh, bait preference varies among rodent species. Considering preference, cost and availability, paddy grains appear the best choice for use as bait for trapping of *R. rattus*. This bait is likely also to be effective where bandicoot rats are dominant or co-exist in high numbers with *R. rattus*.

Table 1. Rats and other animals trapped in the rice fields during the reproductive phase of the 2001 *aman* and 2002 *boro* seasons, Gazipur, Bangladesh.

Attributes	*Boro* season	*Aman* season	Total	Percentage
Trapping duration (nights)	46	68	114	
Animals trapped (total number)				
Rats – *Rattus rattus*	15	48	63	85.13
– *Bandicota bengalensis*	2	2	4	5.41
Shrews		4	4	5.41
Gray mongoose		2	2	2.70
Snakes	1		1	1.35
Total	18	56	74	100

Table 2. Bait preference of *Rattus rattus* during the reproductive phase of the *aman* 2001 and *boro* 2002 seasons, Gazipur, Bangladesh. Means followed by same letter(s) are not significantly different at the 5% level.

Type of bait	Rats trapped per trap per day (mean ± sd)	
	Aman season	*Boro* season
Coconut meat	0.05880 ± 0.04 ab	0.0217 ± 0.02
Snail flesh	0.01470 ± 0.01 b	0.0720 ± 0.01
Paddy grains	0.10780 ± 0.02 a	0.0580 ± 0.03
Dry fish	0.06370 ± 0.02 ab	0.0362 ± 0.03
Level of significance	0.05	Not significant
CV(%)	41.00	79.01

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Pest and non-pest rodents in the upland agricultural landscape of Laos: a progress report

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Abstract. Rodent communities have been monitored on a monthly basis since January 2000 in four provinces of Lao PDR using a regular trapping pattern across five habitats associated with upland agriculture. Rats have been collected sporadically from lowland habitats in two other provinces. The upland environment of Laos supports a rich array of rodent species, the great majority of which probably do little or no damage to crops. We recorded 21 different species of which 6 appear to be important pest species in crop production areas. Two forms of rats from the *Rattus rattus* complex (type A in the north and type B in the south) are the dominant rat species, and crop pest, in all six provinces. Population densities of both regional forms of *R. rattus* clearly fluctuate through the year in response to the availability of food resources, with a decline to very low resident populations and little or no breeding activity through the dry season. However, the same species also occupy the village habitat and these populations appear to be more stable and exhibit continuous breeding, presumably by feeding on high-quality stored grain as well as general refuse and household garden produce. Upland villages thus may represent a critical 'source' habitat for *R. rattus*, with migration into the fields once the cropping cycle is under way. Less certainly, the forest may also act as a refuge habitat through the dry season and a source of emigrants to the fields. Alternatively, the forest may be a 'sink' that absorbs individuals at the end of the cropping cycle but witnesses little, if any, subsequent breeding. These baseline studies provide a solid foundation for identifying key issues for developing ecologically based management of rodent pests and for conserving some non-pest rodent species that are classified by International Union for Nature and Natural Resources (IUCN) as 'vulnerable'.

Introduction

Schiller et al. (1999) made a strong case for more research activity on rodent pests and potential management strategies in the Lao PDR (Laos), especially for the rainfed upland ecosystem which still plays a predominant role in meeting the food requirements of many ethnic groups. In the 2000 production year, this ecosystem accounted for 21% of the total area under rice cultivation in Laos; and it returned approximately 12% of the total rice harvest (Lao PDR Ministry of Agriculture and Forestry records). Most upland rice cultivation in Laos is still based on traditional 'slash and burn' methods of shifting cultivation. However, the productivity of this ecosystem is generally in decline due to myriad problems associated with weeds, insects and rodent pests, and soil erosion and degradation (Schiller et al. 1999; Roder 2001).

Rodent damage is cited by farmers as being second only to weeds as a cause of poor rice yields in the uplands (Schiller et al. 1999). Rodents are a chronic problem in most areas, although the severity of the damage varies from year to year and between localities. In addition, episodic but irregular rodent irruptions are sometimes responsible for extreme crop losses, occasionally leading to widespread famine (Singleton and Petch 1994; Schiller et al. 1999). These events are attributed locally to *nuu khii* (literally, rat of bamboo flower) and they are distinguished from the problem of chronic crop damage.

The research activities reported here commenced in 1998 and followed on from an earlier process of problem definition (Singleton and Petch 1994). Here, we provide a brief overview of progress made in respect to three main issues: (i) identification of the rodent species present in the various production environments and assessment of their pest or non-pest status; (ii) patterns of habitat use by the various rodent species in the upland system; and (iii) the breeding biology of the main rodent pest species. A companion paper by Douangboupha et al. (this volume) examines the historical pattern of *nuu khii* outbreaks across four provinces and speculates on possible causes.

Materials and methods

Research activities have concentrated on upland habitats in four provinces: Luang Prabang, Oudomxay and Houaphanh in the northern agricultural region and Sekong in the southern agricultural region. Some preliminary fieldwork was conducted also in lowland rice production areas in Sayabouly province, in the west of the country, and in Vientiane Municipality. Annual rainfall is highest in Sekong (>2000 mm) and lowest in parts of Luang Prabang and Sayabouly (<1440 mm; Sisophanthong and Taillard 2000). Houaphanh is generally at higher elevation than the other provinces and is significantly cooler in the winter months. Summer temperatures in Sekong are several degrees higher than in the more northerly provinces. The intensity of upland shifting cultivation is highest in Luang Prabang and Oudomxay (Sisophanthong and Taillard 2000).

In each of the four main study areas, rats were trapped on a regular basis starting in January 2000. Each month, traps were set for four consecutive nights in each of five habitats: upland rice field, upland maize or mixed cropping field, lowland rice field, forest, and village (around rice stores). Essentially, three kinds of traps were used: (i) a trap–barrier system (TBS) using multiple-capture traps, set with a linear barrier system in the upland crop/maize habitat and as an enclosed square around a village rice store; (ii) single-capture live cage-traps, set in the lowland rice crop and forest; and (iii) kill-traps of various kinds (large and small snap-traps, and traditional snares) set in all habitats except the village. Additional sampling was carried out in each province at variable intervals to investigate the breeding activity in the common pest species—for this purpose, rats were trapped, dug from burrows and hunted within the same general habitat types.

Rats were identified to species with reference to a taxonomic key developed by K. Aplin for Lao rodents (translated into Lao by B. Douangboupha), measured, weighed and dissected to assess reproductive status. Representative specimens, including whole bodies, skins or heads, were preserved in 70% ethanol. These are lodged in the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Australian National Wildlife Collection (ANWC), Canberra.

Results and discussion

Identity of the major agricultural pest species of Laos

Francis (1999) lists a total of 28 murid species and 3 rhizomyids (bamboo rats) for Laos as a whole, with a further 6 murid species expected on broader distributional grounds. We recorded a total of 20 species from our combined field areas, either from direct trapping or through purchase from villagers or markets (Table 1).

Ten species are classified in Table 1 as definite or probable agricultural pests in Laos. These include five species of *Rattus*, three of *Mus* and two of *Bandicota*.

Rattus rattus is by far the most abundant pest species in the upland ecosystem of Laos. There are two genetically distinct forms of *R. rattus* in Laos (see Aplin, Chesser and ten Have, this volume). Both forms were captured within their respective geographical areas in all habitat types, including villages, upland and valley floor cropping areas, and the forest margin. No other species of *Rattus* were caught other than in Houaphanh. Most importantly, we did not find any evidence either of the rice-field rat, *R. argentiventer*, or the lesser rice-field rat, *R. losea*. Both of these species are recorded from lowland areas of Laos—the former in Khammouane province in Central Laos (Francis 1999) and the latter from several localities in central and southern Laos (Musser and Newcomb 1985; Francis 1999). Neither species was found in suitable habitat in a broad lowland valley in Sayabouly province. Here, and on the Vientiane Plain, lowland rice fields harbour populations of *R. rattus*. Further geographical sampling is needed to map the current range of *R. argentiventer* and *R. losea* in Laos. This will provide a valuable baseline against which to chart any future range expansion by these potentially significant pest species.

Table 1. List of the murid and rhizomyid rodents of Laos, divided into four categories according to probable pest and conservation status. Species in **bold type** have been confirmed from our trapping and other collections. Species marked with an asterisk (*) are only provisionally recorded from Laos. The two taxa listed as ‘sp.’ in the right-hand column were mentioned as possible new species by Francis (1999).

Definite or probable pests	Possible pests	Non-pests but common	Non-pests and rare?
Murinae	Murinae	Murinae	Murinae
Bandicota indica	***Rattus nitidus***	***Berylmys bowersi***	***Berylmys berdmorei***
*B. savilei**	***Leopoldamys edwardsi***	*Chiropodomys gliroides*	*Be. mackenziei**
Mus caroli	***L. sabanus***	***Maxomys surifer***	***Chiromyscus chiropus***
M. cervicolor	*Mus cookii*	***Mus pahari***	*Dacnomys millardi*
M. musculus	*M. shortridgei*	*Niviventer confuscianus**	*Hapalomys delacouri**
*Rattus argentiventer**		***N. fulvescens***	*Maxomys moi*
R. exulans		***N. langbianis***	*Maxomys* sp.
R. losea		*Vandeleuria oleracea*	*Niviventer* sp. cf. *N. tenaster*
***R. rattus* type A**		Rhizomyidae	***Rattus sikkimensis***
***R. rattus* type B**		***Cannomys badius***	Arvicolinae
		Rhizomys pruinosus	*Eothenomys melanogaster**
		Rh. sumatrensis	*E. miletus**
			Placanthomyinae
			*Typhlomys cinereus**

The Pacific rat, *R. exulans*, has been collected in several localities on the Vientiane Plain, but not so far in any of the upland sites. This is somewhat perplexing, as *R. exulans* elsewhere extends to high elevations and is perfectly at home in village and garden habitats. In parts of the Pacific region where *R. exulans* and *R. rattus* coexist, it is generally the latter that occupies the houses (Marshall 1977)—it is possible that *R. exulans* is excluded from upland villages in Laos by the presence of the larger *R. rattus*.

Two *Bandicota* species are listed as potential pest species in Table 1. *Bandicota indica* has been trapped on a regular basis only in Luang Prabang and Sekong but it is nowhere abundant in the uplands. The smaller *B. savilei* is recorded only from specimens photographed by one of us (BD) in Savannaket province in central Laos. Musser and Brothers (1994) record this species from near the Mekong River in Ubon Ratchathani province of Thailand, immediately west of Champassak in southern Laos. Although *Bandicota* species are generally regarded as agricultural pests, it is not proven that they cause much damage to crops in Southeast Asia (Aplin, Chesser and ten Have, this volume).

Mus species were generally collected in small numbers and mainly by the TBS method. In Sayabouly province, *Mus caroli* was taken from burrows dug into narrow bunds in lowland rice fields—farmers claimed that their main activity in the fields is to clean up any cut tillers and panicles left behind by *R. rattus*.

All of the pest species mentioned so far probably contribute to the chronic annual damage that occurs throughout the uplands to varying intensity. Major outbreak events, attributed by many Laotian farmers to *nuu khii*, may in some cases involve extreme population increases or unusual movements of this same suite of species (Douangboupha et al., this volume). However, there are indications that some of these events might involve dramatic increases of different forest-dwelling species, possibly driven by the mass flowering and seeding of bamboos across large areas with subsequent outpouring into the agricultural landscape. To date, this process has not been well documented, despite reports of similar phenomena across large parts of South and Southeast Asia (see Chauhan, this volume).

Five other species are classified as possible agricultural pests in Laos, either because they were caught on a regular basis within cropping areas (*Leopoldamys* spp. in Sekong) or because they are known to damage crops in surrounding countries (*Rattus nitidus*, *Mus* spp.). *R. nitidus* was caught together with *R. rattus* type A and *R. sikkimensis* in forest margin habitat in Houaphanh. This species is an important agricultural pest in parts of southern China, but in Southeast Asia it is more often associated with upland village habitats (Aplin, Chesser and ten Have, this volume). In Houaphanh, *R. rattus* type B is the common village rat.

Bamboo rats are most often found in proximity to bamboo groves where they probably feed mainly on the rhizomes and young shoots. However, Marshall (1977, p. 392) reported some damage caused by these animals to cultivated tapioca and sugarcane. In the uplands of Laos, bamboo rat burrows, both active and abandoned, are frequently found in and around active fields. However, according to farmers in Luang Prabang province, the burrows are originally constructed under cover of forest or regrowth, but come to be located in garden areas when wooded areas are subsequently cleared for cultivation.

Some non-pest species were occasionally caught in traps set in upland fields (e.g. *Maxomys surifer* in Oudomxay, *Niviventer* spp. in Houaphanh). These captures may reflect low-level crop damage by these species, however they might equally reflect foraging in the fields for insects or other prey items. Twelve of the non-pest species are themselves considered to be rare in Laos and three of these are rated ‘vulnerable’ in the International Union for Nature and Natural Resources (IUCN) Red List. However, there does not seem to be any particular reason to believe that these taxa are under any special threat in Laos.

Habitat use and activity cycles

The trapping data from each of the four provinces present a similar picture—in all cases, trends in rat abundance are clearly linked to major events and phases of the cropping calendar. The pattern for Houay Khieu, Lamam district, in Sekong is shown in Figure 1. The period September–November 2000 saw the relatively late ripening and harvest for both upland and lowland crops, perhaps reflecting the late onset of the wet season in 2000. Rat numbers in all cropping areas fell in December, as harvest was completed, but increased around the village store as this was replenished. Rat numbers in the forest/bamboo habitat also declined through this period.

January and February 2001 saw a break in trapping effort at Houay Khieu and also represents the peak of the dry season. Maize and other upland crops were planted in March in response to early rains—rat numbers in this habitat and in the forest/bamboo were high at that time and remained so through to the harvest of upland crops and maize in August. A temporary surge in forest/bamboo rat numbers in June appears to be mirrored by a similar increase in rat captures in other habitats. Rat numbers were high in upland and lowland rice crops through June to September but showed a marked decline after harvest (September for upland rice; October–November for lowland rice). Capture rate around the village grain store increased sharply after harvest of all crops was complete, suggesting a process of immigration of rats from field to village.

The role of the forest ecosystem in these population cycles is unclear at present. At Lamam during 2000–2001 most of the forest captures were of *R. rattus*, with smaller numbers of *Leopoldamys* spp. and other species. Fluctuations in rat numbers in the forest appear to be linked to capture rates in the cropping areas, yet there is no obvious lag and thus no clear indication as to whether the forest is acting as a 'source' or a 'sink' habitat. One point favouring identification of forest as a source habitat is the decline in forest captures after harvest—a sink habitat would presumably be receiving immigrants at this time, as indeed the village appears to be doing.

Rat numbers in the forest habitat may start to increase immediately upon the arrival of the wet season. As food resources and ground cover start to develop in the upland fields over the followed weeks and months, rats may undergo some migration into the fields, perhaps coming both from the forest and from the village where their numbers have been maintained over the dry season by stored food and general refuse.

Breeding biology of *Rattus 'rattus'*

Although breeding data for *R. rattus* are available from five different months and from all four provinces, the coverage remains incomplete (Table 2). Nevertheless, there are enough data to suggest year-round breeding,

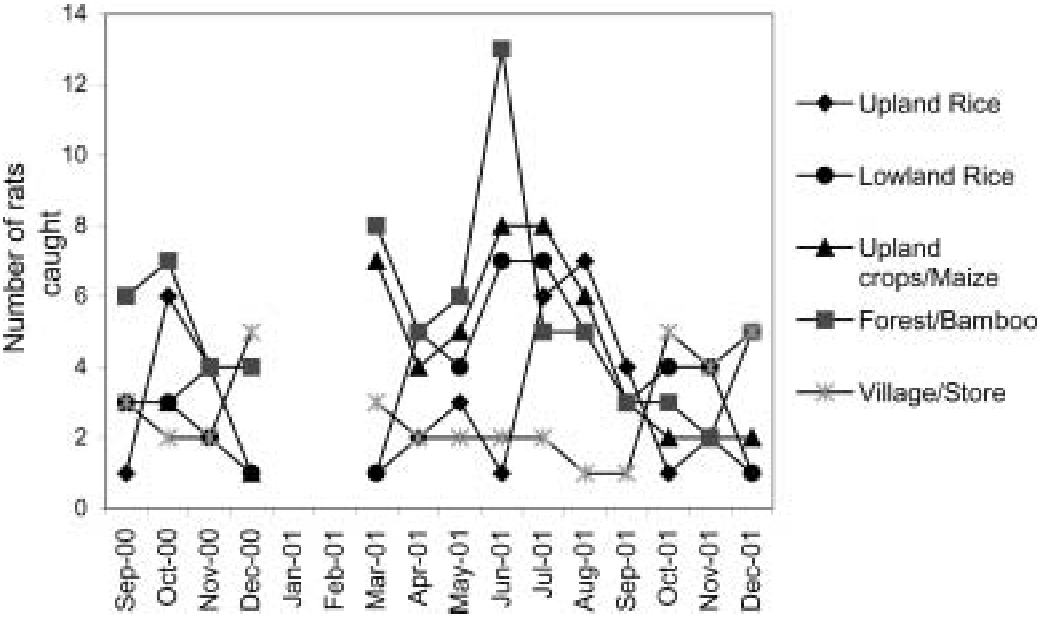

Figure 1. Monthly rat captures in five habitats at Houay Khieu in Lamam district, Sekong. Each trapping period represents 312 trap-nights, with 48 trap-nights in upland rice, 88 in lowland rice, 68 in upland crop/maize, 88 in forest/bamboo, and 20 around the village store. The village stores traps and 20 of those in the upland crop/maize were multiple-capture traps in linear trap–barrier systems; the remaining traps include a standard mixture of single-capture cage-traps, snap-traps and traditional snares. Upland crops and maize were harvested in August 2001; upland rice in September 2001; and lowland rice in October/November 2001.

Table 2. Monthly breeding data for *Rattus rattus* types A and B from intensive sampling across four provinces (*R. rattus* A from HP = Houaphanh, LP = Luang Prabang, OD = Oudomxay; *R. rattus* B from SK = Sekong). Samples were obtained by trapping, hunting and digging of burrows across a variety of cropping habitats. Total % breeding includes females that have embryos and/or placental scars. No sampling in October 2001 and in January and February 2002.

Month	Province	Number of adults	% pregnant	% with placental scars only	Total % breeding
Aug 2001	LP	6	66.7	16.7	66.7
Aug 2001	OD	39	59.0	30.8	89.7
Aug 2001	HP	13	46.2	38.5	84.6
Sep 2001	SK	98	39.8	54.1	93.9
Sep 2001	HP	4	75.0	25.0	100.0
Nov 2001	HP	12	0.0	83.3	83.3
Dec 2001	HP	13	0.0	84.6	84.6
Mar 2002	LP	27	55.6	25.9	81.5
Mar 2002	OD	27	48.1	51.9	100.0
Mar 2002	HP	42	54.8	23.8	78.6

except perhaps for a lull during the dry season (November to January?). This requires confirmation. Breeding in *R. rattus* was well and truly under way in at least three provinces by March 2002, with a high proportion of females already showing uterine placental scars from recent litters. The number of embryos ranged up to a maximum of 10 in the three populations of *R. rattus* type A, and to 14 in the Sekong population (*R. rattus* type B).

Year-round breeding of *R. rattus* has been reported elsewhere in Asia including Jodphur in the Indian arid zone (Advani and Rana 1982) and in a monsoonal environment in Mizoram, eastern India (Chauhan and Saxena 1992). However, previous studies of reproduction in members of this group have reported much lower pregnancy rates, typically no more than 20–30% of adult females. It is possible that the removal of animals from breeding burrows during this study has resulted in an over-representation of pregnant females. However, breeding data from the regular trapping (unpublished data) also point to very high reproductive rates in Lao *R. rattus*. Moreover, comparably high pregnancy rates are reported for other *Rattus* species in tropical agricultural contexts (Brown et al. 1999). The regular trapping data also show that breeding of *R. rattus* continues through the dry season within the village habitat, presumably reflecting the continued availability of high-quality food.

Conclusion

Much has been learned over the last few years regarding the rodent communities and general rodent ecology in the upland agricultural environment of Laos. We now know that the dominant pest species across most of Laos are two distinct, but closely related, members of the *R. rattus* complex, one found in the northern provinces and the other found in the south. Rather surprisingly, these species are dominant also in some lowland cropping systems, such as Sayabouly, where lowland rice is grown across a broad valley floor, and on the Vientiane Plain.

The emerging models of upland rodent ecology have important implications for rodent management in Laos. If the upland villages represent the major source habitat for the *R. rattus* population that attacks the crops, then a vigorous rodent control campaign in the villages just before the onset of the wet season might serve to reduce subsequent crop damage in the fields. This could be conducted without fear of non-target impact on native rodents, none of which seem to use the village habitat or its immediate surrounds. These targeted campaigns could replace the general bounties, which provide money for any rat species collected, that have been implemented in recent years (Singleton and Petch 1994).

On the other hand, if the field population of *R. rattus* is derived in part or whole from the forest habitat, proactive rodent control might be very difficult without harming native species. One solution may be to apply a trap–barrier system plus trap crop (TBS+TC) method of the kind that has been successful in controlling rodent damage in lowland irrigated rice systems (Singleton et al. 1999). However, there are significant technical challenges to be overcome before this system can be applied in the upland cropping environment, including:

- selection of an appropriate lure crop or range of crops;
- redesign of the barrier to operate without a moat and with a pest species that is a proficient climber; and
- consideration of optimal placement relative to the diverse habitat types in the upland cropping environment.

Acknowledgments

Our sincere thanks to the five provincial staff members who have run the trapping programs and conducted the majority of other project activities over the past two years. Work in the uplands of Laos was supported by Australian Centre for International Agricultural Research (ACIAR) project AS1/98/36 and work in the lowlands by the Rodent Ecology Work Group of the International Rice Research Institute.

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Rodent communities and historical trends in rodent damage in the Mekong Delta of Vietnam: establishing an ecological basis for effective pest management

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Abstract. The Mekong Delta region of Vietnam features a variety of natural and agricultural landscapes that differ in flooding and cropping regimes, and in the nature of the associated pest rodent communities. Areas with regular, extensive floodwater inundation tend to show a predominance of *Rattus argentiventer* over other species. In contrast, areas that experience localised flooding support a broader range of species with less obvious dominance within the community. However, cropping regime is also important, and areas where two or three rice crops are grown each year also tend to show a dominance of *R. argentiventer* over other species. Historical records spanning the last decade show a general increase in rodent damage to crops, especially in those provinces that have seen a recent increase in cropping area or frequency. However, flood-prone provinces in the centre of the delta proper share a more complex history of rat damage that appears to correlate with inter-annual variations in river outflow associated with the El Niño cycle. Our improved understanding of the ecology and history of rodent problems in the Mekong Delta region allows us to frame a number of specific hypotheses that can be tested through studies of spatial and temporal patterning, and through manipulative experiments. Insights gained in this way will provide the necessary ecological foundation for sustainable, non-chemical rodent control under the variable conditions offered by the Mekong Delta.

Introduction

Several recent and ongoing projects in Southeast Asia are assessing the applicability of the community trap–barrier system (CTBS) as a potential method for chemical-free rodent control in the lowland rice cropping environment (Brown, Tuan et al., this volume; Russell et al., this volume; Sudarmaji, Rochman et al., this volume). The TBS approach, first developed by Lam in Malaysia for the control of the rice-field rat, *Rattus argentiventer*, was subsequently trialled and found to be effective in controlling the same species in irrigated rice crops in Indonesia (Singleton et al. 1999). However, extension to other countries within Southeast Asia requires a process of continuous assessment and adaptation of the technology. To be effective on a broad scale, it must be applicable across a range of subtly different ecosystems that differ, not only with respect to cropping systems, natural hydrology and water management systems, but which also host contrasting suites of rodent species. In addition, there is a growing awareness of the importance of social and cultural factors in determining the likely success of the CTBS approach (King et al., this volume; Morin et al., this volume; Sang et al., this volume).

Here we report on aspects of rodent community structure and community ecology in the Mekong Delta region of southern Vietnam. We also present new data on historical trends in rodent damage across the 21 provinces that make up the Delta region. These data were collected during a project funded under the Australian Agency for International Aid (AusAID) Capacity-building for Agriculture and Rural Development (CARD) scheme. Other elements of this multidisciplinary project are reported by Morin et al. (this volume), Palis et al. (this volume), and Le Quoc Cuong et al. (this volume), while Nguyen Tri Khiem et al. (this volume) describe the results of an associated study of the live-rat trade in the southern Mekong Delta. The results presented here provide a biological foundation for these other studies, and also, a platform for the formulation of a new set of hypotheses regarding the likely applicability of the CTBS approach in differing areas of the Mekong Delta.

Study area and methods

The Mekong Delta

The Mekong Delta region of southern Vietnam covers 39,500 km^2 or 12% of the total country area and is home for just over 15 million people (22% of total population). Much of the delta area was cleared of forest cover only quite recently, with a major increase in rice cropping area occurring between 1994 and 1996. This process continues with removal of mangroves and *Melaleuca* forest, especially due to the increasing human population and the expansion of shrimp aquaculture in the southern provinces.

Annual rainfall across the delta region is 2000–2500 mm, with most rainfall in the wet season (April to November). Regular flooding occurs during October and November, driven by monsoonal rains in more northerly parts of the Mekong River Basin. The likelihood and depth of inundation varies markedly across the Delta (Figure 1) and this has important implications for rodent ecology. Provinces located to the east of Ho Chi Minh City technically lie outside of the Mekong River Basin and are under the influence of local rainfall patterns; these include Ho Chi Minh City province itself and Tay Ninh, Binh Duong, Binh Phuoc, Dong Nai, Ba Ria Vung Tau and Binh Thuan. The main project activities have been conducted in Tien Giang and Soc Trang provinces, however associated projects have allowed information to be gathered in Ho Chi Minh City province, and in Bac Lieu and Binh Thuan provinces.

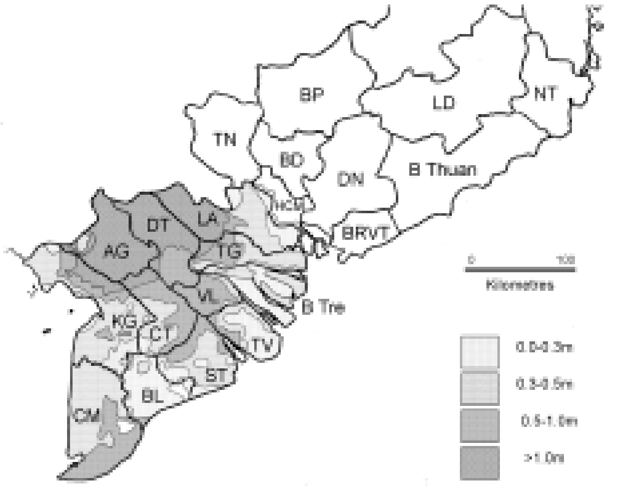

Figure 1. The Mekong Delta region of Vietnam showing the provinces and the approximate depth of seasonal inundation (based on Figure 4 in Hirsch and Cheong 1996). The provinces are abbreviated as: AG, An Giang; BD, Binh Duong; BL, Bac Lieu; BP, Binh Phuoc; BRVT, Ba Ria Vung Tau; B Thuan, Binh Thuan; B Tre, Ben Tre; CM, Ca Mau; CT, Can Tho; DN, Dong Nai; DT, Dong Thap; HCM, Ho Chi Minh City; KG, Kien Giang; LA, Long An; LD, Lam Dong; NT, Ninh Thuan; ST, Soc Trang; TG, Tien Giang; TV, Tra Vinh; VL, Vinh Long.

Cropping systems

In many parts of the Mekong Delta, rice production is supported by a dense network of irrigation canals. Where irrigation water can be accessed year-round, many farmers produce three crops each year. However, planting and harvesting times may be asynchronous, with adjacent fields differing in growth stage by several weeks or more. Two crops are usually grown in areas that lack access to irrigation water. Depending on the flooding regime, these are grown either as a floodwater recession crop in the dry season (December to March) followed by a rainfed early wet season crop (late March to early July) and then an extended period of inundation; or as two successive wet season crops (April to July; August to October), with an extended fallow period through the dry season. In most areas, short-maturing (90 day) rice varieties are now predominant, although traditional varieties (usually 120+ days) are sometimes also grown.

The rice cropping system in many regions is interspersed with villages and numerous small ‘upland’ areas where farmers grow fruit trees, vegetables and sugarcane. This heterogeneity is most prominent in areas that experience limited or no flooding, and in areas that are strictly rainfed.

Historical information

Information on rodent damage was obtained from records compiled over the last decade by staff of the Southern Regional Plant Protection Centre (SRPPC) in Tien Giang. During the cropping season, rodent damage is reported every 14 days by provincial officers of the sub-Plant Protection Department (sub-PPD). These data represent a summary of information provided by individual villages within each province. The sub-PPD officers estimate the total number of hectares that have experienced ‘significant’ rodent damage during the reporting period. These data show a clear geographical pattern suggesting limited observer bias. Data on the total number of hectares under rice cultivation also were compiled. A rat damage index (RDI) was developed as follows: for each province the mean number of hectares showing damage was calculated, and values for each year were scored as a ratio to that mean value. RDI values range from below 0.1 to slightly more than 3 (a score of 1 would indicate average damage for that province). Two provinces were subdivided during the 1990s: Minh Hai was divided to form Bac Lieu and Ca Mau; and Song Be to form Binh Phuoc and Binh Duong. We pooled the data from the subdivided provinces for consistency across the time period.

Information on rodent species and communities

The previous studies by Sang (1998) and Brown et al. (1999) relied principally on field identifications and the taxonomy of van Peenen et al. (1969) and Cao Van Sung (1984). Because there are known taxonomic problems in several groups of Southeast Asian rodents, we collected large series of voucher specimens with associated tissue samples appropriate for DNA analysis (to be reported elsewhere).

Rodent specimens were obtained from three provinces within the Mekong Delta proper (Tien Giang, Soc Trang and Bac Lieu) and from Ho Chi Minh City and Bin Thuan provinces to the east. They were captured by a variety of methods, including individual cage-traps, multiple-capture traps set within CTBS units, and by digging burrows. Some specimens were purchased from people involved in the live rat-meat trade. The voucher specimens are lodged in the Australian National Wildlife Collection (ANWC), the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Canberra, and at the Institute of Agricultural Science, Ho Chi Minh City. In Tien Giang province, systematic sampling using cage-traps was carried out over several periods during March–July 2002 at three sites (two at Cay Lay village; one at Cay Be).

Results and discussion

Historical and geographical patterns of rodent damage

The total area under rice cultivation within the study area has increased by more than a million hectares since 1990 and now stands at just over 4×10^6 ha (Figure 2). Across the entire region, the area of crops damaged by rats was very low during the early 1990s, with a dramatic increase since 1993 (Figure 2). In part, this reflects a lack of data from some provinces from the early period. However, the same trend is observed in individual provinces, with a ten-fold or higher increase in reported damage across four of the six provinces with data from 1991–93. An interesting trend is the apparent decrease in rodent damage in 1995 compared with the preceding and following years. This is consistent with data presented by Brown et al. (1999) for the Mekong Delta and for the whole of Vietnam. Also of interest are the very high values for 1998–99 and the reduction in 2000.

In the majority of provinces, including all of those in the western part of the Mekong Delta, the area of reported rodent damage has increased steadily through the 1990s (Figure 3a). This increase appears to have begun somewhat earlier in some areas than in others, e.g. An Giang and Kien Giang show a steady increase since the early 1990s, while Bac Lieu in the south shows a dramatic increase in the area damaged since 1997. These differences reflect the spatial pattern of land reclamation for intensive rice growing in the Mekong Delta, most notably the progressive blocking of saline intrusion that has allowed intensive rice production across large areas of Soc Trang and the Bac Lieu area of former Minh Hai province.

Three provinces in the core of the delta (Long An, Dong Thap and Tien Giang) show a very different historical pattern, with a major peak in rodent damage in 1993–94 and another in 1998–99 (Figure 3b). These provinces have a longer history of intensive rice cropping, and they also experience heavy seasonal inundation (Figure 1). The period of reduced rat damage in 1995–97 corresponds with three successive years of heavy rainfall in the Mekong River Basin and widespread flooding, which was terminated by the widespread droughts and reduced Mekong outflows associated with the 1997–98 El Niño (McPhaden 1999). Song Be province to the east of the Mekong Delta shows a similar but lower two-peaked pattern of rat damage (Figure 3b).

A third major pattern, featuring a strong peak in rat damage during the El Niño years, is observed in three provinces to the east of the Mekong Delta proper (Figure 3c). These provinces share considerable areas of elevated ground where rainfed rice systems predominate.

Two provinces do not seem to fit into any of these general patterns. Tay Ninh, situated in the hinterland of Ho Chi Minh City province had consistently high reports damage other than for one low point in 1999. Ben Tre, at the mouth of the delta, reported small areas of rat damage with a peak in 1999.

The substantial and systematic variations in rodent damage appear to reflect the contrasting landscape ecology of different parts of the Mekong Delta and adjacent region. In part, these contrasts relate to the differing hydrological conditions that exist between the inland, inundated, region of the delta compared with the slightly more elevated and better draining coastal and eastern zones.

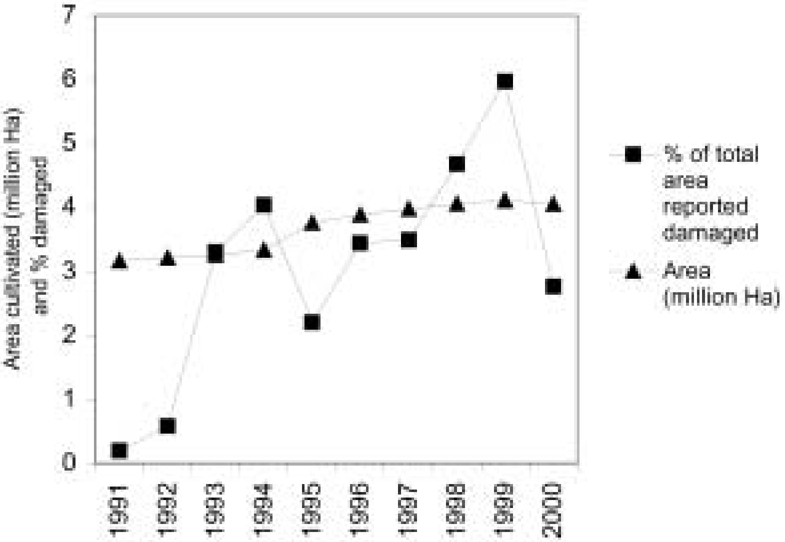

Figure 2. Recent historical trends in the area of cultivated rice in the Mekong delta region of Vietnam and in the proportion of total area reported as damaged by rats.

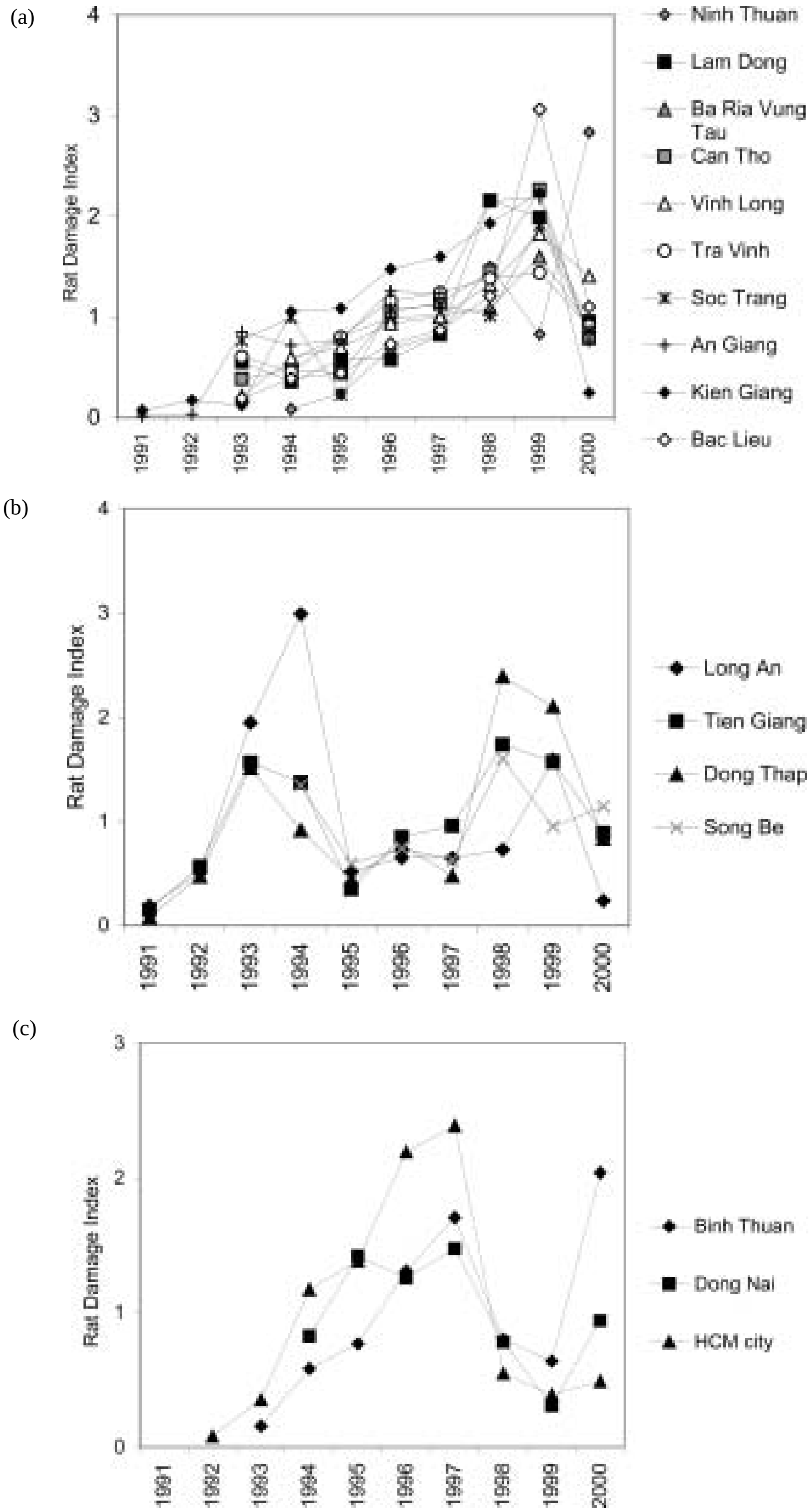

Figure 3. Recent historical trends in rodent damage in various geographic sub-regions of the Mekong Delta area, as indicated by the rat damage index (see Methods): (a) trends in ten predominantly western and southern provinces of the Mekong Delta proper; (b) trends in three inland provinces of the Mekong Delta proper and one to the east (Song Be); and (c) trends in three provinces to the immediate east of the Mekong Delta.

The contrasting histories of rodent damage also appear to reflect differences in cropping history between the provinces. Areas of the delta that have been cleared and drained for rice production over the last decade typically show a marked increase in the extent of rodent damage, as do areas that have converted from an annual wet-season crop to a more intensive pattern of two or three consecutive crops as a result of improved control of saline intrusion or simply improved access to irrigation water. In contrast, areas of the delta that have supported dense human populations for longer periods typically do not show any simple increase in rodent damage through the last decade, but rather, more complex patterns such as the possible link to flooding intensity.

Rodent species and communities of the lower Mekong Delta

All available information on rodent community structure in the Mekong Delta and areas to the immediate east is summarised in Tables 1 and 2. As reported previously by Brown et al. (1999), *R. argentiventer* is the dominant species in most parts of the Mekong Delta proper. A random sample of rats purchased from a rat-meat ‘factory’ in Soc Trang consisted of >95% *R. argentiventer*, while in Bac Lieu, the dominance of this species was probably even greater (the higher percentage of *B. indica* in our voucher sample is due to deliberate selectivity to sample for zoonoses; Singleton, Smythe et al., this volume).

Our studies indicate a lower regional diversity than reported previously by Brown et al. (1999), with eight species confirmed and one or two others potentially present. Previous records of *Rattus koratensis*, *R. germaini*, *R. rattus*, *R. flavipectus* and *R. nitidus* are here treated as reflecting phenotypic variation within one or more members of the *Rattus rattus* complex. As discussed by Aplin, Chesser and ten Have (this volume), the Mekong Delta supports what appears to be an endemic Southeast Asian species of this group and it may also host populations of the introduced ‘Oceanian’ black rat. *R. germaini* and *R. flavipectus* are synonyms of *R. rattus* in the broad sense (Musser and Carleton 1993). *R. nitidus* and *R. koratensis* (more properly known as *R. sikkimensis*) are valid species of *Rattus* (Musser and Carleton 1993) but neither was encountered during our studies, nor were they mapped for this region by Lunde and Son (2001). Records of *B. bengalensis* reported by Brown et al. (1999) probably represent a mix of *B. savilei* and some immature *B. indica*. We have encountered *B. savilei* only in Ho Chi Minh City and Binh Thuan provinces and are confident that the species is either rare or absent from the greater part of the delta proper. True *B. bengalensis* is found on the Indian subcontinent, east to central Myanmar (Aplin, Frost et al., this volume).

R. losea was more abundant than *R. argentiventer* in two provinces: Kien Giang in the far west and Ho Chi Minh City (Cu Chi district) in the east. This species is moderately abundant in Tien Giang province, especially at Cay Be village. As noted by Sang (1998) for Kien Giang, these sites share significant areas of upland that do not become inundated during normal flooding events. *R. losea* is rare in Soc Trang and Bac Lieu, and appears to be absent from Binh Thuan. The species is present in the coastal lowlands of central Vietnam and is abundant in the Red River Delta of northern Vietnam (Brown, Tuan et al., this volume). The northern and southern populations are morphologically and genetically distinct and may represent subspecies or sibling species (K. Aplin, T. Chesser and J. ten Have, unpublished).

The other *Rattus* species (*R. exulans*, *R. norvegicus* and members of the *R. rattus* complex) are nowhere particularly abundant, except perhaps *R. rattus* in Ben Tre (Table 1). However, higher abundance for this species reported by Brown et al. (1999) may reflect some confusion between this species and either *R. argentiventer* or *R. losea*. *R. norvegicus* was encountered rarely but in a variety of contexts, from small towns to rice fields at considerable distance from any town or buildings.

Bandicota species generally accounted for less than 5% of captures in areas sampled by Brown et al. (1999) and Sang (1998). From examination of the live rat-meat samples, we estimate that they are even less abundant in Soc Trang and Bac Lieu. All specimens examined to date from within the Mekong Delta proper have been referable to *B. indica*, the larger of the two species found in Vietnam.

Table 1. Relative abundance (%) of various rodent species across nine provinces in the Mekong Delta, based on live-trapping as described by Brown et al. (1999). *Rattus* species are regrouped as described in Methods.

Species	Kien Giang	Minh Hai	An Giang	Can Tho	Dong Thap	Vinh Long	Long An	Tien Giang	Ben Tre
Bandicota spp.	2.8	1.4	2.2	5.2	4.0	0.4	6.7	4.6	3.0
R. argentiventer	28.4	57.3	68.6	67.8	69.7	75.4	63.4	72.0	50.2
R. exulans	1.8	0.3	2.4	1.3	0.7	0.8	2.5	3.3	1.8
R. losea	45.9	18.7	12.8	10.5	11.0	8.9	8.9	5.3	9.8
R. norvegicus	3.4	3.8	1.2	1.5	2.3	1.2	1.3	2.7	2.5
R. rattus complex	11.9	17.5	11.2	13.6	12.3	13.3	17.2	10.5	30.9
Mus spp.	5.9	1.0	1.6	0	0	0	0	1.5	1.7

Table 2. Relative abundance (%) of various rodent species obtained through live-trapping (*) and opportunistically across six provinces, as described in Methods. Data for Kien Giang province (Hatien district) are from Sang (1998).

Species	Kien Giang*	Tien Giang* (Cay Lay)	Tien Giang* (Cay Be)	Tien Giang	Soc Trang	Bac Lieu	Ho Chi Minh City	Binh Thuan
Bandicota indica	3.5	1.1	11.3	0	1.2	17.7	7.7	41.4
B. savilei	0	0	0	0	0	0	2.6	37.0
Rattus argentiventer	37.6	75.5	51.6	79.5	95.2	77.2	23.1	19.1
R. exulans	2.8	0	0.8	1.3	0	0	2.6	0.6
R. losea	45.3	18.2	33.1	3.8	2.4	1.3	51.3	0
R. norvegicus	0.5	2.2	2.4	7.7	1.2	1.3	0	1.9
R. rattus complex	8.7	3.1	0.8	7.7	0	2.5	2.6	0
Mus caroli	–	0	0	0	0	0	10.3	0
Mus sp.	1.0	–	–	–	–	–	–	–
No. in sample	966	79	124	78	83	79	39	162

In Tien Giang, this species made up 11.3% of captures at Cai Be, but only 1.1% at Cai Lay, sampled at the same times of year. Further east, in Ho Chi Minh City province (Cu Chi district) and in Binh Thuan, both *Bandicota* species were collected in approximately equal numbers. Aplin, Frost et al. (this volume) give details of the distribution and breeding activity for both species. As with *R. losea*, the strong impression is that both *Bandicota* species favour areas where there is considerable local relief; presumably for *Bandicota* spp. this relates to the size of their burrow systems.

Mus species are poorly represented in all of the collecting undertaken so far. However, farmers do not seem to regard them as a major pest and they may be genuinely uncommon in most areas. Specimens of *Mus caroli* were dug from burrows in Cu Chi district.

These observations suggest that landscapes characterised by regular, deep inundation favour populations of the rice-field rat, *R. argentiventer*, over other rodent species. Even so, there are indications that populations of this species also decline annually and sharply over the period of inundation (Brown et al. 1999). Data presented here on rodent damage through the period 1991–2000 suggest that extreme flooding events, such as occurred over several years in the mid-1990s, may lead to a reduction of crop damage during the subsequent dry season. This might be due to flooding of elevated areas that normally function as refugia for *R. argentiventer.*

Conclusion

The general ecological and historical observations made here enable us to frame a number of specific hypotheses that now need to be tested through more detailed studies of spatial and temporal patterning in rodent communities, rodent densities and crop damage, and through well-designed manipulative experiments. These are:

- that rodent distributions and local diversity across the region are correlated with frequency and depth of floodwater inundation;
- that high local rodent diversity, maintained by areas of upland habitat, suppress the rate of population increase of the rice-field rat through competition for resources (especially nesting sites);
- that areas of regular, prolonged inundation, with associated low rodent diversity, provide an opportunity for the rice-field rat to assume dominance within the local rodent community;
- that low-frequency, high-magnitude flooding events lead to a general collapse of local rodent populations, with a slower rate of recovery than under normal conditions; and
- that areas with continuous rice cropping will support higher and less-variable rodent densities than areas where cropping is interrupted by flooding or prolonged periods of fallow.

Each of these hypotheses is testable; moreover, in each case, the outcomes would provide valuable insights into the complex relationship between landscape ecology, environmental variability, rodent community ecology and agronomy. Gaining these insights is necessary if we are to succeed in developing sustainable, non-chemical solutions for rodent control under the variable conditions offered by the Mekong Delta.

Acknowledgments

These studies were partially funded by the Government of Vietnam and by the Australian Agency for International Development (AusAID) under their Capacity-building for Agriculture and Rural Development (CARD) program. We thank Peter Brown for comments on the manuscript.

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Relationship between rodent damage and yield loss in rice in the Mekong Delta, Vietnam

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Abstract. The rice-field rat, *Rattus argentiventer*, is an important pre-harvest pest of irrigated rice in the Mekong Delta of Vietnam. This species is difficult to trap and little, therefore, is known about the association between population densities of this rat, damage to tillers, and yield loss. We examined the relationship between rodent damage to rice and yield loss at three different stages: seedling (15–20 days after sowing; DAS), tillering (35–40 DAS) and booting (55–60 DAS). Rats confined in small enclosures (3 × 3 m) within the rice crop, for 2 days or for the entire cropping season, were used to generate damage to the crop. The crop was able to compensate for rat damage at the seedling stage. At both the tillering and booting stages, damage to the crop was strongly associated with rodent density, and yield was highly negatively correlated ($r > 0.94$) with rodent damage. There was no compensation by the rice crop to rodent damage at the tillering or booting stage. The lack of compensation at 35 DAS is early compared with the few previous studies reported elsewhere in Asia and may be because a fast-growing (90 days) variety of rice was used in this study compared to slower-growing varieties (110–120 days) in previous studies. Our results raise the important question: how early during tillering do rice crops lose their capacity to compensate for damage caused by rats? This study examined also the use of sweet potato on small bamboo sticks as a simple index of rodent density. The method provided a good indicator of low population densities of rats up until the rice crop began to ripen (day 70 in a 90-day growing season). After this, the rats strongly preferred rice to sweet potato. However, this simple index was unable to distinguish between the range of rodent densities (one to six rats per 100 m^2) in this study.

Introduction

Rodents are the most important mammalian agricultural pests at the global level. Rats damage and destroy many crops pre-harvest, are a major pest for grain stored post-harvest, and are a major forest pest because of their debarking activity of broadleaved trees. Too little is known worldwide about the amount and value of damage inflicted annually by rodents (Rennison and Buckle 1987). In 2001, in Asia alone, it was estimated that just pre-harvest damage by rats removes enough rice to feed 180 million people for a year (Singleton 2001). This same study reviewed rodent impacts pre- and post-harvest in rice-dominated agro-ecosystems and concluded that they are the major single pest in these systems, typically causing annual losses pre-harvest of 5–20% (see also Geddes 1992). The significance of rodents in Asia is further emphasised by the statistics that rice provides 35–60% of the total food energy for the three billion people living in Asia and more than 90% of the world’s rice is produced and eaten in Asia (Kush 1993).

Rodents are also carriers of a variety of diseases that can infect both humans and livestock. These diseases are of great social and public-health importance. However, their socioeconomic importance has not been properly evaluated (Mills 1999).

The main pest species of rats in the south of Vietnam (Mekong Delta) are the rice-field rat (*Rattus argentiventer*), the black rat (*Rattus rattus*), the lesser rice-field rat (*Rattus losea*), the Norway rat (*Rattus norvegicus*), and the Polynesian rat (*Rattus exulans*). Minor pest species are house mice (*Mus* spp.) and the bandicoot rat (*Bandicota indica*). Since 1990, the average rice-growing area severely damaged by rats in the Mekong Delta has been around 100,000 ha per year, with loss in rice production of about 10–15% (H.V. Chien, unpublished data). However, these losses vary considerably from season to season and year to year.

This study was carried out in Tien Giang province from 2000 to 2001 in order to study the relationships between:

(a) rodent population density and damage to rice tillers;
(b) the number of tillers damaged and yield loss at three stages of rice growth (seedling, tillering and booting); and
(c) a simple index of rat activity and rat density.

Materials and methods

Study site

Two series of experiments were conducted in 2000 and 2001 at the Southern Regional Plant Protection Center, Chau Thanh district, Tien Giang province in the Mekong Delta region of southern Vietnam. Up to three irrigated rice crops are grown in this region each year. The variety of rice used in the various studies was IR 9729-67-3. The rice was directly seeded at a rate of 200 kg/ha and had a 90-day growing period. The study animals were *Rattus argentiventer* and were in a weight range of 150–200 g.

Experiment 1: the effect of damaged tillers on yield loss

This was evaluated at three stages of rice growth: seedling stage (15–20 days after sowing; DAS), tillering stage (35–40 DAS), and booting stage (55–60 DAS).

For each stage, there were three treatments and three replicates over plot sizes of 3 × 3 m and following a randomised complete block design (RCBD). The treatments were two, three and four male rats per plot, with one set of control plots (no rats). Each treatment plot ($n = 30$, 3 treatments × 3 crop stages × 3 replicates, plus 3 control plots) was fenced by plastic to a height of 1 m, with 3 m between plots. For each treatment, rats were released for two nights, and then they were caught by hand and killed.

Experiment 2: evaluation of the incidence of tiller damage during the rice cropping season

There were five treatments plus one control and three replicates of each. The study followed a randomised complete block design (RCBD). In this experiment, the plot sizes were 10 × 10 m and rats were maintained in fenced plots ($n = 15$, plus 3 controls) for the entire cropping season. The respective plots contained: 1 male rat only; 1 female rat only; 1 male and 1 female rat; 2 male and 2 female rats; 3 male and 3 female rats; and no rats in the control.

Assessment of crop damage and yield

The percentage of damaged tillers was calculated using equation (1). Yield was estimated by multiplying the weight of mature rice grains per panicle by 1000 and by the number of panicles per m^2. The actual yield was estimated by weighing rice harvested per plot at a grain moisture content of 14%.

Assessment of rat activity

Signs of rat activity were assessed at 15-day intervals. Twenty pieces of sweet potato held by bamboo sticks 50 mm above the ground were added to each plot. The percentage of pieces gnawed by rats provided an index of activity.

Statistical analysis

Least standard errors, correlation indices and linear regressions were calculated using the statistical software packages SPSS and IRRISTAT.

Results and discussion

Experiment 1

Seedling stage (15–20 DAS)

In the treatment plots, rodent damage to tillers ranged from 23–76% and yields from 4.00–4.30 t/ha. There were no significant yield differences between treatment and control plots (Table 1). Yield decrease was highest at 4% in the treatment that had four rats. However, there was no significant correlation between damage and yields (Table 2; $r = -0.414$ ns).

The association was modelled by the simple linear functional form of the equation:

$$Y = 4.0975 - 0.00048X \qquad (2)$$

Where, (Y) represents yield loss and (X) represents damage to tillers.

Therefore at the seedling stage (15–20 DAS), the rice plants compensate even when damage was as high as 76%.

Tillering stage (35–40 DAS)

In the treatment plots, rodent damage to tillers ranged from 18–47% and yields from 1.65 to 2.85 t/ha. There were significant yield differences ($P < 0.05$) between treatment and control plots (Tables 1 and 2). Yield loss was negatively correlated with rat density ($r = -0.945$). Yield loss was highest (52.9%) when there were four rats per plot (4.4 rats/m^2 or 4444 rats/ha).

The estimated linear regression between yield loss (Y) and damage to tillers (X) was:

$$Y = 3.8446 - 0.049X\text{, with } X_{\min} = 18 \text{ and } X_{\max} = 47 \qquad (3)$$

Therefore at the maximum tillering stage of the rice crop, there was no productive compensation by rice plants—damaged tillers produced new growth, but these were non-productive tillers.

End of booting stage (55–60 DAS)

On the treatment plots, rodent damage to tillers ranged from 19–33% and yields from 1.40 to 2.50 t/ha. There were significant yield differences ($P < 0.05$) between treatment and control plots (Tables 1 and 2). Yield loss was negatively correlated with rat density ($r = -0.995$).

$$\text{Damaged tillers (\%)} = \frac{\text{Total number of damaged tillers in treated plot}}{\text{Total number of tillers in the control plot}} \times 100 \qquad (1)$$

Table 1. Incidence (%) of tillers damaged by rats over two nights and actual yields at three stages of rice growth.

Number of rats	Seedling stage		Tillering stage		Booting stage	
	Incidence (%)	Yield (t/ha)	Incidence (%)	Yield (t/ha)	Incidence (%)	Yield (t/ha)
2	26	4.30	19	2.40	20	1.65
2	23	4.15	18	2.65	19	2.50
2	28	4.00	26	2.30	20	1.95
3	41	4.10	23	2.85	25	1.90
3	34	4.05	27	2.50	27	1.50
3	38	4.15	32	1.75	22	1.95
4	76	4.05	47	1.65	19	1.65
4	54	4.00	45	2.05	29	1.75
4	56	4.05	38	2.25	33	1.40
Control	00	4.20	00	4.20	00	4.20

Table 2. Actual yields and percentage of yield decrease compared with control plots. Note: numbers followed by the same letter are not significantly different at the 5% level.

Number of rats	Seedling stage		Tillering stage		Booting stage	
	Yield (t/ha)	Yield decrease (%)	Yield (t/ha)	Yield decrease (%)	Yield (t/ha)	Yield decrease (%)
2	4.15a	1.2	2.45b	41.7	2.03b	51.7
3	4.10a	2.4	2.40b	42.8	1.78b	57.6
4	4.03a	4.0	1.98b	52.9	1.60b	61.9
Control	4.20a	0.0	4.20a	00.0	4.20a	00.0

The estimated linear regression between yield loss (Y) and damaged tiller numbers (X) was:

$$Y = 4.0375 - 0.0934X, \text{ with: } X_{\min} = 19 \text{ and } X_{\max} = 33 \quad (4)$$

Therefore, at the end of the booting stage of the rice crop, there was no productive compensation by rice plants to rodent damage.

Together, these results confirm previous observations that rice crops are able to compensate for rat damage inflicted early to the crop provided the tillers are able to re-grow (Buckle et al. 1985; Singleton et al. 2002). However, these previous studies suggested that the rice crops were able to compensate, at least partially, for rat damage until the maximum tillering stage. There was no compensation demonstrated in this study at the tillering stage. We qualify this by referring to productive growth; there may have been some compensation by rice plants in the weight of seed produced from the undamaged tillers. The lack of compensation at a relatively early stage of production may be because a fast-growing (90-day) variety of rice was used in this study compared to varieties with 110 to 120-day growing seasons in the previous studies. Our results raise the important question: how early during tillering do rice crops lose their capacity to compensate for the damage caused by rats?

Experiment 2

Yields of rice per plot were highly negatively correlated with rodent density (Table 3).

The relationship between indices of rat activity based on the percentage of pieces of sweet potato gnawed and known rodent density was not the same for all stages of the rice crop. There were consistent differences at all stages between one rat present and two to six rats present. However, only at 30 DAS was there a significant positive association with rodent density (Table 3).

Overall, indices of rat activity from 30–60 DAS were high, and then rapidly decreased once the crop was at the ripening stage. These results were not influenced by different growth rates of the rat populations within each plot because the average recruitment per plot was 6.7, 5.3 and 4.7 rats for 1, 2 and 3 pairs of rats, respectively, and the young were pre-weanlings. An expected result was a decrease in yield with rat density (Table 3). The finding that sweet potato is a good indicator of low densities of the rice-field rat up to the ripening stage of the rice crop is important because this species of rat is difficult to trap (Leung et al. 1999). However, this simple index was unable to distinguish consistently between the known rodent densities. Further studies across a wider range of population densities are warranted.

Table 3. Signs of rat activity (% sweet potato eaten) during the cropping season and actual yields in each of the plots (DAS = days after sowing, CV = coefficient of variation). Note: numbers followed by the same letter are not significantly different at the 5% level.

Treatment	30 DAS (%)	45 DAS (%)	60 DAS (%)	75 DAS (%)	85 DAS (%)	Yield (t/ha)
1 male	11.67a	30.00ab	53.33b	33.33b	11.67ab	3.87b
1 female	15.00ab	31.67ab	50.00b	40.00b	10.00ab	4.00b
1 pair	35.00bc	48.33b	66.67bc	45.00b	16.67ab	2.80c
2 pairs	45.00cd	68.33b	76.67bc	68.33c	23.33b	2.10d
3 pairs	58.33d	71.67b	81.67c	73.33c	21.67b	1.53d
Control	00.00a	00.00a	00.00a	00.00a	00.00a	4.87a
CV (%)	42.60	57.70	25.10	27.70	72.90	10.70

Conclusions

In short-maturing irrigated rice crops in Tien Giang province, damage by rats was compensated for at the seedling stage, but not at the tillering and booting stages. There was strong compensatory growth by rice plants when damage occurred during tillering, but this growth did not result in productive seed. There was a strong association between damage to tillers and reduction in crop yield.

Sweet potato was a good indicator of rodent activity up to the ripening stage of the crop. Thereafter, the rats preferred the rice to the sweet potato.

Acknowledgments

This study was partially funded by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) from a grant provided by the Australian Agency for International Development (AusAID) under their program for Capacity-building for Agriculture and Rural Development.

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The rodent density–damage function in maize fields at an early growth stage

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Abstract. The relationship between the population density of *Mastomys natalensis* and percentage crop damage at planting of maize was determined in experimental maize fields in Morogoro, Tanzania. The experimental design was completely randomised with 21 plots of size 70 × 70 m. We determined rodent density using the capture–mark–release (CMR) technique in each of the plots. The best model for the data was determined using Akaike information criterion values in order to establish the relationship between rodent density and rodent damage. The relationship between rodent density and rodent damage is sigmoidal ($r^2 = 0.55$, $n = 44$, $p = 0.001$).

Introduction

The problem of rodent damage in agriculture is complex because almost any crop can be the target of rodent attack (Taylor 1972; Fiedler 1988). Dramatic rodent outbreaks have been reported in many countries where intensive and extensive cultivation of agricultural crops is undertaken (Singleton and Redhead 1990). Such outbreaks, particularly in cereals such as rice, maize, wheat and barley, have caused serious losses and widespread food shortages (Walker 1990). Damage ranges from negligible destruction to total crop loss. For example, regional reports from Lindi in Tanzania showed that yield loss due to rodents was 85,108 tonnes (i.e. 71,236 for cereal and 13,872 for pulse crops) in 1989/90 (Mwanjabe et al. 2002). These losses could feed 290,669 people in Lindi (i.e. 700 g/person/day for cereals and 100 g/person/day for pulses).

For decisions to be made about rodent control in any cropping system, the density of rodents must be estimated. However, little is known about rodent density–crop loss relationship functions. It has been reported that there is a positive correlation and linear relationship between rodent density, damage, and yield loss in fields of rice at maturity in Southeast Asia (Walker 1987, 1990). While it is theoretically and widely assumed that there is a positive linear relation between the number of rodents and damage, in practice this may not be so, since the damage curve always reaches a necessary asymptote of 100%.

The current study was carried out to determine and describe the rodent density–crop loss functions in maize fields in Morogoro, Tanzania. Here we present the data about damage occurring just after maize seeds have been planted.

Materials and methods

Location of experimental fields

Field experiments were carried out in two locations at Sokoine University of Agriculture, Morogoro, Tanzania. The first location is 510 m above sea level (asl), 6°50'S, 37°38'E, within the university farm. The second location (Solomon Mahlangu Campus) is 480 m asl, 6°46'S, 37°37'E. The area has a bimodal rainfall patterns with a ‘short rain season’ in October–December and a ‘long rain season’ from March–June. The study was conducted during the long rain seasons in 1999, 2000 and 2001. The exact timing of the field observations depended on the date of sowing, which was in turn dependent on the timing of rainfall.

Density of rodents and agronomic practice

Twenty-one maize fields, each 70 × 70 m, were used in the study. The size of the plots corresponds to the field size in smallholder farms in Tanzania. The plots were located a minimum of 80 m apart or, in four cases, were fenced. The plots were experimental fields of other ongoing studies with different treatments manipulating the level of predation, dispersal, land management or cropping system. Details of those experiments are less relevant here, but the important point is that through these treatments we could make observations in fields with a considerable range of rodent densities. The rodent population size in each field was estimated with closed-model capture–mark–recapture estimates (estimator Mh in CAPTURE; White et al. 1982) based on sessions of three consecutive trapping nights with 49 Sherman live-traps at fixed trapping points in a square trapping grid with 10 × 10 m mesh size in each plot. We estimated population size before ploughing and after planting and used the average of both estimates as a measure of rodent density at planting in each field.

All fields received similar standard agronomic treatments, i.e. early ploughing, application of triple superphosphate (TSP) fertiliser (20 kg P_2O_5/ha) before planting, and nitrogen fertilisers (40 kg N/ha) twice as a top dressing three weeks after sowing and booting stages. Three maize seeds (variety Staha) were planted per hole, with a planting spacing of 90 cm × 60 cm. Weeding was carried out twice.

Assessment of crop damage

Crop damage assessment was carried out at the seedling stage, 10 days after planting. We used a non-stratified systematic row-sampling technique, described by Mwanjabe and Leirs (1997), where sampling units were maize rows, four rows apart, leaving out the two outer rows. The assessor walked along maize rows across the plot, counting seedlings at each hole. Since three seeds had been planted per hole, we calculated the difference between observed and expected number of seedlings, and expressed the difference as a percentage damaged.

Relationships between rodent density and rodent damage

In order to find out which model represented the relationship best, first the data points were presented in a scatter plot, and we identified different biologically meaningful function types (Harshbarger and Reynolds 2000). Computer software (Sigmaplot, Excel, and Table curve 2D) was used for curve fitting. We calculated Akaike's information criterion (AIC) values for those models and compared (Akaike 1973). Therefore, the model with the lowest AIC (and thus lowest parsimony) was chosen to be the best model for the relationship.

Results and discussion

Twelve models were tested for the relationship between rodent density and damage and AIC values compared (Table 1). The relationship was best described by a sigmoidal function with three parameters ($r^2 = 0.55$, $n = 44$, $p = 0.001$) (Figure 1). The function has an intercept of about 14%, which corresponds to a realistic background germination failure rate. It is obvious from the curve of the best model that even at a low level of rodent density, there is considerable damage and the rodent damage increases with increasing rodent density from the beginning. However, rodent damage reaches an asymptotic level (constant level of damage) at high rodent density (>40 animals per plot, which is equivalent to 80 animals/ha). Interestingly, a simple linear regression is almost equally good as a best model.

There is considerable variation around the curve, indicating that effects other than rodent density, e.g. rainfall, should be included in future multivariate analysis. In terms of rodent management, therefore, the results show that if populations are high, there is little point in controlling rodents unless densities can be reduced to fewer than 20 animals/ha.

Table 1. Relationship between rodent density and percentage damage at the seedling stage using Akaike's information criterion (AIC) values obtained from best fitting models.

No.	Model and its coefficients	AIC
(1)	Sigmoidal, sigmoid with three parameters	238.84
(2)	Linear regression with two parameters	240.32
(3)	Logarithm first order	240.59
(4)	Hyperbola with two parameters	240.68
(5)	Sigmoidal, logistic with three parameters	241.89
(6)	Sigmoidal, sigmoid with four parameters	241.93
(7)	Exponential rise to maximum with three parameters	242.63
(8)	Sigmoidal, logistic with four parameters	243.38
(9)	Hyperbola with three parameters	244.32
(10)	Logarithm second order	244.90
(11)	Power with three parameters	244.96
(12)	Logarithm third order	247.33

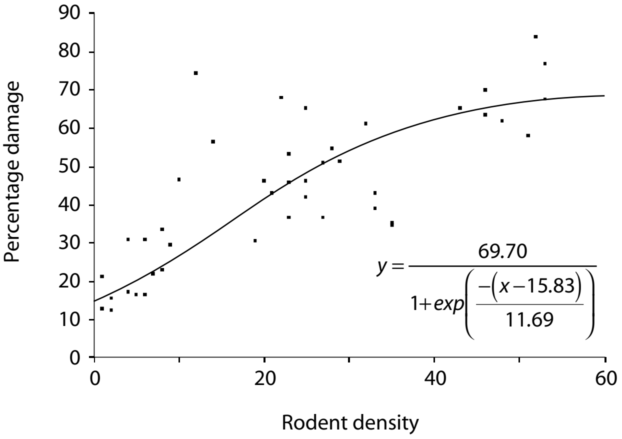

Figure 1. Relationship between the density of *Mastomys natalensis* per hectare and the percentage of damage at sowing of maize crops in Tanzania. A sigmoidal curve best described these data and accounted for 55% of the variation.

The relationship between rodent damage at planting and the actual effect on the final yield needs to be investigated further. Although compensation could occur after rodent damage, it has been reported to be minimal in maize (Myllymäki 1987). On the other hand, at low rodent damage levels, farmers may actually thin the seedlings to two seedlings per planting hole to reduce competition between plants. It is also important to note that different causes of crop loss interact and the yield response is usually variable at a given location and time (Walker 1990) due to environmental factors, e.g. rainfall. Further analysis is currently in progress.

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Commercial use of rats and the use of barn owls in rat management

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Abstract. More than 50 years experience in rat population control throughout Indonesia has not succeeded in overcoming the numerous problems associated with rats. Today, rats remain a major pest, with economic loses estimated at US$25 million per year. The intention of this paper is to offer new technologies for the utilisation of rats and provide a new paradigm for rat management.

Impacts of rodent pests and traditional methods of control

There are at least six species of rodents that cause significant losses to agricultural production in Indonesia: *Rattus argentiventer*, *R. diardi*, *R. exulans*, *R. tiomanicus*, *R. norvegicus* and *Bandicota indica* (Kalshoven 1981). Farming communities of the past and present have attempted various mechanical, chemical and biological methods to decrease these rat populations. Farmers recognise the role of snakes, predatory mammals, and predatory birds in limiting rodent populations, but predators are becoming fewer. Formerly, rats served an important role in traditional medicine and it is estimated that when this practice ceased, economic losses by rats increased.

Mechanical and chemical control methods are conducted year after year to eliminate rats. In Java, in 1961, there were major outbreaks of rodent populations in some localities, leading students of the Faculty of Agriculture, Gadjah Mada University, to develop an extension program for rat control in Bojonegoro subdistrict, Central Java. They modified a midget duster into a fumigator. This simple fumigator, '*Emposan Gama*', burned rice straw and sulfur granules, producing smoke containing CO_2 and SO_2 that was forced into rat burrows. Rats inside the burrows suffocated. This simple technology has been widely adopted in Java. Another simple technology, developed in the 1990s, is the trap–barrier system (TBS) which, together with ecologically based rodent management, is effective in decreasing damage to rice crops and in increasing yields (Singleton et al. 1998).

Despite these efforts and promising progress in reducing impacts, rats remain the most important agricultural pest in Indonesia. In a national panel discussion on rats in Jatisari, West Java, in May 2001, it was reported that total losses due to rice-field rats, *R. argentiventer*, reached US$22.5 million per year. Other commodities that suffer significant rodent damage, mainly caused by *R. tiomanicus*, are cocoa, coconut and oil palm (Sipayung et al. 1990). House rats (*R. exulans*, *R. norvegicus*, *R. rattus*) and bandicoot rats (*B. indica*) cause serious problems in traditional markets, grain stores and around houses. At this meeting, it was estimated that total annual losses due to rats to agricultural produce in Indonesia was >US$50 million.

Discussion

Integrated management

The concept of integrated pest management (IPM) was introduced to Indonesia in 1983 to promote the control of brown planthoppers in rice crops. The impact of IPM was impressive, with the use of insecticides reduced from 17,300 t in 1986 to about 3000 t in 1989.

The government of Indonesia now encourages the use of ecologically based management for the control of rodents (Research Institute for Rice 1998). However, in Central Java, 94% of trained farmers would only implement IPM to manage rodents if the government provided subsidies, particularly for chemical rodenticides (Eddy Mahrub et al. 1995).

In contrast to farmers in other regions of Southeast Asia (see Nguyen Tri Khiem et al., this volume), farmers in West Java usually do not use rats commercially. Such use of rats may be an advantage when implementing ecologically based rodent management because the additional benefit from selling rat products makes it more likely to achieve positive benefit–cost ratios. Rat skins could be used as materials for various handicrafts, while the rat body could be processed for animal feeds. In Java in 2001, we conducted a training course dedicated to commercial use of rats by farmers (20 participants from 6 provinces).

How can the attitudes of farmers regarding rats be changed from disgust to the perception of potential economic benefits? In the past, local governments paid bounties for dead rats turned in by farmers of about rupiah (Rp)200 to Rp1,000 per individual. In 2001, the Sleman subdistrict government spent Rp22,500,000 on rat bounties. Also in 2001, the General Chairman of the Indonesian Society of Farmer Groups, who attended a special discussion with farmers about rat control, estimated that it might be possible to sell animal feed produced from rat bodies for Rp10,000 per kg. This encouraged some farmers to set up home businesses producing rat pellets or rat meal as animal feed for chickens, dogs and fish. In the future, rat meat could be produced for food for human consumption. This is already practised in Central Java and North Sulawesi, but religious and personal beliefs must be overcome.

In addition, rat skins may be used for making wallets, bags or clothing. These handicrafts are marketable, either for domestic or foreign consumers. Farmers can collect and preserve rat skins in salt for 3–4 months, but specialists should do tanning to minimise the risk of environmental pollution by chemicals used in the tanning process.

Predators of rats

The promotion of predators may be another way to increase the effectiveness of ecologically based rodent management. The barn owl, *Tyto alba*, is a night active predator of rats and may prove useful for controlling rodent populations. Barn owls breed naturally in oil palm plantations (Sipayung et al. 1990; Heru et al. 2000). Artificial breeding has been successful in Java and we have established a breeding colony in a cocoa plantation in North Segayung, Batang, Central Java which has been maintained for 5 years. More than 60 progeny were produced from one of the nest boxes (S. Mangoendihardjo, unpublished data). The owls have been observed to spread about 8 km from the breeding site.

Conclusion

We suggest the utilisation of rats in assisting ecologically based rodent management to control rats in West Java. However, it is important to change the attitude of people towards the use of rats. The establishment of breeding barn owls in agricultural land in West Java is promising for their potential use in rat control. Rats should be considered as animals having economic value and the barn owl should be protected.

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The efficacy of a trap–barrier system for protecting rice nurseries from rats in West Java, Indonesia

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Abstract. The rice-field rat, *Rattus argentiventer*, causes substantial damage to freshly sown rice nurseries in West Java, Indonesia. Rice nurseries surrounded by a plastic barrier with multiple-capture rat traps (trap–barrier system; TBS), or a barrier system (BS) consisting of plastic and no traps, were compared for their effectiveness to reduce rodent impacts against untreated nurseries that did not have a barrier to rats. There were 10 replicates of each treatment and the study was conducted for one wet and one dry season. The study clearly demonstrated the substantial impact of rats on unprotected rice nurseries for the two major crops in West Java—the dry and wet season rice crops. Both the TBS and BS provided significant protection to rice nurseries. There was no rat damage in nurseries protected by a TBS in either season. In the 1996 dry season, nurseries surrounded by a BS had 7% (±2.0 se) of seedlings damaged, whilst those with no barrier had 88% (±8.1) of seedlings damaged. In the 1996/97 wet season, nurseries surrounded by a BS had 14% (±3.1) of seedlings damaged, whilst those with no barrier had 97% (±2.1) of seedlings damaged. The mean number of rats caught per day per trap in a TBS led to the recommendation of four traps per nursery in the dry season but only two in the wet season. Whether farmers opt to use a TBS or BS will depend on the weight they give to having approximately 10% of their seedlings damaged by rats versus the expense of purchasing four live-capture rat traps.

Introduction

The rice-field rat, *Rattus argentiventer*, is the most important pre-harvest pest of rice crops in West Java (Geddes 1992; Singleton and Petch 1994). These rats can damage rice tillers from transplanting to just before harvest (Singleton et al. 1998). Rats also cause significant damage to seedlings in rice nurseries before they are transplanted. In West Java, the most common method of rodent control in the rice nurseries is a physical barrier made from plastic sheeting. These barriers are erected to deflect rats from the nurseries. However, the nurseries are planted during land preparation, when food is limiting for rat populations. Therefore, these rice nurseries are prone to rat damage. When rat densities are high, farmers often have to replant their seedbeds. If a farmer has to replant then his crop will be transplanted late. This in turn can lead to high damage before harvest if rats aggregate at the late-planted crops (Jacob, Nolte et al., this volume).

The addition of multi-capture live-traps to a plastic fence (trap–barrier system) has proven a successful method of managing rodent impacts to crops after the rice has been transplanted (Singleton et al. 1998, 2002). This study examines the efficacy and benefit–cost of a trap–barrier system for controlling losses by rats to seed nurseries in a region where rice is the dominant crop. The replicated study was conducted over the two main rice-cropping seasons in West Java.

Materials and methods

The study was conducted in rice paddies of farmers near Sukamandi, West Java (6°20'S, 107°39'E) during the 1996 dry season (19 April to 12 May) and the 1996/97 wet season (13 October to 2 November 1996). In this region, the rice is sown in a small nursery 3 weeks before being transplanted into the rice paddies. There were two treatments and a control: a trap–barrier system (TBS), a barrier system without traps (BS), and no fence (control). Each had 10 replicates, separated by a minimum of 200 m. Each rice nursery was approximately 10 m × 15 m. The BS consisted of a plastic fence. The TBS consisted of a plastic fence and one multiple-capture trap made of wire mesh ($600 \times 240 \times 240$ mm) placed along each side of the fence. Each trap was located within the TBS, with its opening flush with a hole in the fence. The traps were checked in the morning of each day and all rats were removed. The number of rats caught over a period of 20 days was recorded. The fences were inspected each morning and any holes found in the fences were patched immediately to maintain the fence in good condition.

Cost of TBS and BS

The cost for materials and labour (2002 prices) to build the barriers were as follows: 50 m of new plastic, US$2.25; bamboo sticks, string and staples, US$1.9; installation, US$1.5. The four traps cost US$14. Therefore, a BS cost US$5.65 and a TBS US$19.65.

Assessment of rat damage to seedlings

Rodent damage to rice tillers is distinctive. Rats cause a clean cut near the base of the seedling at approximately a 45° angle. The percentage of damaged seedlings was assessed visually at 10 and 20 days after the rice seeds were planted. Two people independently assessed the level of rat damage and a mean of the two estimates was used.

Statistical analyses

Sex differences in the number of rats caught per season were analysed using a one-way analysis of variance. The data on tillers damaged were analysed using a repeated measures analysis of variance. Standard errors of the mean are given in brackets.

Results and discussion

1996 dry season

More males (64%) than females were caught in the TBS ($F_{1,18} = 6.84$, $P = 0.002$; Table 1). The reason for this is unclear. Perhaps male rats were more trappable following a short fallow and high disturbance of the cropping landscape during land preparation, or perhaps they simply move more and are therefore more likely to come in contact with nurseries protected by a TBS.

Despite daily observation and maintenance of the plastic fencing, rats gained access to the nurseries and they caused damage to the seedlings in the BS treatment.

There was a significant treatment effect ($F_{2,27} = 89.98$, $P < 0.001$). There was no rat damage in the nurseries protected by a TBS. In the nurseries protected by a BS, the mean percentage of seedlings damaged by rats was 7% (±2.0) after 20 days. Severe rat damage was observed in the unprotected plots; the mean percentage of seedlings damaged by rats was 88% (±8.1) after 20 days (Figure 1). There was no significant difference in damage to seedlings 10 and 20 days old ($F_{1,27} = 2.67$, $P = 0.065$).

1996/97 wet season

There was no difference in the number of males and females caught in the TBS ($F_{1,18} = 0.02$, $P = 0.902$; Table 1).

Again, there was rat damage to the seedlings in the BS treatment despite the fences being maintained as a ‘barrier’ with no holes during the 20 days.

There was a significant treatment effect ($F_{2,27} = 251.0$, $P < 0.001$). There was no rat damage in the nurseries protected by a TBS. There was a significant difference in damage to seedlings after 10 and 20 days ($F_{1,27} = 25.68$, $P < 0.001$) (Figure 1). This suggests that perhaps rice seedlings less than 10 days old are more attractive to rats than those 11–20 days old. In the nurseries protected by a BS, the mean percentage of seedlings damaged by rats was 14% (±3.1) after 20 days. Severe rat damage was observed in the unprotected plots; the mean percentage of seedlings damaged by rats was 97% (±2.1) after 20 days (Figure 1).

Economics and efficacy of the different treatments

The major cost was the purchase of new live-capture traps. The time to process rats caught by the TBS was minimal compared to the average of 10 h (1.3 days of labour) over the 20 days to check and maintain the TBS or the BS. The daily labour cost is approximately rupiah (Rp)15,000, so it only cost Rp20,000 (≈US$2) to maintain the respective fences over the 3 weeks.

In West Java, seed nurseries clearly need to be protected from the severe impact of rats. Where there was no barrier erected to protect the nurseries, farmers had to replant new seed in each season when high losses were suffered. A TBS or BS provided substantial reductions in rodent damage. In determining whether to use a TBS or a BS to protect the rice nursery, farmers need to weigh the extra cost of new traps against losses of about 7 to 14 % of their seedlings. Recommendations on the number of traps per TBS are based on the number of rats caught per day per trap. In the dry season there were mean captures of up to 12 rats per trap, whereas in the wet season the mean was usually ±4 rats per trap. Therefore, the recommendation is to use four traps per TBS in the dry season and only two in the wet season for a 10 m × 20 m nursery. An added consideration for determining whether to adopt a TBS rather than a BS is that once farmers have purchased the traps they can be used for many seasons.

Table 1. Rats captured over 20 days in the trap–barrier system protecting rice nurseries of farmers near Sukamandi in the 1996 dry season and the 1996/97 wet season.

Season	Number of rats caught per replicate										
	Sex	1	2	3	4	5	6	7	8	9	10	Total
Dry	Male	33	14	15	15	13	13	33	22	24	7	189
	Female	17	12	5	10	14	4	8	17	14	5	106
Wet	Male	6	3	9	3	3	12	6	9	2	2	55
	Female	4	8	5	3	5	7	10	8	1	4	55

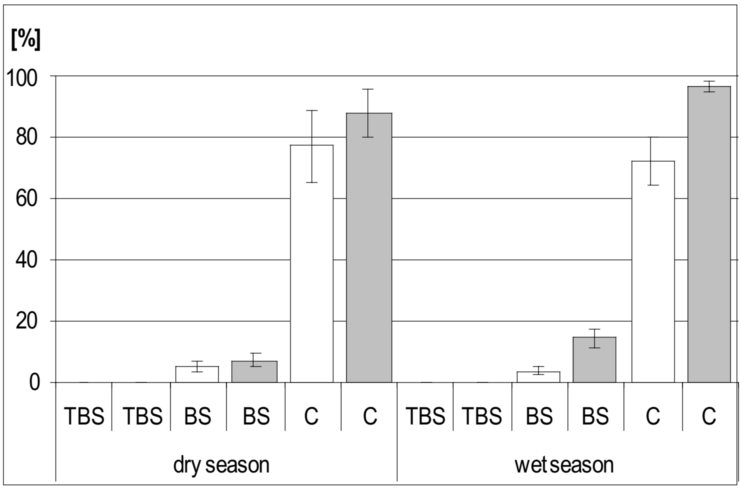

Figure 1. Rat damage (± 1 se) to rice seedlings in nurseries for three different treatments during the dry season 1996 and wet season 1996/97; damage at day 10 (unshaded), damage at day 20 (shaded). TBS = trap–barrier system, BS = barrier system, C = control with no barrier.

During the wet season one-third fewer rats were caught compared with the catch during the dry season, but rat damage was higher in the wet season. There are two likely explanations for these results. First, rats are more nutritionally stressed after the 3 months fallow at the end of the dry season (there is only a 1 to 1.5 month fallow at the end of the wet season) and therefore may be more active in their search for food. Second, rats, particularly male rats, may be more trappable during the beginning of the dry season. This could be related to there being a predominance of younger cohorts at the end of the wet season. More studies are required to distinguish between these two possibilities.

Conclusion

Rats cause substantial damage to both rice nurseries and to rice crops after they have been transplanted. A TBS that contains a rice crop transplanted three weeks earlier than the surrounding crops is effective in reducing crop losses caused by rats once the rice crop has been transplanted (Singleton et al. 1998, 2002). This is the first study to examine the efficacy for using a TBS or a BS for protecting rice nurseries against rats.

This study clearly documented the substantial impact of rats on unprotected rice nurseries for the two major crops in West Java—the dry and wet season rice crops. Both the TBS and BS provided significant protection to these nurseries. Whether farmers opt to use a TBS or a BS will depend on the weight they give to having approximately 10% of their seedlings damaged by rats versus the expense of purchasing two to four live-capture rat traps.

Acknowledgments

We thank Jumanta, Tedi Purnawan and Elon Rasdan for their expert technical assistance with this study. The project was supported by funds from the Australian Centre for International Agricultural Research (AS1/94/20).

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SYMPOSIUM 5: POPULATION ECOLOGY AND MODELLING

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Outbreaks of rodents in agricultural systems: pest control problems or symptoms of dysfunctional ecosystems?

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Abstract. House mice in Australia and Brandt's voles in China are used to illustrate the factors that lead to episodic rodent management problems in agricultural systems. Outbreaks can develop rapidly in both species, depending on the population density at the onset of breeding, the rate of increase over the breeding season, and the duration of the breeding season. The available data suggest that these demographic parameters are determined by independent processes, which means that knowledge of all three is required to predict outbreaks reliably. As well as dealing with uncertainty in predicting outbreaks, management of both species could be improved by identifying and enhancing natural regulatory processes like predation and minimising agricultural practices that tend to increase the likelihood of outbreaks.

Introduction

Rodents are pests in agricultural systems in many parts of the world. They can have high intrinsic rates of increase so that severe agricultural impacts occur over time scales similar to the production of crops or management of livestock in both temperate and tropical environments. A recent review highlighted the problems with eruptive species on several continents (N.C. Stenseth et al., unpublished). In these cases, the difficulty of managing a pest species is compounded by uncertainty in when to apply controls.

In this paper we explore two questions relating to eruptive rodent species in agricultural systems. Firstly, why do outbreaks occur irregularly? Secondly, to what extent is the likelihood of an outbreak increased by the special characteristics of agricultural systems? House mice (*Mus domesticus*) in Australia and Brandt's vole (*Microtus brandti*) in Inner Mongolia are used as case studies to illustrate some of the features of eruptive pest rodent species. Under favourable conditions, populations of both species can increase from low abundance to exceed damage thresholds within one breeding season. Both species decline rapidly from high population densities, and then persist at relatively low abundance for extended periods. In some areas, the period of low abundance can continue even though environmental conditions appear to be suitable for supporting much larger populations.

House mouse

Outbreaks of house mice occur irregularly throughout the cereal production areas of eastern and southern Australia (Saunders and Giles 1977; Mutze 1989; Singleton and Redhead 1989). For example, there were at least 12 outbreaks in Victoria between 1905 and 1997, with an apparent increase in frequency over the last two decades (Singleton and Brown 1999). Outbreaks cause high economic losses to grain-growers, major social problems, and environmental problems through extensive use of chemicals. They are usually associated with years of above-average crop production, which in turn is linked to winter–spring rainfall (Pech et al. 1999). However, outbreaks do not occur in all years, or in all areas, with apparently suitable climatic conditions.

Brandt's vole

Brandt's vole is endemic to the grasslands of central Inner Mongolia, eastern Mongolia and adjacent parts of Russia. It is considered a pest species because it competes with livestock, contributes to soil disturbance (and hence desertification) through burrowing activities and, particularly during outbreaks, is a reservoir for zoonoses such as bubonic plague. Zhang et al. (2002) compiled a history of outbreaks of Brandt's voles in Inner Mongolia over the last 50 years based on reports in the scientific literature, detailed demographic data from several sites and reports of bubonic plague spilling over into the human population. Approximately 15 outbreaks occurred during this period, though some appeared to be relatively localised. Problems with Brandt's voles and with desertification have become more severe in recent decades, leading to an increased requirement to manage the problem.

Ontogeny of an outbreak

The rapid increase in abundance of rodents from low numbers to an outbreak depends on three factors: (1) the population density at the start of the breeding season, N_B, (2) the rate of increase over the breeding season, and (3) the duration of the breeding season, T_B. For simplicity, it is assumed that the population increase during the breeding season can be characterised by a single exponential rate, r_B.

House mouse

N_B depends on the population density during the previous breeding season and the rate of decline over the non-breeding season. For house mice, there is a significant negative correlation between these two parameters (Davis et al., this volume). Both parameters are unaffected by the winter-to-spring rainfall immediately preceding an outbreak that explains most of the variation in r_B, with the result that there is no significant correlation between r_B and N_B (Davis et al., this volume; N.C. Stenseth et al., unpublished). This is consistent with the more general model for the rate of increase developed by Pech et al. (1999), which included a small, density-dependent component that had an effect only at very high densities (i.e. the density late in the breeding season). Singleton et al. (2001) used data on the breeding status of mice at Walpeup in north-western Victoria to calculate T_B for each year between 1982 and 2000. The relationship between T_B and N_B is weakly negative (R^2 = 0.265, Figure 1a) due mainly to the value for one year (1993–94). Deleting this year, R^2 = 0.042. There is no correlation between r_B and T_B (Figure 1b).

Brandt's vole

Fewer data are available to assess all three factors for Brandt's vole. Shi et al. (2002) and Zhang et al. (2002) reported a negative correlation between the rate of increase in the non-breeding season and the population density at the end of the previous breeding season. These two parameters determine N_B, which is highly variable. r_B is not affected by population density but there is a convex upwards relationship between r_B and pasture conditions, reflecting the preference of Brandt's voles for short grass habitat (Zhang et al. 2002). However, populations have low, sometimes negative, values of r_B when grass is very short (< 50 mm) and sparse (< 40% cover), probably due to a shortage of food, and in tall, dense grass (>200 mm, >70% cover), which is thought to interfere with social interactions and with the ability of voles to detect predators (Zhong et al. 1999). Plant biomass during the breeding season is determined by precipitation over the preceding winter (Zhang et al. 2002) and grazing by livestock (Zhong et al. 1999). Hence, there is no significant correlation between N_B and r_B (Zhang et al. 2002). Breeding data from 3 years at a site central to the distribution of Brandt's vole in Inner Mongolia indicate relatively minor variation in T_B (Shi et al. 2002). Early spring rain and flooding of burrows can result in low survival rates of unweaned voles, delaying the effective start to recruitment. However, the frequency of these impacts on vole demography has not been reported so that it is possible that T_B for Brandt's voles may be relatively invariant. In this case, there is unlikely to be any significant correlation between T_B and r_B or between T_B and N_B.

The characteristics of N_B, r_B and T_B for house mice and Brandt's voles are summarised in Table 1.

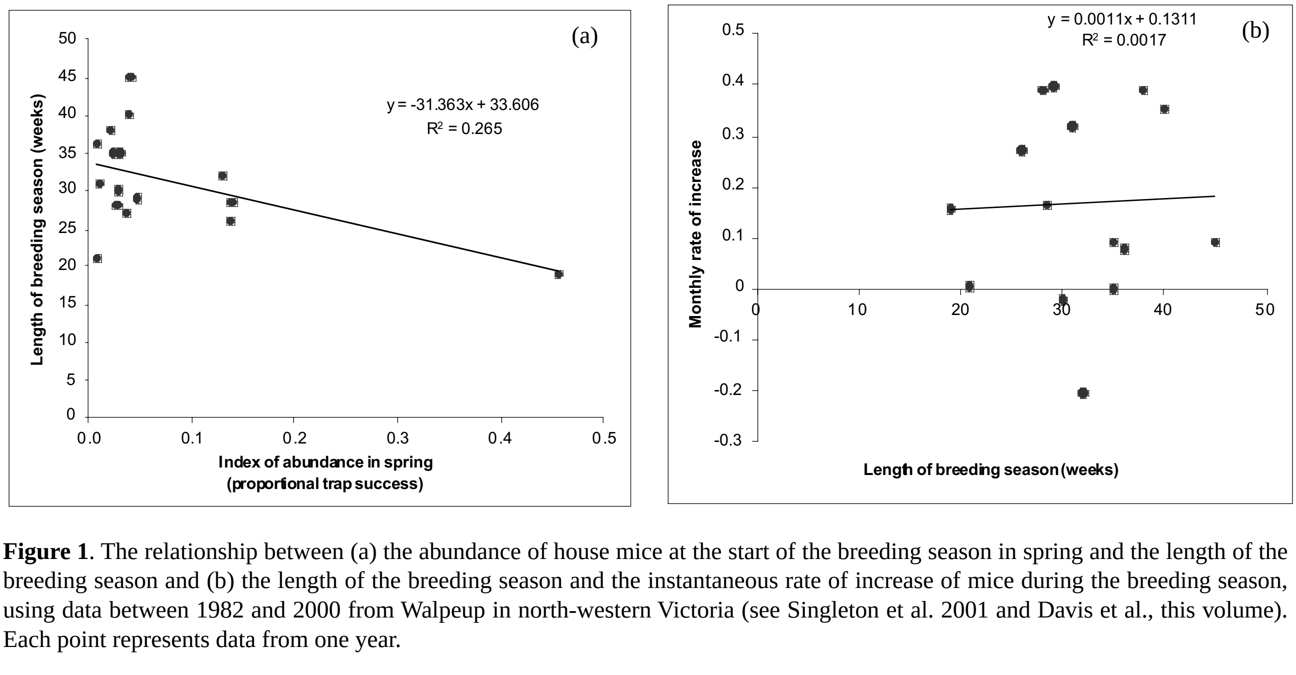

Figure 1. The relationship between (a) the abundance of house mice at the start of the breeding season in spring and the length of the breeding season and (b) the length of the breeding season and the instantaneous rate of increase of mice during the breeding season, using data between 1982 and 2000 from Walpeup in north-western Victoria (see Singleton et al. 2001 and Davis et al., this volume). Each point represents data from one year.

Table 1. Summary of the characteristics of three key demographic parameters that determine the rapid development of outbreaks of house mice and Brandt's voles. N_B is the population density at the start of the breeding season, r_B is the rate of increase over the breeding season, and T_B is the duration of the breeding season (see text for details).

Demographic parameter	House mouse	Brandt's vole
N_B	density-dependent decline from the end of the previous breeding season in both species	
r_B	positive linear relationship with winter-to-spring rainfall	convex upwards relationship with grass height and cover during the breeding season
T_B	highly variable	limited data: probably consistent duration

Discussion

Timing of outbreaks

All three factors, N_B, r_B and T_B, are important in determining the change in population size over the course of the breeding season, as is the subsequent decline in population density to set the initial conditions for the start of the next breeding season. For very low starting densities, there may be insufficient time during the breeding season for the population to reach economically damaging thresholds, even with high rates of increase. Also, high rates of increase may not generate large populations if the breeding season is short. Therefore an outbreak is more likely to occur if a rodent population begins with a relatively high spring density and has a high rate of increase over an extended breeding season. However, outbreaks of house mice occurred in north-western Victoria in two years (1988–89 and 1994–95) with high spring densities but only average rates of increase (Davis et al., this volume), which suggests that an outbreak depends on the joint probability of high values for at least two of the three factors.

For house mice and Brandt's vole, two of the key factors leading to outbreaks, N_B and r_B, are influenced by climatic conditions one year apart, so that between-year variability in the climate will contribute to the erratic occurrence of outbreaks. The third factor, T_B, may be reasonably consistent for Brandt's vole due to the highly seasonal climate in Inner Mongolia, but r_B can be affected by variations in the level of grazing by livestock that are likely to be influenced independently by socioeconomic factors. T_B is the least well understood of the three factors for house mice. The onset of breeding for mice may be determined by access to high-quality food (see, for example, Bomford 1987a,b) which in turn depends on climatic conditions in late winter and early spring. Interspecific competition is unlikely to be important because, over a 20-year period in north-western Victoria, more than 100,000 house mice were caught but only one other small mammal, a carnivorous marsupial mouse, *Sminthopsis murina* (G. Singleton, unpublished data). Ylönen et al. (2002) have demonstrated that the behaviour of mice in areas with different plant cover is consistent with a response to changes in the risk of predation. This risk avoidance behaviour can delay body growth rates and breeding in mice (Arthur and Pech, this volume). However, there is little information about the relative importance of factors, such as disease, predation or lack of food due to intraspecific competition or farm management (e.g. time of harvest or grazing by livestock) or stochastic rainfall events, that could influence when breeding starts and finishes.

For both house mice and Brandt's vole, the lack of significant correlations between N_B, r_B and T_B, implies that they are likely to be determined by unrelated processes. The result is that outbreaks are difficult to predict without knowledge of all three factors. Since 1999, the model developed by Pech et al. (1999) has been used to successfully forecast the probability of an outbreak of house mice at one locality in north-eastern Victoria (Pech et al. 2001). The model uses the cumulative winter rainfall from April to October to predict changes in the rate of increase of the next 6 to 9 months but the accuracy of predictions is greatly improved by field estimates of N_B. Also, the model implicitly assumes that T_B is constant, which leads to error in estimating the magnitude of an outbreak (Pech et al. 2001). A logistic model using winter and spring rainfall to predict the occurrence of outbreaks, rather than detailed changes in the abundance of mice, has had limited success for Walpeup in north-western Victoria (N.C. Stenseth et al., unpublished) and for the mallee region of Victoria and South Australia (Kenney et al., this volume), particularly because it predicts more outbreaks than occur. Similar results have been achieved for predicting outbreaks of Brandt's vole (N.C. Stenseth et al., unpublished). The conclusion is that predictions of outbreaks of house mice and Brandt's vole that are based on a single explanatory variable, such as precipitation, will have a high level of error, requiring farmers to take this uncertainty into account when choosing a management strategy (N.C. Stenseth et al., unpublished).

Links between agricultural systems and the causes of outbreaks

For both house mice and Brandt's voles, there are two components that set the initial density, N_B: the density at the end of the previous breeding season and the rate of decline of the population during the non-breeding season. The former component is determined primarily by climatic conditions at least a year before an outbreak occurs. Brandt's voles cache food for winter (Zhong et al. 1999) and competition for this resource may cause the density-dependence in over-winter survival (Zhang et al. 2002). Therefore, grazing by livestock, which can lead to changes in pasture composition and biomass, may modify the strength of the density-dependence. For house mice, Arthur and Pech (this volume) found that the survival rate declined with increasing density when they were exposed to predation by foxes (*Vulpes vulpes*), feral cats (*Felis catus*) and raptors, in short grass habitat. This impact would be enhanced by prophylactic measures such as the control of weeds along fence lines recommended by Singleton and Brown (1999), although conservation farming practices, such as stubble retention, could reduce predation risk and lead to higher survival of mice and higher densities, N_B, at the start of the breeding season. However, the regular monitoring program conducted since 1982 at Walpeup in Victoria has not detected any consistent trend in the size of the over-wintering population that could be attributed to changes in farming practices.

There are several ways that r_B and T_B could be modified by the activities of pastoralists or farmers over the period from spring to autumn. In Inner Mongolia, grazing by livestock has a direct impact on the structure, species composition and biomass of the plant community (Zhong et al. 1999) and hence will affect r_B. Large increases in the number of livestock over the last 50 years appear to have shifted the balance between precipitation-driven grass growth and off-take, so that the conditions preferred by Brandt's vole now tend to occur in years of near-average rainfall (Zhang et al. 2002). Hence, there has been an increase in the frequency of outbreaks compared to earlier periods when short-grass conditions were more likely in exceptionally dry years. In addition, campaigns to control voles may have resulted in secondary poisoning of predators and hence reduced their ability to regulate prey populations (Zhong et al. 1999). In grasslands elsewhere in China, control of small mammals has led to a measurable decline in many species of birds, including raptors such as black-eared kites (*Milvus lineatus*) and upland buzzards (*Buteo hemilasius*) (Lai and Smith 2002). However, little is known about the potential for predators to regulate populations of Brandt's voles in Inner Mongolia.

Recent changes in a range of farming activities may have contributed to increasing problems with outbreaks of mice in south-eastern Australia (Singleton and Brown 1999). These include activities that may directly increase r_B and extend T_B, such as increased diversity and asynchrony in crops, and others such as clearing of remnant native vegetation that might indirectly benefit mice by reducing the abundance of predators. The analysis by Sinclair et al. (1990) suggests that aggregation by raptors could regulate mouse populations at low density in localised irrigation areas. In regions with extensive dryland cropping, a significant impact of predation is more likely during the decline phase of an outbreak when there has been sufficient time for a build-up in raptor populations, particularly Australian kestrels (*Falco cenchroides*) and black-shouldered kites (*Elanus notatus*) (see, for example, Davey and Fullagar 1986).

In contrast to Brandt's vole, the house mouse is an introduced species in Australia, which increases the potential for safe and effective use of biological control agents. The serological prevalence of some mouse-specific viruses, such as mouse cytomegalovirus, minute virus of mice and mouse parvovirus, vary with the density of the host population, but there is no evidence that any of these pathogens could maintain the population at low density (Singleton et al. 2000). In fact, the lack of competition with small native granivorous mammals may be due to the impact on these species of pathogens introduced and spread with the house mouse (Smith et al. 1993).

Conclusion

Irregular outbreaks of house mice in Australia and Brandt's vole in Inner Mongolia appear to be caused primarily by irregular fluctuations in key climatic parameters, and exacerbated by a loss of potential regulatory processes such as predation. For house mice, up to 70% of outbreaks can be predicted from the amount of rain that falls during winter through to early summer (Kenney et al., this volume), a remarkably strong relationship given the independence of N_B, r_B and T_B. Eruptions of Brandt's vole are correlated with positive phases of the southern oscillation index, which is in turn linked to climate, and most outbreaks occur in years with uniform, near-average precipitation (Zhang et al. 2002). However, for both agricultural systems, existing models tend to predict many more outbreaks than actually occur. This suggests that additional factors that have yet to be identified often prevent outbreaks from developing. The challenge is to identify these factors and, if possible, enhance their effectiveness to counter the tendency of current agricultural practices to generate outbreaks of rodents.

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Rodent problems and management in the grasslands of China

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Abstract. In this paper, we review rodent problems and their management in the steppe grassland of Inner Mongolia, alpine meadows in Qinghai–Tibet, and grassland in Xinjiang. The behaviour, ecology and population dynamics of the major rodent species, including functionally similar species such as pikas, and their interactions with grassland ecosystems have been extensively surveyed. Cultivation and overgrazing by livestock are recognised as key factors in accelerating rodent infestation in grasslands. Therefore, improved management of livestock and crop production is an essential component of the solution to the rodent problem. As well as ecologically based management, species-specific control techniques such as immunocontraception are recommended for future rodent management in the grasslands of China.

Introduction

China has huge grasslands covering about 0.28 billion ha, and ranking first in the world. However, the grasslands produce only 8% of the total domestic meat production and 25% of the total domestic requirement for wool. Production input per unit area in grasslands is about 10 or 20 times less than in advanced countries and, in some regions, is becoming worse due to poor management. For example, in 1959, 6–13 Mu (1 ha = 15 Mu) were needed per sheep in Qinghai but this increased to 10–46 Mu per sheep by 1984 because of the degradation of the grassland. Despite this deteriorating trend, there is substantial scope for increased livestock production through better grassland management.

Rodent pests cause serious problems in the grasslands of China. They infest about 10–20% of the total area of grassland every year, and the annual loss of grass biomass has been estimated at 40–50 billion kg. In Qinghai and Tibet, expensive rehabilitation programs are required for 4 million ha of ‘black sandy land’, which have resulted from soil erosion attributed to rodents. Also, rodent populations in the grasslands of Inner Mongolia and Xinjiang are important reservoirs for many serious diseases, including plague. Therefore, better management is urgently needed for pest species of rodents and other small mammals in grasslands.

The major pest species differ from region to region in Qinghai, Tibet, Inner Mongolia and Xinjiang. The following is a brief overview of the environment and rodent problems of these grassland regions.

Grassland in Inner Mongolia

Inner Mongolia is located in the north of China. Western Inner Mongolia is mostly desert, while the east is mostly a huge grassland. The altitude is about 1000 m and the climate is cool and dry: annual average temperature ranges from –1 to 10°C, and annual rainfall varies from 200–400 mm. The dominant plant species are *Caragana microphylla*, *Cleistogenes squarrosa*, *Stipa krylovii*, *Aneurolepidium chinense* and *Artemisia frigida.*

Rodents, and other small mammals such as pikas, cause serious problems in grasslands. They consume about 10–20% of the grass and require constant monitoring by local government to prevent the spillover of epidemics, such as plague, to the human population. Of the 36 ‘rodent’ species in this region, the main pest species are *Rhombomys opimus* in the western part of Inner Mongolia, Brandt’s vole (*Microtus brandti*) and the Daurian pika (*Ochotona daurica*) in central-eastern areas, *Microtus gregalis* and the grassland zokor (*Myospalax aspalax*) in the far east, Mongolian gerbils (*Meriones unguiculatus*) and Mongolian lemmings (*Lagurus prezewaskii*) in the central-north, and the Mongolian gerbil in the central-south. Overall, Brandt’s vole and the Mongolian gerbil are the most serious pests in the grassland of Inner Mongolia, and rodenticides are commonly used whenever outbreaks occur.

Brandt’s vole is a species with complex social behaviour. Voles that survive over winter usually produce 3–4 litters within a breeding season, whereas the first cohort of a year produces 2–3 litters and the second cohort 1–2 litters.

The third and fourth cohorts do not breed until the next year. Litter size is 8 on average, but can be up to 14, and the breeding season is from March to September. The gestation period is 21 days, and lactation lasts for 15 days. It takes 52–62 days for a male to mature, and 55–65 days for a female. Brandt's voles live in groups, ranging in size from 2–3 in spring, 6–8 in early summer, and up to 22 or even 30 in a nest system in late summer or autumn. Population outbreaks of Brandt's voles occur irregularly, with an interval of 5–7 years (Li and Liu 1999; Z. Zhang et al., unpublished data). The autumn density can range from low values around 2.4 voles/ha to outbreaks at 528.8 voles/ha. Brandt's voles cache plant material, about 11 kg/nest, for over-wintering. Thus, the estimated damage is 0.49 kg/vole during the non-growing season of grass, and 0.36 kg/vole during the growing season. Populations of Brandt's voles are hosts for diseases such as salmonellosis, plague, tularensis, and tick-borne rickettsiosis. The threshold for implementing control in spring is 23 voles/ha, or 385 active holes/ha (Zhong et al. 1991, 1992).

Mongolian gerbils are considered very serious pests in grassland and farmland, and they harbour diseases that are a danger for human health. They prefer drier habitats in grassland and also occur in the transition zone between grassland and farmland. Populations fluctuate greatly every 4 or 5 years: for example, outbreaks occurred in 1964, 1969 (Xia et al. 1982), 1975, 1985 and 1989 (Li and Zhang 1993). The outbreaks coincided with high rainfall, which usually generates good production of grass and abundant food for gerbils.

Overgrazing is a key factor facilitating rodent infestation. Successional transitions in both plant and small mammal communities result from increasing levels of grazing by livestock (Zhong et al. 1985). For example, without overgrazing, *A. chinense and S. krylovii* are the dominant grasses and *O. daurica*, *Citellus dauricus* and *Cricetulus barabensis* are the dominant rodent species at Xilinhot (rainfall 350–400 mm) in central Inner Mongolia. After heavy grazing by livestock, the abundance of *A. frigida, Potentilla acaulis* and *C. squarrosa* increases in the plant community, while Brandt's vole, which prefers sparse short grass, becomes the dominant rodent species. Under extreme grazing pressure, *Planta annua* is the dominant plant, and the Mongolian gerbil, which prefers eroded habitats, replaces Brandt's vole. Therefore, control of grazing by livestock is very important for rodent pest management in Inner Mongolian grasslands. For example, from 1987 to 1989, the population density of Brandt's voles decreased by 78% and the biomass of grass increased by 40% in areas where overgrazing was prevented compared to a control area (Zhong et al. 1991).

Alpine meadow in Qinghai–Tibet

Qinghai and Tibet are two important areas for livestock production in China. In Qinghai, grasslands occur at altitudes from 2500 m to 4500 m and the annual average temperature ranges from –5 to 8°C. In Tibet, the altitude of grassland is over 4500 m and the annual average temperature ranges from –3 to 12°C. There are about 0.15 billion ha of grassland, of which millions of hectares are infested by rodents and pikas, with a substantial impact on livestock production. There are estimated to be about 1.5 billion plateau pikas (*Ochotona curzoniae*) and 0.15 billion plateau zokors (*Myospalax baileyi*), which are the two major pest species in the alpine meadow ecosystem. They consume approximately 20–30 billion kg of fresh grass each year, equalling the annual food intake of 20 million Tibetan sheep.

The plateau pika is distributed over about 32% of the grassland in Qinghai. Population densities oscillate greatly, ranging from less than 1 pika/ha to 150 pikas/ha (Fan et al. 1999). Pikas live in social groups and have a breeding season from March to September. They reproduce two or three times a year, average litter size is 4.7 ± 1.3, and the male:female sex ratio is 87:100, resulting in high rates of population increase. The maximum life span of a pika is 957 days (average is 120 days). For the first cohort of a year, the male's life span is 108 days, and the female's life span is 106 days. For the second cohort, the life span is reduced to 58 days for males and 66 days for female. Survival rates for the third cohort are even lower, with life spans of 25 days for males and 15 days for females (Wang and Dai 1990). Pikas prefer habitats with low sparse grass, and benefit from heavy grazing by livestock. The daily food intake per pika is 60 ± 8 g fresh grass. About 6.2 million KJ/ha.yr of the primary grass production is consumed by pikas, about 1.3 times that for all sheep. Pikas also spread diseases like salmonellosis, plague, tularensis, tick-borne rickettsiosis and pseudotuberculosis.

The plateau zokor lives underground and occurs in nearly 12% of grassland. Population densities are usually stable and can reach over 70 zokors/ha in seriously infested areas. Plateau zokors are mostly solitary and have a breeding season from March to July. They reproduce only once a year, with an average litter size of 2.7 ± 0.1. Each year, one zokor produces 242 mounds, or about 1024 kg of soil, which cover approximately 23 m^2 of grassland. In areas with very high population densities, zokor mounds can cover the whole surface (up to 2683 mounds/ha). The population density of zokors is significantly correlated with the loss of grass (Fan et al. 1988): mounds cover grass and zokors' feeding activity destroys the roots of grass.

The management of livestock is very important for rodent control because overgrazing is the major factor causing serious rodent infestations. In Qinghai, plateau pikas and zokors can be controlled effectively by rodenticides, followed by the use of herbicides to control weeds and exclosures to reduce grazing by livestock, and then re-planting of grass. The threshold for initiating control is 4 zokors/ha, and 30 pikas/ha (or 150 mounds/ha). However, traditional bait delivery techniques do not work well for zokors because of their fossorial behaviour. A baiting machine has been invented that places baits in artificial tunnels, which connect with the active tunnels of zokors. This technique increases the efficiency of control from 60% to about 80%, and the work efficiency is more than 20 times greater than traditional manual baiting (Jing et al. 1991). Recently, a bacterial toxin called botulin toxin-C was invented for killing pikas and zokors. Population reductions of over 90% can be achieved using this toxin (Wang and Shen 1988).

Grassland in Xinjiang

Xinjiang is a fourth province with grasslands that are important for livestock production in China. Rodents cause major problems in the grasslands of northern Xinjiang. The Xinjiang lemming (*Lagurus luteus*) is the most serious pest species in this region. The abundance of this rodent oscillates greatly every 4 or 5 years. Population densities can reach 2080 active holes per ha and grasslands are severely damaged during outbreaks. Large die-offs can occur after outbreaks but the cause is unknown. For example, in the early summers of 1959, 1982, 1989 and 1993, massive die-offs of lemmings were observed in rivers and lakes (Yu X., Zhao F. and Ye Y., unpublished data).

Recommendations for management

Long-term studies in the grasslands of Inner Mongolia and alpine meadows of Qinghai–Tibet have demonstrated that overgrazing and cultivation facilitate rodent infestations. Conversely, outbreaks of rodents lead to degradation of the grasslands and reduce agricultural production by decreasing the carrying capacity of livestock. Also, the damage to the grasslands can cause other serious environmental problems. The recent frequent sand storms sweeping across Beijing from Inner Mongolia were attributed to the deterioration of grasslands, partly accelerated by rodent activity. In the headwaters of the Yellow River and the Yangtze River, two of the most important rivers in China, serious problems with soil erosion have been exacerbated by rodent damage to vegetation. In response, the Chinese central government has launched a large program for managing rodent problems in grasslands. As usual, poisons, including botulin toxin-C, are the common tools for rodent management. These methods can only solve the rodent problem in the short term. Integrated management emphasising an ecological approach, combined with fertility control, is required for a sustainable solution.

For heavily degraded grassland, chemical control of rodents should be considered first, followed by weed control and re-sowing of grasses. Grazing by livestock should not be permitted in the first year of rehabilitation, and limited grazing is acceptable only after the grassland has fully recovered. For lightly degraded grassland, rodent control may not be necessary but the other rehabilitation techniques are required. Grazing can be resumed when the grassland has recovered. Poisoning of rodents, chemical control of weeds, and re-sowing of grass are all essential for the restoration of abandoned, formerly-cultivated grassland (Fan et al. 1999).

Traditional chemical control causes environmental pollution and risks to humans, livestock and wildlife. Therefore, it is necessary to develop non-toxic, non-polluting and sustainable control techniques for managing grassland rodents. The development of agents for fertility control, especially immunocontraceptive vaccines, is a recent area of research that may result in new tools for managing rodents. An immunocontraceptive vaccine that stimulates an animal’s immune system to block fertilisation, implantation or embryo development could be delivered in a non-toxic bait using traditional techniques. Immunocontraception has the advantage of being species-specific, non-polluting and humane, with little or no undesirable consequences for agricultural production or the environment. In Australia, major advances have been achieved in the development of immunocontraceptive vaccines for the management of house mice (*Mus domesticus*) (Chambers et al. 1999). In addition, population models have shown that this control technique is potentially very effective for rodent management (Zhang 2000; Shi et al. 2002; Davis et al., this volume).

Acknowledgments

This research was partially supported by Chinese Academy of Sciences (CAS) project KSCX2-SW-103, the CNSF projects (39730090, 39825105) and the Australian Centre for International Agricultural Research.

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Simulation of fertility control in an eruptive house mouse (*Mus domesticus)* population in south-eastern Australia

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Abstract. We simulated fertility control of house mice during and following years that populations erupt by combining time-series abundance data with estimates of survival based on capture–mark–recapture data. Analysis of seasonal rates of increase suggest that compensation to any method of control that reduces the density of mice is not expected until the winter decline—rates of increase over the annual decrease phase are density-dependent while rates of increase over the increase phase are not. Fertility control that sterilises one third of the female mice is predicted to have a large impact on the dynamics of mice such that plague densities are avoided. These results assume that the control agent operates over the whole breeding season and the presence of sterile females does not affect the reproductive output of the remaining fertile females. Nevertheless, we conclude from our simulation that achieving high sterility rates is not necessary for effective management of house mice outbreaks in Australia.

Introduction

House mouse populations occasionally erupt in the grain-growing regions of southern and eastern Australia, causing substantial losses to crops, high social stress through mice invading houses, shops, businesses and hospitals, and environmental and animal welfare concerns because of the high use of poisons (Caughley et al. 1994). Recently, the focus has been on developing species-specific fertility control through the use of immunocontraceptive vaccines (Chambers et al. 1999a; Singleton et al. 2001a). Immunocontraception involves dosing or infecting an animal with a reproductive protein that generates an immune response which blocks fertilisation.

Populations of wild house mice typically have an annual breeding season that begins in early spring and ends in autumn, though there is considerable inter-annual variability in both the commencement of breeding and the length of the breeding season (Singleton et al. 2001b). Seasonality in breeding produces an annual cycle in the abundance of mice. The annual cycle can be clearly seen in periods of high numbers of mice but can be difficult to detect during periods of low abundance. Management of mice using fertility control agents aims to eliminate the rapid seasonal increases in numbers of mice that are associated with eruptions. This concept has been tested in enclosure studies, which indicated that sterilising approximately two-thirds of the population would be sufficient to prevent eruptions (Chambers et al. 1999b).

This paper brings together analyses of time-series data and capture–mark–recapture data from a 19-year study of field populations to predict the short-term effects of fertility control on the population dynamics of house mice.

Materials and methods

Study site

Mice were live-trapped using Longworth traps at regular intervals of approximately 6 weeks near Walpeup in north-western Victoria (35.08°S, 142.02°E) from 1983 to 2001. Between 1990 and 1992, trapping was opportunistic and there was no trapping during the summer of 1999. Details of the trapping protocol are given in Singleton (1989). Between October 1983 and July 1984, there was a more intensive capture–mark–recapture study during a period when the population density of house mice increased from low levels to the extremely high levels that are characteristic of a plague.

Concurrent to the capture–mark–recapture study, traps were set in nearby farmland to collect data on the breeding ecology of wild house mice. Necropsies of female mice provided information on the commencement and end of the breeding season (Singleton et al. 2001b). Finally, daily rainfall is recorded at the Mallee Research Station and these data were used to calculate cumulative rainfall between April and October each year, which is positively correlated with crop yield and has been used to model the rate of increase of mouse populations (Pech et al. 1999).

Statistical analyses

To obtain an index of abundance of mice at the farm scale, data from all farm habitats were pooled. For each night in which the number of recaptures was greater than seven, a capture probability was calculated as the number of recaptures divided by the number of marked mice (if there was more than one night in a trapping session for which this was possible, then a mean capture probability was calculated for the session). For each session which included one or more such nights, a farm-scale estimate of abundance was generated by dividing the mean trap success by the mean capture probability. For the remaining sessions, mean trap success was divided by a seasonal average capture probability. In all cases, the estimate was scaled by trapping effort.

For each annual cycle in the time-series data, a single average rate of population change was calculated over the increase phase and a single average rate for the winter decline. These rates of population change are represented as monthly instantaneous rates of increase, defined as

$$r_{b,t} = \frac{1}{L_t}\ln\left(\frac{N_{end,t+1}}{N_{start,t}}\right) \tag{1}$$

and

$$r_{d,t} = \frac{1}{T_t}\ln\left(\frac{N_{start,t}}{N_{end,t}}\right) \tag{2}$$

where $N_{start,t}$ and $N_{end,t+1}$ are, respectively, indices of abundance at the start and end of the annual increase in mouse abundance that begins in calendar year t and ends in year $t+1$, L_t is the length of time (months) between the start and the end of the annual increase that begins in year t, and T_t is the length of time (months) between the end of the previous annual increase and the beginning of the next. $N_{start,t}$ is defined as the abundance of mice at the last trapping occasion that is less that 9 weeks (the generation time for house mice) after the commencement of breeding. The observed peak in abundance was used to set $N_{end,t+1}$ because there was little correlation between the timing of the observed peak in abundance and the reported end of breeding.

Simulation of fertility control

Fertility control was simulated using the historical time-series data by reducing $r_{b,t}$ (as described below), using a statistical model to predict $r_{d,t}$ (see Figure 1) but retaining the observed values of the date of commencement of breeding and the duration of the increase and decreases phases, L_t and T_t. In the season that fertility control was applied, the observed monthly rate of increase, $r_{b,t}$, was replaced by

$$r_{b,t}(x) = \ln[\phi_t + (1-x)R_t] \tag{3}$$

where ϕ_t represents the monthly survival of trappable mice during the seasonal increase that begins in calendar year t (estimated from capture–mark–recapture data), x represents the proportion of female mice that are sterile, and R_t is the monthly *per capita* recruitment rate over the breeding season that begins in calendar year t and ends in year t+1 calculated as

$$R_t = exp(r_{b,t}) - \phi_t \tag{4}$$

Simulations began with the onset of breeding and were run for 2 years. The value of $r_{b,t}$ in the second breeding season of a simulation was not changed from its observed value. The demographic rates, R_t and ϕ_t, and the seasonal instantaneous rates all refer to the trappable population. While this population includes some sexually immature animals at some times of the year, we do not attempt to introduce age structure here.

Results and discussion

Rate of increase

The time-series data on the abundance of mice are shown in Figure 1a. There was high between-year variability in the rates of increase during the seasonal increase ($r_{b,t}$). These rates are positively correlated with April–October rainfall, with 45% of the variance accounted for (Figure 1b). Rate of increase, $r_{b,t}$, is *not* correlated with the starting density in spring (Figure 1d).

There was also between-year variability in $r_{d,,t}$. This is negatively correlated with mouse population density at the end of the preceding seasonal increase. It has a stronger negative correlation with both *peak* density during the preceding seasonal increase and *average* density over the seasonal increase. The latter variable explains 84% of the variation (Figure 1c).

Simulation of fertility control

Figure 2 shows a simulation of fertility control for 1983–84, when a mouse plague caused significant losses in crop production, and the consequences of fertility control for the following summer (1984–85). The fertility control agent was assumed to act over the whole of the first breeding season such that $r_{b,t}$ was given by equation (3) with x set to 0.33. For values of x higher than a third, the predicted impact on the abundance of mice is greater than that shown in Figure 2 with trajectories following the same pattern (results not shown). Survival (ϕ_t) over the increase phase in 1983–1984 was set to the maximum observed monthly apparent survival rate of 0.85 (S. Davis, unpublished data).

We have implicitly assumed that:

(i) the survival rates of sterile mice are the same as those for fertile mice;

(ii) the duration of each increase and decrease phase is unaffected by the presence of sterile female mice;

(iii) reproductive parameters such as age at sexual maturity, proportion breeding, litter size and survival of pups are unaffected by the presence of sterile females;

(iv) the fertility control agent is active at the commencement of breeding; and

(v) the fertility control agent affects new cohorts as they appear so that the proportion of female mice that are sterile is constant over the course of the increase phase of the population.

In the simulation of fertility control, compensation did not occur during the seasonal increase but did occur during the winter decline through density-dependent survival. Controlling mice over the seasonal increase resulted in lower densities throughout the increase phase and consequently relatively better survival of mice over winter. This source of compensation can result in higher spring densities the following season than if no control was applied (Figure 2).

This is a potential cause for concern if control of mice in one year results in a high spring density the following year when, if conditions are good, control may need to be

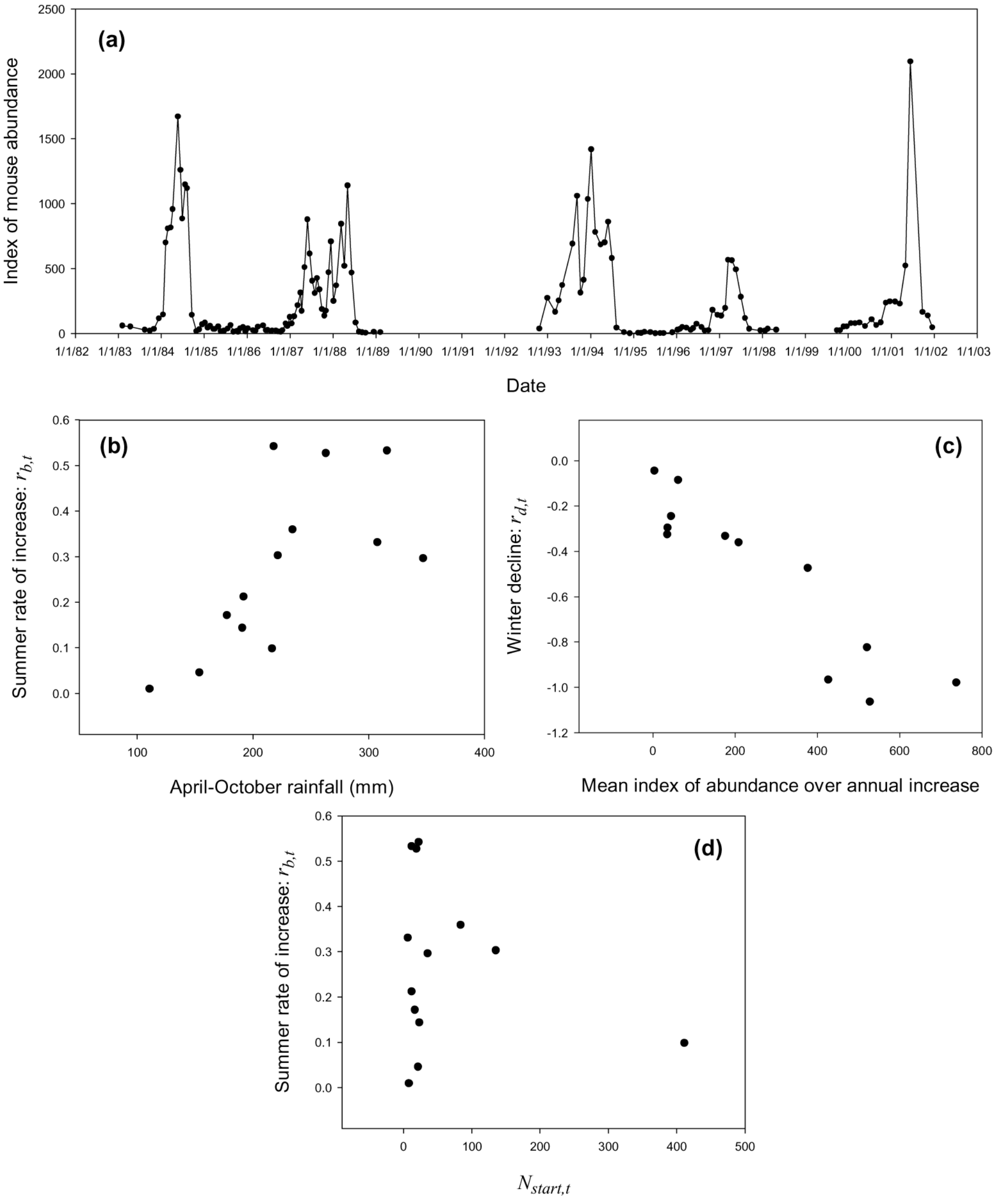

Figure 1. (a) Time-series data on the abundance of house mice (see Methods for definition of the index used). (b) Correlation between the rate of increase during the annual increase phase ($r_{b,t}$) and April–October rainfall (mm) (regression coefficients are –0.1379 and 0.0018 with P values 0.3556 and 0.0121 respectively). (c) Correlation between the rate of increase (decline) over winter ($r_{d,t}$) and mean index of abundance over the preceding increase phase. The linear regression used for simulation purposes was $r_{d,t} = -0.1472 - 0.0013M_{t-1}$, where M_{t-1} is the mean index of abundance over the annual increase phase beginning in the previous year, t–1 (P values for the regression coefficients are 0.0486 and <0.0001 respectively). (d) Lack of correlation between the rate of increase during the annual increase phase ($r_{b,t}$) and starting density in spring ($N_{start,t}$) (regression coefficients are 0.2996 and –0.0004 with P values 0.0004 and 0.4223, respectively).

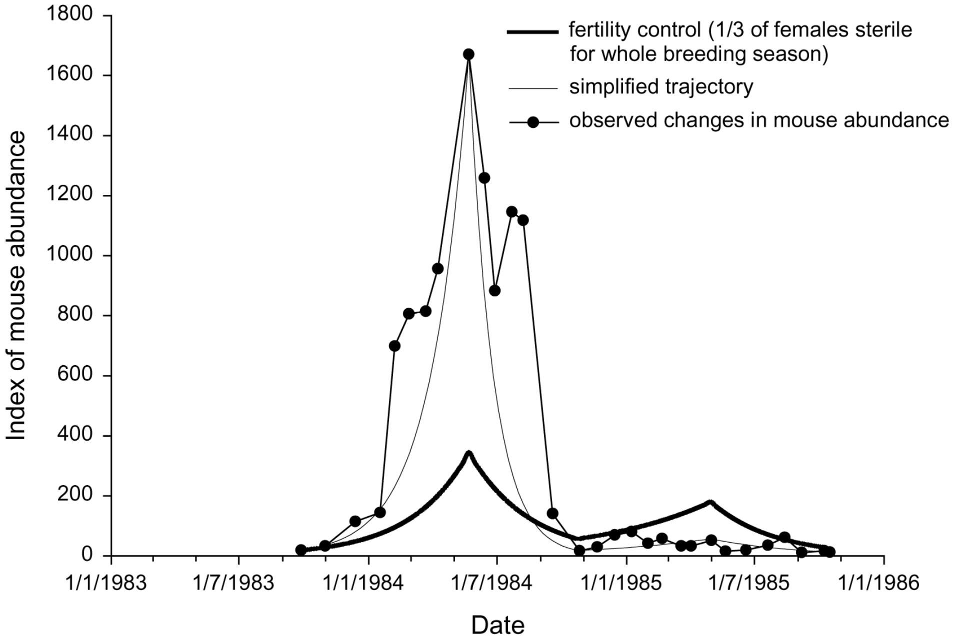

Figure 2. Observed changes in mouse abundance, simplified trajectory (using average instantaneous rates of increase over the increase and decrease phases) and simulation of fertility control, all shown for two annual cycles starting from the beginning of the breeding season in the spring of 1983. Fertility control is modelled as a reduction to recruitment (by a factor of one third) during the whole of the first breeding season but not the second.

repeated in order to prevent an outbreak. This is relevant to all methods of managing mice, rather than being particularly associated with fertility control. Also, if control is highly effective then, despite enhanced winter survival, control in one year may not create management problems in the following year.

The modelled effect of fertility control on house mice populations shown in Figure 2 is similar to that predicted for Brandt's voles (*Microtus brandti*) in Inner Mongolia (Shi et al. 2002). This is because populations of house mice and Brandt's voles have the same seasonal structure in demographic rates: density-dependent survival over winter, and a rate of increase during the breeding season that is independent of density and determined by extrinsic environmental factors.

The simulation may underestimate the true impact of imposing life-long infertility on mouse populations because (a) the maximum observed value for apparent survival was chosen, and (b) in the second year of the two-year simulation, $r_{b,t}$ was not reduced even though a small proportion of over-wintering mice would be infertile.

Conclusion

The predicted impact of fertility control that sterilises a third of the female mice is high in the season that it is applied. This prediction relies on the analyses of the time-series data, which show that the observed rate of increase of house mice during the seasonal increase is independent of density. On this basis, there will be no compensation to fertility control during the seasonal increase phase, at least through density-dependent factors, until the following winter decline. We conclude that achieving high sterility rates is not necessary for effective management of eruptive populations of house mice in Australia.

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Predicting house mouse outbreaks in the wheat-growing areas of south-eastern Australia

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Abstract. Outbreaks of house mice (*Mus domesticus*) occur irregularly in the wheat-growing areas of south-eastern Australia and impact on agricultural production. Prediction of mouse outbreaks has been successful in the central mallee region of Victoria and we have attempted to extend this prediction to a wider region of Victoria and South Australia. We developed two models: (1) a qualitative outbreak prediction from winter and spring rainfall and (2) a quantitative prediction of maximum autumn density of mice from winter and spring rainfall and spring mouse abundance. Both models have achieved some success at prediction. For the qualitative model we can achieve 70% correct predictions from winter and spring rainfall. The quantitative model is less satisfactory, and although it gives some predictability of high autumn densities, it misses too often the severe outbreaks that cause most damage. We highlight the demographic problems that need further analysis to increase our predictive abilities for mouse outbreaks.

Introduction

House mouse outbreaks are an undesirable feature of the wheat-growing regions of south-eastern Australia. Detailed studies of local populations have been carried out at different sites for more than 40 years, and these studies provide a wealth of demographic data for understanding the causes of these outbreaks (Newsome 1969a,b; Redhead and Singleton 1988; Mutze 1989, 1991; Singleton 1989; Singleton and Redhead 1990; Boonstra and Redhead 1994; Pech et al. 1999; Singleton et al. 2001). If one understands the mechanisms behind demographic changes, the next step is to construct models to predict outbreaks. For the house mouse in south-eastern Australia, a detailed modelling effort was undertaken by Pech et al. (1999), concentrating on the data available from one site in the central mallee region of Victoria. The Pech model has been quite successful in predicting changes in mouse numbers in the central mallee, and the objective of this paper is to try to extend this modelling effort to a broader spatial scale. In particular, we ask this question: Can we achieve a predictive model of house mouse plagues that can be used throughout the mallee region of Victoria and South Australia both to assist farmers and to add to our understanding of the ecology of mouse plagues?

Materials and methods

Quantitative house mouse data were available from two main sites: Walpeup in the Victorian mallee (G.R. Singleton, unpublished data) from 1983 to 2002 and Roseworthy in South Australia from 1979 to 2001 (G. Mutze, unpublished data). In addition, quantitative data were available from four other sites in Victoria and South Australia from 1998 to 2002 (Figure 1). Longworth and Elliott live-traps were set in crops (typically 6 × 6 grids, 10 m spacing) and along fence lines (10 m spacing). Mouse abundance was estimated by adjusted trap success, and the general methods are described more completely in Mutze (1991) and Singleton et al. (2001).

Qualitative house mouse data were dichotomised at 0 = no outbreak, 1 = outbreak. These qualitative data were gathered from Saunders and Giles (1977), Mutze (1989), and Singleton and Redhead (1989), and during the last 20 years from direct reporting from farmers and state agricultural scientists. We have used qualitative mouse data from the nine statistical local areas shown in Figure 1 for 1960–2001. Not all areas have data for each year, but there are many more qualitative data available from a larger area than there are quantitative data.

The schematic model for house mouse outbreaks is shown in Figure 2, and is based on the assumption that food supplies drive changes in density. Mutze et al. (1990) and Pech et al. (1999) used wheat yield as a surrogate measure of food supplies, and we have followed their lead in this paper. Wheat yield data from the period 1960 to 2001 were obtained from the Australian Bureau of Statistics for the statistical local areas shown in Figure 1. Monthly rainfall data for the same time period were obtained from the Australian Bureau of Meteorology for sites in or near the areas shown in Figure 1. In a few cases for which rainfall data were missing from one station, we used a nearby station for that time period. In general, monthly rainfall data are highly correlated for nearby sites. In addition to temperature and rainfall, we have computed two weather variables to add in the analysis—actual evapotranspiration and soil water deficit. Actual evapotranspiration (AET) is a complex function of temperature and rainfall in association with potential soil water storage. Soil water deficit measures the shortage of water in the soil, and is maximal under drought conditions. Monthly actual and potential evapotranspiration were calculated for all the rainfall stations from temperature and rainfall data. We used the methods of Thornthwaite and

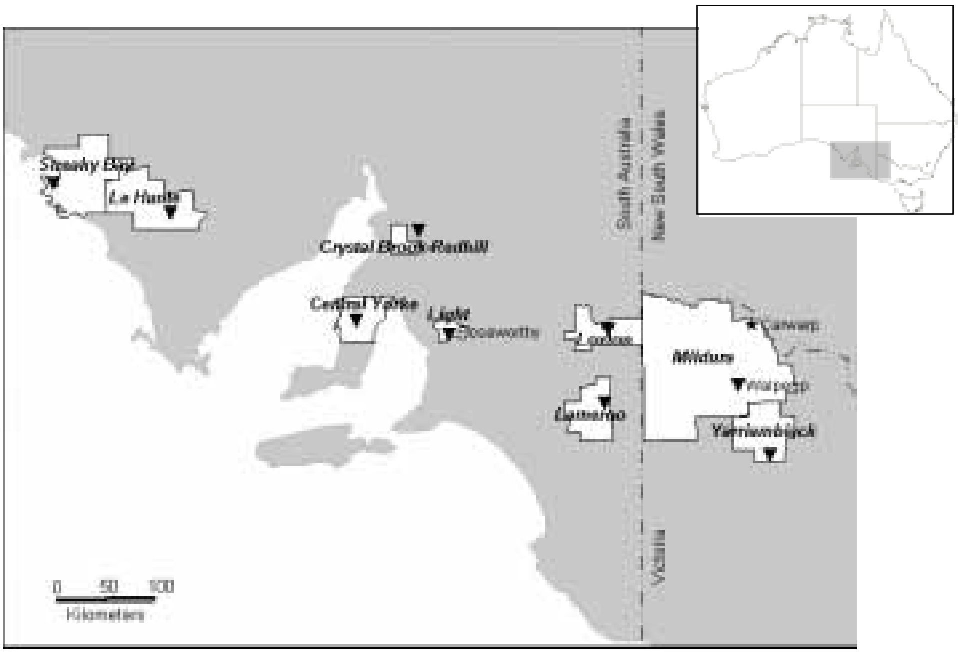

Figure 1. Location of the study areas utilised in this analysis. The nine statistical local areas from which wheat production and qualitative mouse outbreak data were obtained are outlined. The meteorological sites from which rainfall and temperature data were obtained are indicated by a ▼ for each study area. The major long-term study sites of Roseworthy and Walpeup are shown. Quantitative data from 1998–2002 was also obtained from four sites at Loxton, Lameroo, Yarriambiack, and Carwarp.

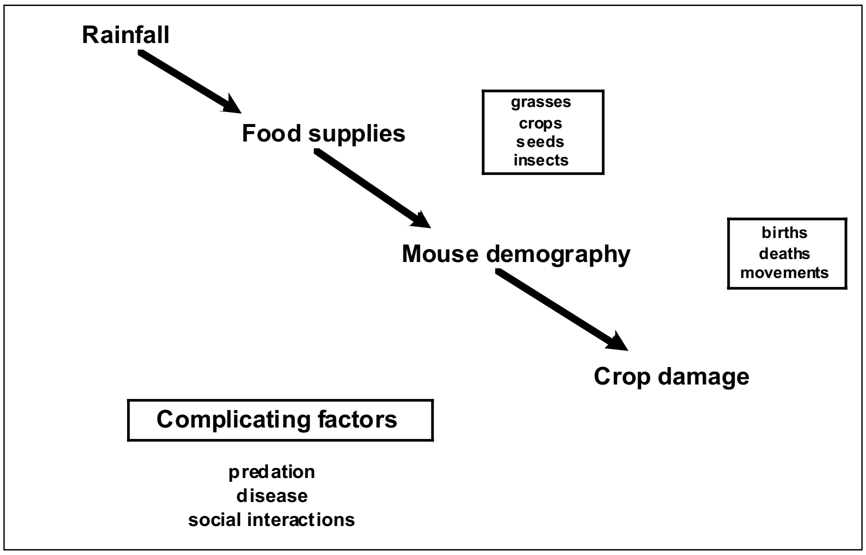

Figure 2. Schematic illustration of the current model for house mouse population dynamics in the grain-growing regions of south-eastern Australia. Food supply is the central variable, but the roles of predation, disease, and social interactions are not clearly understood with respect to how they can modify the basic food-density relationship.

Mather (1957) to estimate actual and potential evapotranspiration and soil water deficit for the areas shown in Figure 1. These estimates agreed with the general maps published by Wang (2001).

These biophysical data were used in logistic regression to estimate the probability of an outbreak for all sites and years for which we had data since 1960 (*n* = 255 site-years). This approach is similar to that used by Mutze et al. (1990). For sites and years in which we had quantitative data, we used robust multiple regression to attempt to predict the maximum autumn mouse density for that year. The models developed by Pech et al. (1999) and Pech et al. (2001) are based on predicting the rate of increase of mice, so that knowing the starting density of mice and some measure of food resources, one could predict the rate of increase and hence the abundance for the next time step (122 days in the 2001 model). We have adopted a different statistical approach in trying to predict the much simpler qualitative outcome of whether or not there will be an outbreak, and the more difficult quantitative prediction of how large the population will be in autumn, on the assumption that higher abundance in autumn translates into higher crop damage (Caughley et al. 1994).

All statistical analyses were carried out with NCSS 2001 (Number Cruncher Statistical System, Kaysville, Utah, <www.ncss.com>).

Results and discussion

We present our results as a series of questions with relevant data.

Can we achieve a good qualitative prediction of mouse outbreaks?

We used logistic regression to predict the probability of a mouse outbreak using 255 annual observations over the 9 sites. The best predictors were November rainfall and May to September rainfall, and the resulting logistic regression was as in equation (1) below, in which rain is in mm. The resulting logit can be converted to a probability by equation (2).

Classification of the 255 observations was correct 70% of the time (Table 1). We explored many possible alternative predictive models. Adding December rainfall to the above model did not improve predictability. Adding wheat yield to the regression improved predictability but by 3% only. Using wheat yield alone we could predict with 67% accuracy, slightly less than with rainfall alone. Soil water deficit and actual evapotranspiration were of no use in improving predictability. We conclude that the above logistic model based on rainfall is the most useful one at present for predicting qualitatively the chances of a mouse outbreak.

Can we achieve a good quantitative prediction of mouse outbreaks?

We used multiple regression to try to predict the maximum abundance of house mice in autumn from sites with detailed data on mouse abundance. A total of 43 site-years were available, most from the two sites of Walpeup and Roseworthy. The best variables for prediction were December rainfall, April to October rainfall, and September mouse abundance (indexed by adjusted trap success). Equation (3) was obtained, in which rain is in mm and mouse abundance is measured in adjusted trap success. This model, although highly statistically significant, gives an average absolute residual error of 26% in trap success, and is particularly poor in predicting the very highest mouse abundances observed. It is most sensitive to September abundance estimates.

Conclusion

Of the two models, we think the logistic model may be more useful to farmers who need to know in advance when to expect high mouse numbers in autumn. The quan-

Table 1. Classification table for the prediction of house mouse outbreaks in the Victorian and South Australian mallee regions from the logistic regression given in the text for 1960 to 2001. Boldface items indicate mistakes in classification. Outbreaks are classified qualitatively on the basis of moderate or severe damage to crops

		Estimated from model		
		No outbreak	Outbreak	Total
Actual event	No outbreak	149	**62**	211
	Outbreak	**14**	30	44
	Total	163	92	255

Equations:

$$\text{Logit}(Y) = 2.7325 - 0.0277\ (\text{November rain}) - 0.00780\ (\text{May to September rain}) \quad (1)$$

$$\text{Prob(outbreak)} = 1/[1 + e^{\text{logit}(Y)}] \quad (2)$$

$$\text{Maximum autumn abundance} = -27.158 + 0.5308\ (\text{December rain}) + 0.1468\ (\text{April to October rain}) + 1.183\ (\text{September trap}) \quad (3)$$

titative model may be more useful for developing understanding, and could become useful in practice if a simple way of estimating September mouse abundance can be developed.

Future work should involve a more detailed comparison of the relative predictive abilities of the Pech 1999 model, these two models of house mouse dynamics, and that of Mutze et al. (1990). We need to explore what determines the start of the spring breeding season, which is highly variable in house mice. Insects and grass seeds are major components of spring diet (Tann et al. 1991), and the start of breeding could be examined with simple models that predict the onset of insect activity and grass seed production in response to preceding weather patterns. It is clear that rainfall is indeed the driver of mouse outbreaks, as shown in Figure 2, but the exact causal pathway by which this is achieved is not yet clear.

Acknowledgments

We thank Dean Jones, Jason Cody, and Fiona Cavanaugh for their efforts in collecting the house mouse data from the Walpeup area, and David Chinner, Frank Anderson and students from Roseworthy Agricultural College for collecting data from Roseworthy. This study was funded by the Grains Research and Development Corporation (GRDC)(CSV 15). AJK was supported by a GDRC Visiting Fellowship.

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The non-lethal impacts of predation on mouse behaviour and reproduction: implications for pest population dynamics

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Abstract. In this paper, we report results from an experiment investigating the influence of habitat structure on the non-lethal effects of predation on enclosed populations of house mice. Mice were enclosed in 50 m × 50 m mouse-proof pens that allowed access to free-living predators, and were subjected to various habitat and predator manipulations. Food was provided *ad libitum*. Under high predation risk, mice selectively used areas of dense cover or refuge, but foraged more readily in open areas when predation risk was reduced by the exclusion of predators. These foraging decisions had consequences for body growth rates and the onset of breeding: in pens with little refuge, mice showed low body growth rates and began breeding later in the season, even though the populations were at low densities and there was free access to good-quality food. In pens where refuge habitat provided safe access to food, mice had higher body growth rates and showed an earlier onset of breeding, despite populations being at relatively high densities. Similarly, the total exclusion of predators from pens with minimal refuge also resulted in mice having higher body growth rates and an earlier onset of breeding. These experiments show that in semi-natural systems the non-lethal effects of predation can have large effects on the physiology of mice with flow-on effects to mouse population dynamics, and that these can be mediated by habitat structure. The implications for the development of house mouse (*Mus domesticus*) outbreaks in south-eastern Australia, which are characterised by an earlier onset of breeding compared to non-outbreak years, are discussed.

Introduction

Models of the population dynamics of pest species often assume the influences of extrinsic factors such as food abundance and predation pressure are independent. However, recent evidence suggests the risk of predation can influence the availability of resources, like food, to prey, and hence these factors may interact in determining prey population dynamics (reviewed in Lima 1998). For example, when facing the risk of predation, prey species may reduce their foraging activity, leading to increased risk of starvation (McNamara and Houston 1987) or decreased reproductive output (Peckarsky et al. 1993).

Outbreaks of house mice (*Mus domesticus*), which occur at irregular intervals in the south-eastern region of Australia, are characterised by an earlier onset of breeding than in other years (Singleton et al. 2001), although this is not in itself sufficient for plague formation. A change in food quality is a probable mechanism driving these reproductive differences, i.e. populations increase when the abundance of high-quality food increases. However, it is possible that high predation risk could offset increased food abundance by making food less accessible to mice. There is some evidence that predators can regulate house mouse populations in the irrigated, rice-growing region of New South Wales through direct predation (Sinclair et al. 1990), but the impact of predation risk on mouse population dynamics has not been investigated.

In this paper, we present a subset of results from a study using house mice contained in pens that were accessible to predators (described in detail in Arthur 2001). Three habitat and predator manipulations (A = low refuge; B = high refuge, with wire netting over felled trees providing small areas of absolute protection; C = total exclusion of predators from a subsection of the pen) were used to compare the behaviour of mice in the short-grass habitat common to all pens with their behaviour in patches of absolute refuge (treatment B) or felled trees set out in small grids (treatments A and C). Supplementary food was provided *ad libitum*. The following hypotheses and predictions were tested:

1. If mice perceive high risk of predation, they should selectively use areas under felled trees or areas covered by netting. Exclusion of predators should reduce the selective use of cover.
2. Selective use of cover in low-refuge pens should result in restricted access to supplemental and natural food, which was predominantly in open areas, result-

ing in reduced body growth of mice, compared to high-refuge and predator-exclusion pens where there was safe access to supplemental and natural food.

3. If access to food influences reproduction in mice, then mice with reduced body growth rates in low-refuge pens should have lower reproductive output than those in the other two pens.

Materials and methods

Study site and experimental design

Experiments were conducted in eight 50 m × 50 m pens that allowed access to free-living predators including feral foxes (*Vulpes vulpes*), cats (*Felis catus*) and native raptors. Prey behaviour was assessed in all pens, but due to disruption by feral pigs (*Sus scrofa*), results for mouse body growth and reproduction are presented for five pens only. A full description of the experimental design is provided in Arthur (2001). Populations were subjected to three habitat and predator manipulations: a low-refuge treatment (short grass habitat with a 5 × 5 grid of felled 3 m tall cypress pine trees); a high-refuge treatment (short grass with patches of absolute refuge of wire netting over felled pine covering 10–15% of the area); and a predator-exclusion treatment (short grass habitat but with predators excluded from a 25 m × 25 m subsection of the pen using fencing—a 5 × 5 grid of felled trees equivalent to that in low-refuge pens was placed within the exclosure). Wheat was provided *ad libitum* in four feed stations per pen either in the open (low-refuge treatment), within the refuge (high-refuge treatment), or within the predator-exclusion area (predator-exclusion treatment). The study was carried out on the eastern foreshores of Burrendong Dam on the central western slopes of New South Wales (32°40′S, 149°10′E) in open grassland. Mouse outbreaks occur in nearby areas where agricultural crops are grown (see, for example, Twigg and Kay 1994).

Assessing mouse behaviour

Mouse behaviour was assessed using the giving-up density (GUD) technique, where 20 pieces of cut up sunflower seed (each piece ~1/3 of a seed) were provided in a non-food matrix of sand. The number of pieces remaining after one night of foraging by mice measures the 'quitting harvest rate', which reflects a trade-off between the benefits and risks of continuing to forage at that harvest rate. The prediction is that animals will have a higher GUD (more pieces of food remaining) when facing high predation risk. Perceived predation risk under the three treatments was compared by measuring the GUD in up to 10 trays placed under cover (under a felled tree in the low-refuge and predator-exclusion treatments; or under netting in the high-refuge treatment), with 10 trays placed in the open (1–2 m from cover). Only data from trays visited by mice were used. Data from multiple assessments in replicate pens were analysed as a split-plot repeated-measures experiment using residual maximum likelihood (REML) estimation.

Analysis of body growth rates

Mouse populations were monitored by live-trapping using type A Elliott traps (9 × 10 × 30 cm) baited with wheat. Growth of mice was analysed by comparing the length of trapped individuals between one trapping session and the next (growth = length at session t +1 – length at session t). Initial length was included as a covariate for the analysis. The data were analysed using REML estimation with pen as a random effect. The limited replication of the experimental treatments leaves few degrees of freedom to test for treatment effects. To overcome the low level of replication, further support for conclusions regarding the effect of treatment on growth was obtained by comparing growth rates in pens at different times and under different treatment regimes (e.g. treatment reversals; Arthur 2001), but results for one period only are presented here.

Analysis of reproduction

At the end of the experiment in September 2000 (early spring), reproductive performance was analysed by comparing the proportion of females >79 mm long with embryos and recent uterine scars. This length was chosen because 80 mm was the minimum length of a female that was either pregnant or had recently given birth at the end of the experiment, based on necropsy (unpublished data). Few animals had old scars, and there were too few animals breeding in low-refuge pens to compare the number of uterine scars as a measure of litter size under the different treatments. The data were analysed using a generalised linear model (GLM) with binomial errors and a logit link function.

Results

Mouse behaviour and predation risk

There was a highly significant location by treatment interaction for GUD (F = 9.53, df = 2,8, P = 0.007; Figure 1). In high-refuge pens, the GUD under the netting was much lower than in the open. In low-refuge pens, the GUD in cover was lower than in the open. In predator-exclusion pens, there was a non-significant difference in GUDs between open and closed locations. Also, GUDs in the open in predator-exclusion areas were generally lower than GUDs in the open in other pens. These results were consistent with a number of other trials presented in Arthur (2001).

Growth of mice

Over the winter to early spring period at the end of the experiment (July–September 2000), mice in low-refuge pens grew much less than those in high-refuge and predator-exclusion pens (Wald statistic for treatment effect = 54.2, 2 df, P < 0.001, length by treatment interaction Wald statistic = 5.8, 2 df, P = 0.055; Figure 2). Points with high leverage have been left in the analysis, however it should be noted that if they are removed, the apparent treatment effects are much larger. To show that treatment effects were consistent between pens with the same treatment, lines have been fitted to the five individual pens. Results from other periods, where different treatments were applied in different pens, confirmed that the results were due to treatment effects and not some underlying feature of each pen (Arthur 2001).

Reproduction

At the end of the experiment in spring (September 2000) a much higher proportion of females >79 mm in length was found to be breeding in the high-refuge and predator-exclusion pens than in the low-refuge pens (deviance ratio 13.5, 2 df, $P < 0.001$; Figure 3).

Discussion

The results from this study indicate that predation risk can have significant non-lethal effects on mouse population dynamics under certain conditions. In low-refuge pens, mice showed an unwillingness to forage in the open. This led to reduced body growth rates, and few mice had begun breeding in early spring. In high-refuge pens, mice also showed an unwillingness to forage in the open, but safe access to supplementary food and 10–15% of the natural food provided by the refuge resulted in higher body growth rates and a high proportion of adult females breeding in early spring. When predators were removed, mice were much more willing to forage in the open, and hence had access to the supplementary food and 25% of the natural food in a predator-exclusion pen. As in high-

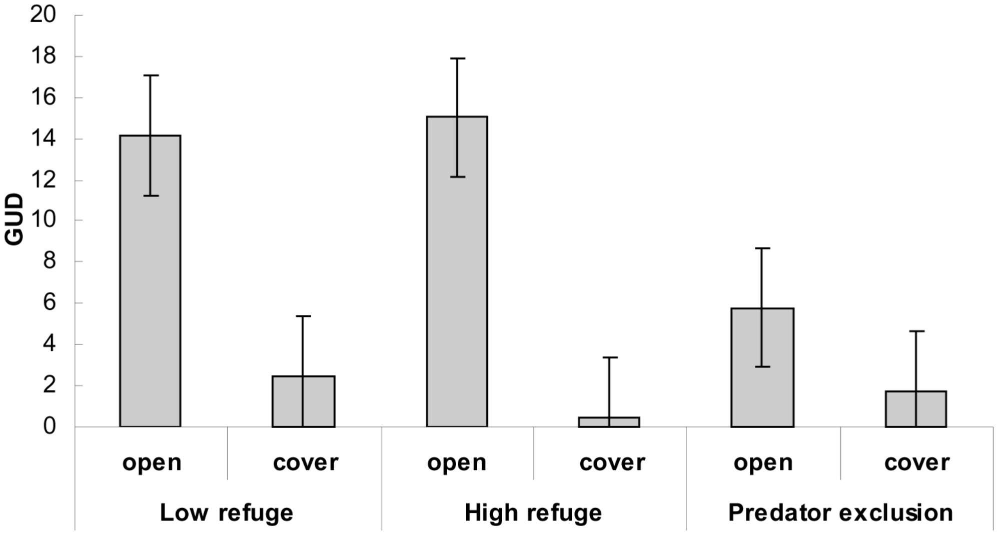

Figure 1. Mean giving-up density (GUD) in open and covered locations under the three different treatment types. Error bars are ± standard errors. Figure redrawn from Arthur (2001).

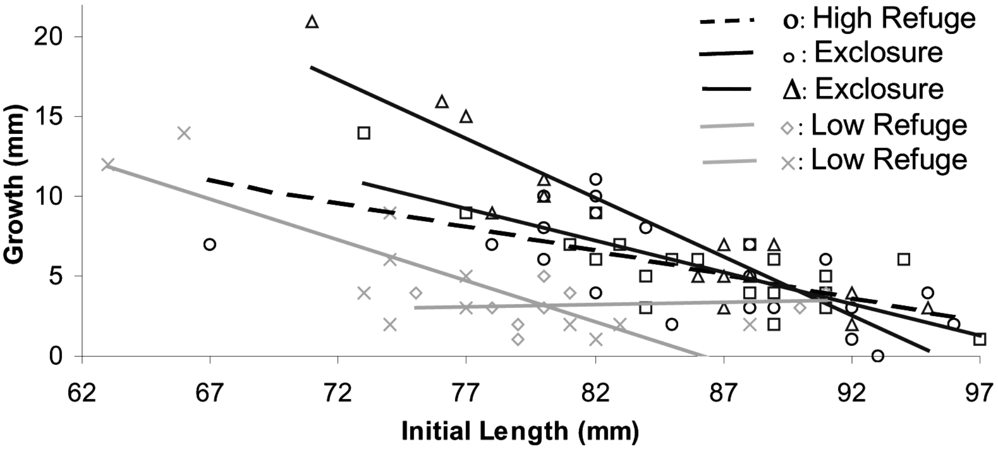

Figure 2. Fitted relationship of growth against initial length of mice for the period July–September 2000, with data grouped by pen. Each data point reflects the growth of one individual over the 84-day period (exclosure = predator exclusion treatment). Figure redrawn from Arthur (2001).

refuge pens, this resulted in higher body growth rates and a high proportion of adult females breeding in early spring. These results occurred despite populations being much higher in the high-refuge and predator-exclusion pens than in the low-refuge pens (Arthur 2001), i.e. the strength of the effect was larger than any effect of population density on mouse reproduction. It is important to note that differences in body growth and reproduction were most evident in winter and spring (Arthur 2001) when cold conditions are likely to result in high-energy requirements for small mammals like house mice. Further results from an experiment conducted in the previous breeding season were consistent with those presented here, and all results are discussed in more depth in Arthur (2001), but here we focus on the implications of these results for rodent management, particularly house mice in Australia.

Populations of house mice in Australia undergo periodic eruptions, with the pattern changing depending on the region (Pech et al. 1999). In the irrigated, rice-growing regions of New South Wales, it has been suggested that mobile predators congregate (Davey and Fullagar 1986) and can regulate mouse populations by direct mortality under certain conditions, preventing eruptions (Sinclair et al. 1990). Populations then erupt due to a combination of wider dispersal of predators and enhanced breeding performance of mice. Based on the results presented here, the latter could be due to a reduction in predation risk associated with the wider dispersal of predators. In the mallee region in Victoria, the availability of high-quality food has been the main focus for models predicting population eruptions of mice, although recent experimental studies have shown that risk avoidance behaviour of mice in areas with short, sparse vegetation is different to those with tall vegetation, e.g. along fence lines (Ylönen et al. 2002). A necessary, but not sufficient, condition for the generation of outbreaks in this region is an early onset of breeding in mid-August (early spring; Singleton et al. 2001). A change in the abundance of high-quality food is a probable mechanism driving these reproductive differences. However, changes in abundance of high-quality food may also be confounded by changes in predation risk. The abundance of high-quality food is influenced by rainfall, which results in extensive vegetation growth along fence lines and other refuge habitats where mouse populations persist between outbreaks. This vegetation growth is likely to greatly reduce the risk of predation of mice by making them less detectable by predators.

Management recommendations for minimising the risk of mouse outbreaks already include controlling vegetation along fence lines to reduce the survival and breeding of mice (Brown et al. 1998). The results presented here suggest that this may also reduce population increases by decreasing the reproductive output of mice due to increased predation risk. However, as the results from the predator-exclusion treatment show, mice will forage willingly in the open if predator activity is low. Hence, we would expect mice to reduce foraging only if predator populations were sufficiently high to generate high predation risk. Future experiments could focus on manipulations of predator abundance and habitat structure to determine whether they interact to influence the build-up of mouse populations in these areas. Studies could assess also whether there is any evidence that mice perceive predation risk at various stages of their population fluctuations.

While habitat and predator manipulations may contribute to management of pests like mice, it is important to note that these manipulations also may have detrimental consequences for other prey species (Pech and Arthur 2001). Predation risk may also be increased for protected native species also, for example. The full impacts of management actions therefore need to be considered carefully before they are implemented.

Acknowledgments

This study was funded by the Pest Animal Control CRC (Cooperative Research Centre) and Commonwealth Scientific and Industrial Research Organisation (CSIRO)

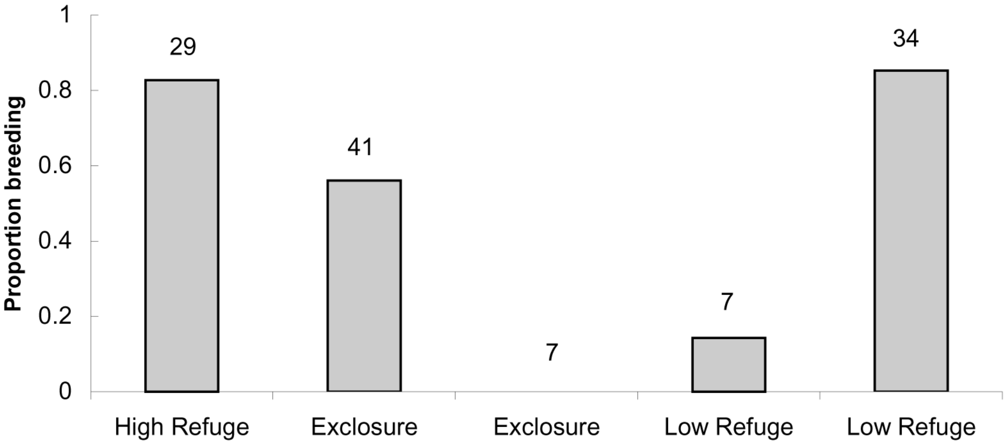

Figure 3. Proportion of female house mice >79 mm in length either pregnant or with recent uterine scars in September 2000 in different pen types. Numbers above columns show sample sizes

Sustainable Ecosystems. Tony Arthur was supported by an Australian Postgraduate Award from the University of Sydney. Dr Chris Dickman was a supervisor of Tony Arthur and provided input into the design and analysis. Bob Forrester provided statistical advice. Alex Drew, Eddie Gifford, Steve Henry, Adam McKeown and Steve Zabar provided field assistance. We thank the Department of Land and Water Conservation for access to the Burrendong Dam field site.

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Seed production, predators and house mouse population eruptions in New Zealand beech forests

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Abstract. Periodic heavy seed production in New Zealand beech forests increases the food supply available to both native birds and exotic pests, including the house mouse. We tracked changes in beech seedfall and mouse abundance as well as rats and stoats in two valleys in Fiordland National Park, New Zealand, between 1999 and 2001. Mouse population eruptions occurred only in areas and years where the beech forest was producing large quantities of seed. This autumn injection of highly nutritious food allowed winter breeding by mice, triggering a population eruption. Beech seed is no longer available after spring and mouse populations crash until the next beech seedfall. The presence of stoats (a predator) did not affect the rate of increase of mouse populations, or have any modifying effect on the influence of seedfall.

Introduction

The beech forests (*Nothofagus* spp.) of New Zealand seed heavily at irregular intervals (Wardle 1984). This seed provides an increase in food supply for native birds, but also results in a cascade of pest animal eruptions (King 1983). Immediate (within 3 months) increases in house mouse (*Mus musculus*), kiore (*Rattus exulans*) and ship rats (*R. rattus*) occur after heavy seedfalls, and a delayed increase in stoat populations (*Mustela erminea*) occurs due to their seasonal breeding. This cascade is a concern for New Zealand conservation because stoats and ship rats are predators of ground-dwelling and hole-nesting native birds. Choquenot and Ruscoe (2000) analysed a long-term data set from New Zealand's North Island to assess the relative importance of intrinsic and extrinsic factors in limiting house mouse populations in beech forest. They found that seed availability was the major predictor of house mouse population increase (r), but that this was modified by some unspecified density-dependent mechanism. They also suggested that rat abundance might have had a negative effect on the rate of increase of mouse populations via competition or predation. In this paper, we test the general model of Choquenot and Ruscoe by analysing data collected from Fiordland National Park in the South Island of New Zealand. In addition, we assess the effect of predation by stoats on the rate of increase of mice.

Materials and methods

Study sites

This study was undertaken in two valleys of Fiordland National Park in south-western New Zealand between 1999 and 2001. The Eglinton Valley comprises a forest dominated by red beech (*Nothofagus fusca*) at low altitudes (approx 450 m above sea level) where the trapping grids were located. Stoats were being controlled in the valley as part of a native bird protection program and that provided us with a predator removal treatment. Between January 1999 and June 2001, 792 stoats were removed from the Eglinton Valley (P. Dilks, pers. comm.). The Hollyford Valley comprises a mixed silver beech (*Nothofagus menziesii*)–hardwood forest. There was no predator removal being undertaken in this valley.

Rodent monitoring

Rodent populations were monitored quarterly from May 1999 to February 2002 on two grids in each valley. Each quarter (February, May, August and November), rodent trapping was undertaken on each grid for five successive nights. Each grid was 25,600 m^2, consisting of 81 trapping stations at 20 m intervals in a 9 × 9 array. At each trapping station, a single Elliott live-capture rat trap was baited with peanut butter and rolled oats and had straw added. All animals caught were tagged with individually numbered ear-tags and given an ear-notch to indicate the trapping session during which they were first encountered. Standard data were collected on all animals caught:

valley, grid, trap location, tag number, notch position, mass (g), head–body length (mm), sex, and reproductive condition.

Beech seedfall

On each grid, four collecting buckets were positioned to catch seed as it fell. The contents of the seed buckets were collected each quarter at the same time as trapping. Seeds (including seedcases) in each bucket were floated in 95% ethanol to determine if they had a kernel (Ledgard and Cath 1983). Only those with a kernel present were used to quantify seedfall (seeds/m^2). Choquenot and Ruscoe (2000) found that seedfall was a significant predictor of the rate of mouse population increase in the autumn and winter months only. In our analysis, seedfall was taken as zero in November and February, while cumulative seedfall was used for May (autumn) and August (winter) within each year. Log (Seedfall+1) was used in the analysis here as was done previously (King 1983; Choquenot and Ruscoe 2000). In laboratory trials, mice open the seed, eat out the kernel, and leave the seedcase (personal observation). An average red beech seed weighs approximately 0.0077g (Lethgard and Cath 1983) of which approximately 50% is kernel weight.

Analysis

Populations were indexed using minimum number of animals known to be alive (*MNA*). Ruscoe et al. (2001), using the first three seasons of this data set, showed that *MNA* was highly correlated with mark–recapture population estimates (r = 0.87). To reduce bias in estimates of mouse population growth between seasons arising from the addition of a constant to mouse *MNA* (N_t), all *MNA*s were transformed using Steen and Haydon's (2000) correction:

$$X_t = N_t + 1 + (0.05\ N_t) \qquad (1)$$

Instantaneous changes in log mouse abundance between seasons (r_t) were estimated from sequential transformed mouse *MNA*s as:

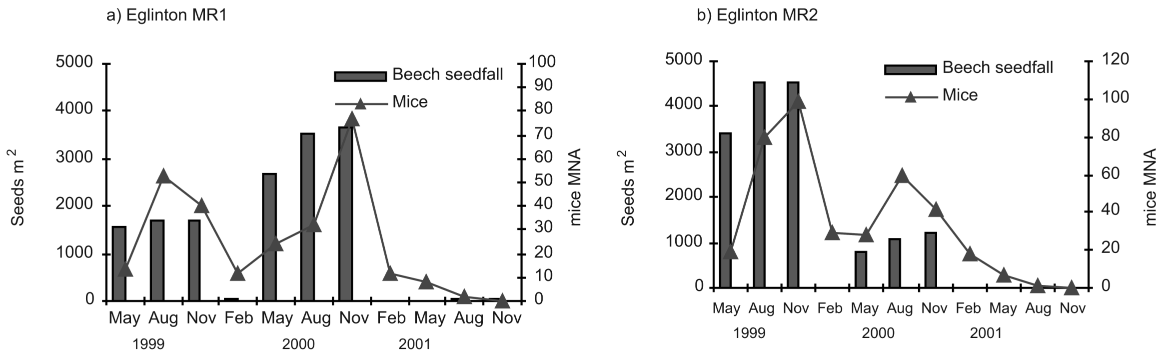
$$r_t = \mathrm{Ln}\ (X_{t+1}) - \mathrm{Ln}\ (X_t) \qquad (2)$$

where time (t) was season. A linear mixed effects model with a first-order autoregressive correlation was used to determine which factors affect mouse r. Valley, Season, log(Seedfall+1), Mouse abundance at the beginning of the quarter, Rat, and Stoat abundance were used as predictor variables and Grid specified as a random factor (S-Plus 6, Insightful, Seattle, USA).

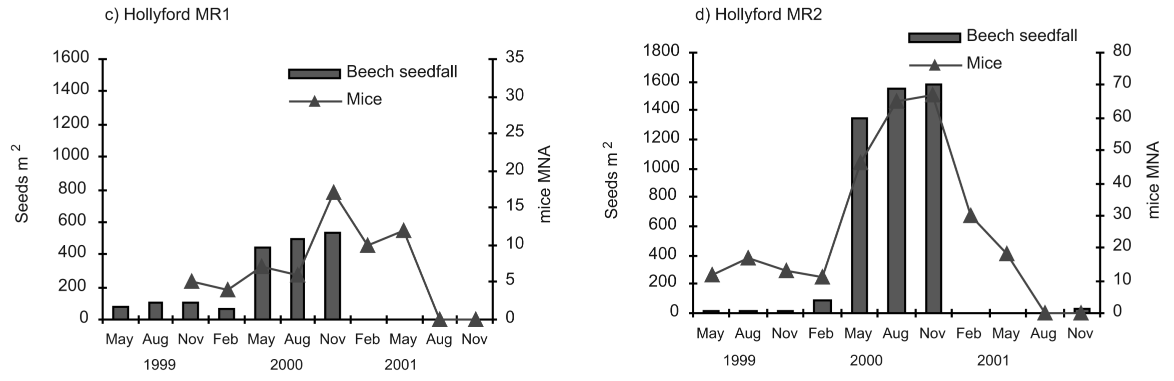
Results and discussion

Effect of seedfall

Mouse abundance on each grid varied with the magnitude of the predominantly autumn beech seedfall (Figure 1). The seedfall represents the density of seed fallen in the 3 months before the trapping date (i.e. May seedfall is that fallen during the February–May quarter). In the Eglinton Valley, there was significant seedfall in both 1999 and 2000, although the magnitude of the seedfall varied


a) Eglinton MR1

b) Eglinton MR2


c) Hollyford MR1

d) Hollyford MR2

Figure 1. Cumulative within-year seedfall and population size (minimum number of animals known to be alive; *MNA*) on each of the grids in the Eglinton and Hollyford valleys from May 1999 to November 2001. Note different scales on the y-axes.

between grids. Seedfall in the second year was higher than in the first year on Eglinton MR1 grid, whereas the pattern was reversed on the MR2 grid, approximately 4 km away. The silver beech in the Hollyford Valley only produced significant seed in the second year and the quantity produced was markedly higher on the MR2 grid than the MR1 grid.

Mouse population changes appeared to follow the pattern of seedfall. In the Eglinton Valley, the highest mouse population peaks were recorded in the year of highest seedfall at each site. Within the Hollyford Valley, both seedfall and mouse numbers were higher on the MR2 grid than the MR1 grid, despite their being only 2 km apart. Mice were present in the Hollyford Valley in 1999 when there was virtually no beech seedfall. This is probably due to the presence of other seed-bearing plants not present in the Eglinton Valley (King 1983). However, the populations crashed to zero detectable in 2001, as did the Eglinton populations, when there was no beech seedfall in either valley. Annual log (Seedfall) was highly correlated with annual peaks (either in August or November) in log(*MNA*) ($r_{10} = 0.957$, $P < 0.001$).

The increase in mouse population size in May of each high seedfall year was due to an increase in young animals entering the trappable population. Young animals (head–body length ≤65 mm) continued to make up >25% of the Eglinton population from May to November 1999 but dropped to 10% in February 2000 (Figure 2). Following the next seedfall, the proportion of young animals increased again in May 2000 but then dropped sharply over the following 9 months. The Hollyford Valley populations followed a similar pattern with more small animals in the population in May. Following the failure of beech seeding in 2001, populations crashed toward zero and no young animals were captured after May 2001 (Figure 2). Average head–body length also changed during the study (Figure 3). Lowest averages were recorded in May 1999 and May 2000, with averages increasing from August 1999 to February 2000. In May 2001, with no seedfall, there was no decline in head–body length because only older animals remained in the population.

As a crude measure of the general ‘health’ of the animals captured, a condition index was generated using the regression method of Krebs and Singleton (1993). Figure 4 shows the mean body condition for larger animals (>65 mm head–body length) for each quarter in each valley. Small animals were excluded because juveniles are growing faster in length relative to weight gain and this results in a higher index that may not reflect general health. Likewise, females that were obviously pregnant were excluded. Results are variable, but for Eglinton the general pattern is that animals were in better condition in May when there was seedfall and subsequently lost condition over the following 9 months (winter to summer). In 2001, when there was no seedfall, the average condition index deteriorated and at that time animals were noticeably ‘lean’ in the field. The results for the Hollyford were not as clear. The mice were in good condition from May to November 1999 despite there being no significant beech seedfall that year in the Hollyford Valley. This suggests that mice could be deriving food from another source in this mixed forest.

The effect of food, predation and competition on the rate of increase of mice

Two other mammal species were present on our grids. Ship rats were present on the grids in most trapping sessions, with up to six ship rats caught over the five nights in Eglinton Valley, and up to 17 ship rats or kiore in the Hollyford Valley. Although the study was not designed to index stoat abundance, we did trap stoats on our grids. During the course of the study, seven stoats were trapped in the Eglinton Valley and 19 in the Hollyford Valley. Stoats are kill-trapped in the Eglinton Valley in an attempt to protect threatened birds and therefore are less abundant. We used these trapping indices of stoat and rat abundance (ship rat and kiore combined) as covariates in the model to describe rate of increase of mouse populations in addition to the effect of stoat removal, which is included in the Valley factor effect.

We assessed the interactive effects of Valley and other predictor variables. There were no significant two-way interaction effects of Valley and Season ($F_{3,20} = 0.0532$, $P = 0.614$), Seedfall ($F_{1,20} = 0.120$, $P = 0.526$), Stoat abundance ($F_{1,20} = 0.0001$, $P = 0.983$), or Rat abundance ($F_{1,20} = 0.202$, $P = 0.413$) on mouse *r*. Three-way interaction effects were investigated but none were significant ($P > 0.2$). When non-significant effects were eliminated from the model, we were left with the main effects of Seedfall ($F_{1,27} = 15.063$, $P < 0.001$), Mouse abundance at the beginning of the quarter ($F_{1,27} = 31.81$, $P < 0.001$), and Season ($F_{3,27} = 15.538$, $P < 0.001$) and Mouse abundance*Rat abundance interaction ($F_{1,27} = 6.050$, $P = 0.021$) that explained 68% of the variation in the data. Examination of the coefficients showed that while seedfall (in May and August only) had a positive effect on *r*, the influence of mouse abundance and rat abundance were both negative.

The lack of significant interaction effects of Rat abundance, Stoat abundance and Seedfall with Valley suggests that, despite the differences in forest type between the two valleys, the effects of these main predictor variables were consistent between the valleys. There was also no main effect of Stoat, or any significant second-order interactions of Stoat with Mouse abundance or Seedfall. Neither Valley (which included the effect of the stoat removal in Eglinton) nor Stoat abundance (as indexed from our trapping) changed the effect that Seedfall or Mouse abundance at the beginning of the quarter, had on mouse *r*. Therefore, we could not detect an effect of predation by stoats on mouse *r*. Mouse population numbers did not reach as high a level in the Hollyford Valley as in the Eglinton Valley. However, it appears that this is more likely due to the differences in food availability between the two valleys than the effect of stoats. Following a high

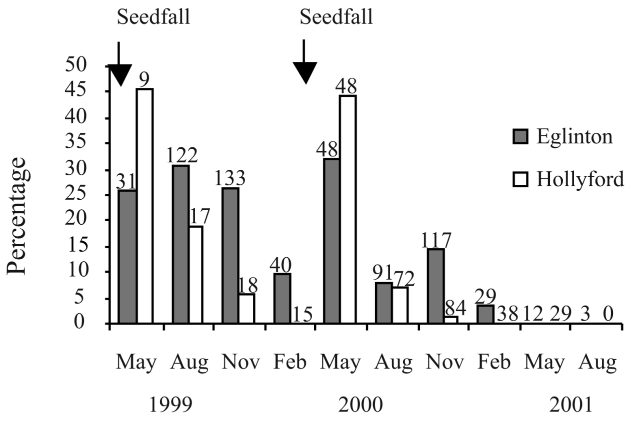


Figure 2. Percentage of small mice (≤65 mm head–body length) in the population for May 1999 to August 2001. Timing of significant seedfall in 1999 (Eglinton only) and 2000 (both valleys) is shown. Sample sizes are shown above bars.

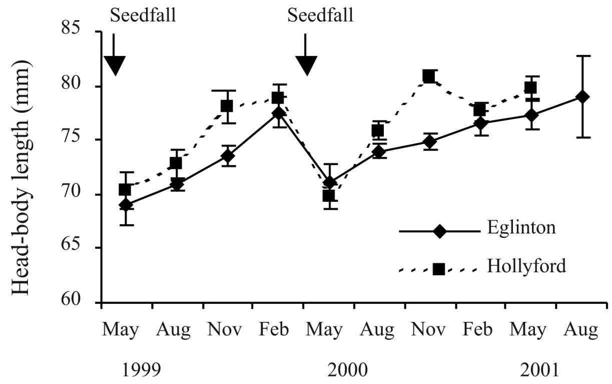


Figure 3. Changes in the mean head–body length (± se) of animals trapped in each valley from May 1999 to August 2001. Timing of significant seedfall in 1999 (Eglinton only) and 2000 (both valleys) is shown.

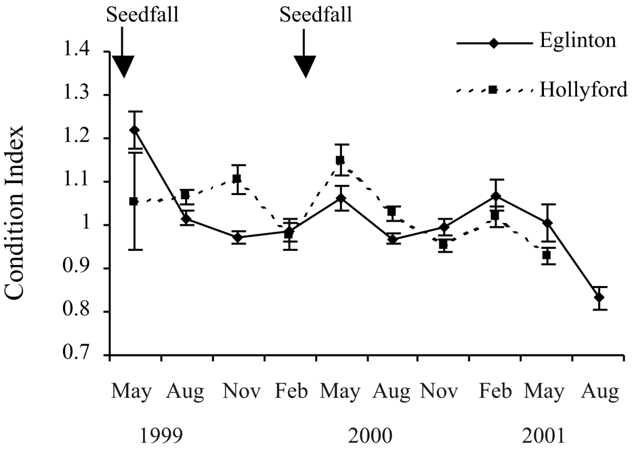


Figure 4. Changes in the mean condition index (± se) of large (>65 mm head–body length) animals in each valley from May 1999 to August 2001. Timing of significant seedfall in 1999 (Eglinton only) and 2000 (both valleys) is shown.

seedfall event, the mouse population decline begins in August or November, and by the following February, mouse populations have fallen to their lowest levels. Stoats only produce offspring in summer (weaned in January–February)—therefore the beginning of the mouse population decline is not related to an increase in stoat numbers. Predators may exacerbate a decline indirectly by influencing the foraging efficiency of prey. We did not find any evidence for stoat abundance affecting the relationship between seedfall and mouse *r* between the two valleys, which suggests that the increased predation pressure in the Hollyford Valley is not sufficient to change mouse foraging behaviour to the extent that it affects population growth and decline.

Conclusion

This study reconfirms the general model of Choquenot and Ruscoe (2000) that the quantity of seed produced by the beeches in New Zealand can be used to predict mouse population growth. We were unable to detect any influence of stoat abundance on mouse population growth during these three years. This leads to the conclusion that these mouse populations are food, rather than predation, limited.

Acknowledgments

Thanks to the many people who helped with field work. Ray Webster helped with analysis and A. Byrom, P. Lyver, S. Richardson and B. Warburton reviewed the manuscript. The study was carried out with Landcare Research Animal Ethics Approval (02/99) and was funded by the Foundation for Research, Science and Technology (Contract C09X0009).

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Impact of farm management practices on house mouse populations and crops in an irrigated farming system

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Abstract. House mice cause serious damage to agricultural crops in Australia. A set of farm management practices was developed with farmers, extension officers and scientists for a complex farming system incorporating irrigated winter cereals, rice and summer crops. This paper reports on the effect of baiting and spraying margins of crops on damage to winter crops when mouse densities were low to moderate. Baiting with zinc phosphide reduced the consumption by mice of census cards by 86%, but there was a 35% reduction on unbaited sites. Populations declined further to low levels before harvest and there was no difference in damage to wheat crops before harvest. Spraying margins of winter cereal crops with herbicides to reduce weeds and grasses significantly reduced plant growth by 47% and abundance of mice on sprayed sites by up to 77%. Damage to crops was <5%, and there was no observed reduction in damage to wheat crops. These were two examples of a range of farm management practices. Further analyses are required to look at the impacts over the whole farm and through the combined effects of the recommended practices. A critical test of the recommended practices cannot take place until an outbreak occurs.

Introduction

The house mouse (*Mus domesticus*) is a serious pest to agriculture in Australia. Mouse populations occasionally undergo widespread irruptions (= mouse plagues) in the grain-growing regions of Australia once every four years on average, but their frequency for any particular region is generally one year in seven (Singleton 1989; Mutze 1991). In 1993/94, a mouse plague caused losses estimated at A$64 million (Caughley et al. 1994), while a mouse plague in the Murrumbidgee Irrigation Area in 1994 caused an estimated A$8 million damage to three irrigated summer crops alone (Croft and Caughley 1995). Farmers generally do not perceive they have a mouse problem until densities are >200 mice/ha. The timing of high numbers of mice in relation to the stage of crop development is critical to the level of pre-harvest losses.

Management of mouse population problems in Australia generally has been reactive rather than preventative. During mouse plagues, large amounts of poisons are distributed to control mouse damage and, in one instance, up to 500,000 ha of land was baited with zinc phosphide (see Singleton 2000 for review). There is conflicting evidence about the effectiveness of broad-scale application of rodenticides such as strychnine and zinc phosphide and possible impacts on non-target species (Brown et al. 2002).

Current research is aimed at examining the effectiveness of a range of farming practices to prevent significant damage by mice. These farming practices have been developed from an understanding of the ecology of house mice in the farming system and of how management actions can be integrated into existing farm management. This strategy is based on the concept of ecologically-based management (Singleton 1997; Singleton and Brown 1999). Farm management practices or cultural practices have been used to control a range of rodent pest species throughout the world and include mowing, harrowing, ploughing, irrigating, grazing, application of herbicides to reduce cover and seed set, and baiting when rodent numbers are high (White et al. 1998; Makundi et al. 1999; Jacob and Halle 2000). These practices have proven to be successful where one crop type is grown or when it is mixed with grazing.

Our study draws together data on the responses of populations of mice to farm management practices in New South Wales (NSW), Australia, in a mixed, summer cropping system. We compare the impact of particular farm management practices on mouse population abundance, biomass of plants along crops margins, and damage to crops.

Methods

Study site

The project began in July 1998 and ran for 4 years. Data were collected from 12 experimental sites managed by 7 farmers. Each site was situated within 30 km of Coleambally, southern NSW (34°51'S, 146°05'E; altitude 126 m). The topography of the region is flat to mildly undulating. The soils are predominantly heavy grey-cracking clays. The climate is Mediterranean, with hot dry summers and cool wet winters. The average rainfall at Griffith (40 km north of Coleambally) is 406 mm/year. Rainfall was below average in 1998 (88.6% of the long-term mean, LTM), above average for 1999 and 2000 (124.2% and 108.0% of LTM, respectively) and below average for 2001 (76.4% of LTM).

The main crops grown in the region are winter cereals (wheat, barley and oats, sown early winter, harvested mid-summer), flood-irrigated rice (sown mid-spring, harvested mid-autumn), and pulse-irrigated summer crops (maize, soybean, canola and sunflower, sown mid-summer, harvested mid-autumn). Fifty per cent of paddocks were double-cropped with a winter cereal followed by a summer crop. The average farm size is 250 ha and consists of 6–11 paddocks, each of approximately 20 ha in size. Some farmers also graze sheep.

Farmer actions for mouse control

A list of farm management practices was developed by an advisory panel for controlling the impact of mice on farms (Table 1). The panel consisted of farmers, representatives from the Irrigation Research and Extension Committee, extension officers from NSW Agriculture and scientists from the Commonwealth Scientific and Industrial Research Organisation (CSIRO). The panel met annually to develop, reconsider and make final recommendations on mouse control actions for summer-irrigated cropping systems. These practices were carried out on replicated treated and untreated sites. In this paper we report on the impact of two mouse control practices.

Impact of zinc phosphide baiting

Farmers on two sites considered that they had a significant mouse problem that warranted use of zinc phosphide. Bait was applied at 1 kg/ha by plane on 14–15 September 1999. The mouse populations were monitored using census cards before and after baiting to determine its effectiveness. Census cards are 10 × 10 cm pieces of

Table 1. List of recommended farming practices to reduce the impact of mice in the irrigated summer cropping area of southern New South Wales.

Action	Timing of action
Summer crop	
Cultivate early	May–Sept., spring, before winter
Sow early (on time)	Depends on rainfall
Harvest cleanly	Harvest
Control weeds/Remove food and cover/Spray	Twice (spray) early and follow up
Winter crop	
Pre-sowing stubble management—burn	Depends on weather
Pre-sowing stubble management—incorporate	Early as possible
Control weeds	Before spring
Sow early (on time)	Depends on rainfall
Sow deeper	At sowing
Increase sowing rate	At sowing
Monitor mice	Pre-sowing
Perimeter bait	Pre- or at sowing
Harvest cleanly	Harvest
Rice crop	
Stubble management—no action	
Stubble management—slash early	Soon after harvest
Stubble management—graze	Soon after harvest
Stubble management—burn early	After harvest
Stubble management—burn later	Following spring
Manage channels and banks	Ongoing
Bait stations	Before breeding season
Harvest cleanly	Harvest
Other actions	
Remove and reduce cover around sheds, buildings and silos	Continuous
Monitor for signs of mouse activity	Key times (early spring and autumn)
Clean up grain spills (silos, field bins)	Sowing and harvest
Mouse-proof houses, and grain and stock feed storages	Continuous
Bait key habitats using bait stations	Before spring

white bond paper (photocopying paper) soaked in vegetable oil and pegged to the ground using rigid wire pegs (10–20 cm long). The cards were set for two nights, but checked each day, and replaced on the first day if there was any evidence of chewing by mice. Cards were set in a 5 × 5 grid, 50 m from the edge of the crop, and 2 lines of 10 cards each were set along the edge of the crop, each line being 1 m apart. A 1 cm^2 grid pattern was printed on the cards. The number of cards chewed out of all cards set per site was used as a measure of mouse abundance.

The level of damage to the wheat crop was assessed on all sites 2 weeks before the farmer's expected date of harvest. Four transects were set through each crop. Each transect was separated by 50 m and was set at least 50 m from edges of crops (roads, fencelines etc). On each transect, damage to plants was assessed at five distances into the crop: 10, 20, 50, 100 and 150 m. Ten plants were assessed at each distance. These plants were selected by choosing every second plant on a perpendicular line from the transect. The number of undamaged tillers and damaged tillers were recorded per plant as well as the number of plants damaged per sampling point and reported as the percentage of mouse-damaged tillers.

Impact of spraying weeds

The impact of spraying weeds and grasses around the edge of winter cereal crops on mouse numbers and plant biomass was assessed using live-trapping (Longworth traps) and estimates of biomass from quadrats. Trapping was conducted in 6 × 7 grids placed 50 m into the crops, and from a trap-line along the edge of the crop, fenceline or channel bank. There were 15 trap stations spaced every 10 m, with 2 traps at each station. Traps were set for two consecutive nights. Biomass of weeds and grasses along the edge of the crop was estimated using photographs of known biomass. Reference photographs of known biomass were taken from 1 m^2 sample plots, which were hand clipped at ground level, dried and weighed (converted to kg/ha). Ten 1 m^2 estimates of biomass were taken from each trap line. Mouse damage to the wheat crop was assessed using the same techniques described above. For some farmers, spraying for weeds was conducted routinely around the whole farm, whereas other farmers conducted spraying specifically for this study.

Results and discussion

The application of zinc phosphide on two sites resulted in an 86.2% reduction in abundance of mice (Figure 1). A reduction of 35.2% occurred on untreated sites. Before harvest (November), mouse populations were low on treated and untreated sites (<0.5% census card take), there was little damage to wheat crops and no treatment effect (treated = 1.4% ± 0.8 se, $n = 2$; untreated = 2.5% ± 0.5 se, $n = 6$; $t_6 = 1.08$, $P = 0.323$). This reduction in mouse abundance after poisoning was consistent to that found in other studies in Australia (Caughley et al. 1998; Brown et al. 2002). However, by November there was a similar reduction in mouse numbers on unbaited sites, hence there was no economic benefit.

Spraying weeds and grasses along fencelines significantly reduced the amount of biomass on the edge of cereal crops compared to unsprayed sites by 46.7% ($F_{1,11} = 13.053$, $P < 0.01$) (Figure 2). Furthermore, the abundance of mice was on average 37.3% (up to 77%) lower

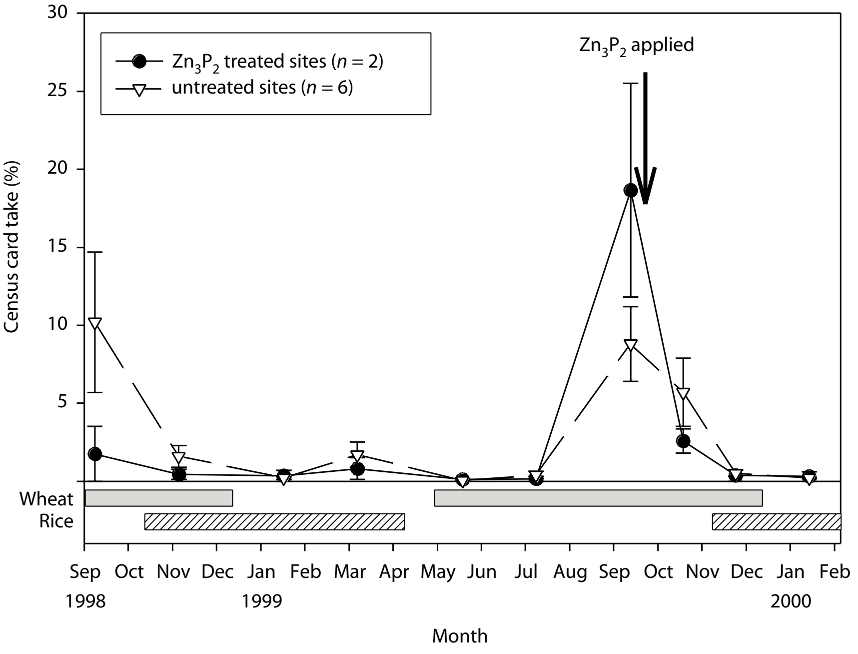

Figure 1. Impact of zinc phosphide (Zn_3P_2) on house mouse abundance measured using census cards on treated and untreated sites (mean ± se). Zinc phosphide was applied aerially on 14–15 September 1999. The horizontal bars represent the duration of the wheat and rice crops.

on sprayed sites compared to unsprayed sites ($F_{1,47}$ = 4.149, $P < 0.05$) (Figure 2). There was no interaction with time ($F_{11,47}$ = 1.005, P = 0.456). Although mouse abundance peaked in June 2000, it was not significantly higher than other months. The average damage to wheat tillers in 1999 was 4.9% (± 0.9 se, n = 3) and 3.6% (± 1.6, n = 3) to sprayed and unsprayed sites, respectively, and for wheat tillers in 2000, damage was 2.3% (± 0.9 se, n = 3) and 0.6% (± 0.3, n = 3) to sprayed and unsprayed sites, respectively. There was no difference in the level of damage between treatments ($F_{1,8}$ = 2.092, P = 0.186), but there was significantly more damage in 1999 compared with 2000 wheat crops ($F_{1,8}$ = 7.221; $P < 0.05$). Farmers generally do not notice this level of mouse damage.

It is possible to reduce the abundance of mice through applying herbicide sprays around the perimeter of crops, however because the abundance of mice was low to moderate and the level of damage relatively low, the impact on damage has not been adequately tested. If mouse populations had been higher, we would have expected to see reductions in damage to crops if these management practices were adopted. Mouse populations decline to baseline levels in November each year in the Murrumbidgee Irrigation Area (P. Brown et al., unpublished data), so damage is generally low before harvest.

Spraying and other forms of habitat manipulation around the perimeter of crops to reduce cover and availability of food have been successfully applied in a range of situations. Black rat (*Rattus rattus*) damage to macadamia orchards in Australia was reduced by 65% through manipulation of adjacent habitats by slashing grasses and applying herbicides (White et al. 1998). In East Africa, environmental manipulation has led to some success in reducing damage caused by rodents, for example, areas that are cleared of bushes or that support grazing usually have a lower carrying capacity of rodent populations, while other practices such as poisoning and trapping remain popular (Makundi et al. 1999).

While individual actions can have positive impacts on mouse populations, it is the combined effect of a range of management practices within a complex farming system that is of interest to farmers. When the study is completed, we will undertake analyses of the responses of mouse populations to a range of farming practices and the associated effects of mouse damage to crops and their yields in both winter and summer crops.

Conclusions

Most of the management of mouse plagues in Australia has been reactive rather than preventative, partly through the availability of broad-acre rodenticides such as strychnine and zinc phosphide. There are a range of farm management practices available that farmers can undertake, or are already undertaking, which can have benefits in terms of reducing mouse abundance and damage to crops. We believe that these could be incorporated within existing management practices for farmers at little cost in terms of time or money, and could lead to significant gains through increased yield, without relying on the use of rodenticides. While the results from this study showed a reduction in mouse abundance, there was no reduction in

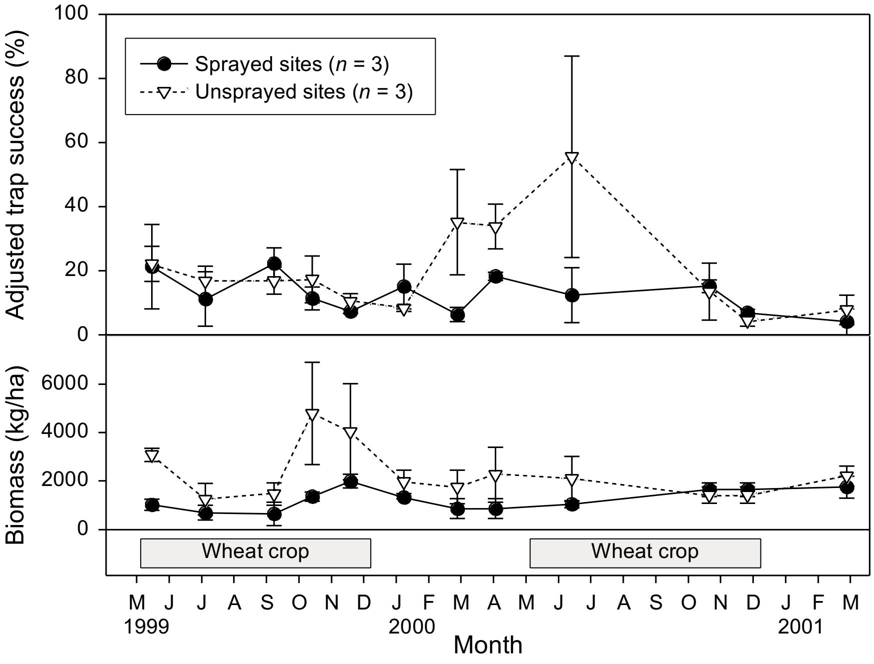

Figure 2. Impact of spraying weeds and grasses around the margins of wheat crops on house mouse abundance (adjusted trap success) and on the biomass of weeds and grasses (kg/ha). Mean ± standard errors are shown. The horizontal bars represent the duration of the wheat crops.

damage to crops when mouse populations were low to moderate. Further work is required when mouse numbers are high and to clarify whether: (1) farmers can do nothing when mice are low and only undertake practices when mice are building up; or (2) farmers that undertake these practices when mouse numbers are low will have less damage when mice are high.

Acknowledgments

We are grateful for the involvement of the farmers in this project: V. Filmer, K. Russell, I. Sutherland, P. and C. Hardy, G. Druitt, T. Graham and M. Bramston. We also thank D. Jones, A. Lewis, K. Leslie, J. Winsbury (CSIRO), R. Eade, J. Osmond (Narrandera Rural Lands Protection Board) and J. Farrell (NSW Agriculture). This project was funded by the Natural Heritage Trust (through the National Feral Animal Control Program of the Bureau of Rural Sciences). This research was conducted in accordance with the Australian code of practice for the care and use of animals for scientific purposes.

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Seasonal differences in bait acceptance by forest-dwelling rats following simulated aerial 1080 possum control operations in New Zealand: interim results

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Abstract. Ship rats (*Rattus rattus*) were trapped following 10 simulated possum (*Trichosurus vulpecula*) control operations using aerially-sown non-toxic baits laced with rhodamine B. These surveys were carried out in different areas and at different times over 3 years in the Whanganui National Park, North Island, New Zealand. Preliminary examination of the data found that between 79 and 100% of ship rats contained traces of rhodamine dye, indicating that they had eaten, or at least handled, baits. Those rats that were caught following winter and spring operations were more likely to contain rhodamine B than those caught in autumn and summer. During these surveys, mice (*Mus musculus*) were incidentally caught in the traps set for rats. The proportions of mice containing rhodamine varied between 40 and 100% and those caught in winter or summer were more likely to have taken baits than those caught in autumn or spring. At the time of writing there was still one more survey to be completed.

Introduction

Aerial 1080 (sodium monofluoroacetate) operations to control possums (*Trichosurus vulpecula*) in New Zealand have traditionally been timed to occur in winter, although they often do not take place until the following spring due to the requirement for a reasonable period of fine weather. Recent work by Landcare Research has shown that there are no seasonal preferences in bait acceptance by possums following simulated aerial 1080 operations (Morgan et al. 2000). This may encourage managers to opt for summer control operations simply because the chances of having predictable periods of fine weather are much higher. Rodent, or at least ship rat (*Rattus rattus*), numbers have been reduced following successful aerial-sown 1080 possum control operations (Innes et al. 1995; Miller and Miller 1995). However, results from aerial 1080 possum control operations in the Pokeka Valley, Wanganui National Park and at Boundary Stream, Hawkes Bay, suggest that rat numbers are not always significantly reduced, even when possums are (McRitchie 2000; J. Campbell, personal observations). Currently, little is known of any seasonal differences in bait acceptance by rats following these aerial 1080 operations. Dowding and Murphy (1994) observed some interesting differences in bait take between male and female rats during an aerial 1080 operation in Northland and suggested there might be seasonal or sexual effects that warrant further investigation. Timing possum control operations to maximise the by-kill of rats, and to coincide with the breeding season of most forest birds, could produce greater conservation gains.

The primary aim of this work was to determine if there were seasonal differences in bait acceptance by forest-dwelling rats following simulated aerial 1080 operations to target possums. In addition, we hoped to determine if there were seasonal differences in bait take between sexes within the sample population of rats. The results from the first 10 surveys of a study conducted over 3 years are summarised here.

Materials and methods

Once each season between October 1999 and July 2002, non-toxic cereal baits (Wanganui No. 7), surfaced-coated with 8% rhodamine B (RB) solution as a marker of bait uptake, were aerially sown at 3 kg/ha over an approximately 90 ha study block in forest in or near the Wanganui National Park, North Island, New Zealand. A new site was selected every season to ensure each survey was independent from previous ones and baits were only sown when we could reasonably predict three fine nights following application. On the fourth day (three nights) after the bait was sown, rats were kill-trapped and possums poisoned using cyanide paste laid near the rat traps for three nights on two randomly-orientated 3.24 ha plots. These plots were separated by an absolute minimum of 200 m within, and no closer than 200 m to the edge of, the 90 ha treatment area. All rats trapped were identified to species, weighed, measured, sexed, and examined internally for the presence or absence of RB (indicating whether or not the rat had eaten non-toxic bait). Usually the RB could be easily detected by eye, however some rodents required inspection under an ultraviolet fluorescent lamp before the marker could be detected.

Statistical analysis

We used an exhaustive CHAID (Chi-squared automatic interaction indicator) analysis to explore predictors (season, sex, year of survey, the night the rat was trapped (1st, 2nd or 3rd night of trapping) and the number of possums poisoned in the survey) that may have affected whether RB was detected in an individual rodent. This algorithm examines all possible splits for each predictor based on chi-square statistics (De' ath and Fabricius 2000) and is implemented in AnswerTree, an SPSS data classification system.

Results and discussion

To date, 10 simulated aerial 1080 operations and trapping surveys had been conducted (two in spring, three in summer, two in autumn and three in winter) and 300 ship rats, two Norway rats (*Rattus norvegicus*) and 98 mice (*Mus musculus*) were caught. The proportion of rats trapped in each survey marked with RB varied between 79 and 100%. We have made two important assumptions with the results from these simulated aerial 1080 operations using non-toxic baits. The first is that the proportions of rodents that would take toxic baits in each season, or within each sex, would be the same as these non-toxic baits. The second is that those animals marked with RB would have consumed lethal doses of a poison and that any sub-lethal doses are not associated with a particular season or sex. CHAID exploration of the pooled data collected to date (Table 1) suggested that those rats that were caught following winter and spring operations were more likely to be marked than those caught in summer and autumn (χ^2 = 8.58, df = 1, P = 0.0034). The CHAID analysis also indicated that those rats caught on the first two nights of trapping were more likely to be marked than those caught on the third night, and that those rats caught on surveys where 124 or fewer possums were poisoned were more likely to be marked than those where 157 or more possums were poisoned (χ^2 = 31.34, df = 1, P = <0.0001 and χ^2 = 9.05, df = 1, P = 0.0026, respectively). Sex or the year that the surveys were carried out did not appear to be important indicators of whether a rat was likely to be marked (χ^2 = 3.13, df = 1, P = 0.0767 and χ^2 = 4.397, df = 1, P = 0.1131, respectively). We used the CHAID analyses in this paper only to provide some indications of the likely predictors of bait acceptance by rats, because at the time of writing there was still one more field survey to be carried out in spring 2002. Also, some of the rodent specimens collected from the 2002 autumn and winter surveys still required examination in the laboratory to confirm that they were not marked with RB, thus the proportions given here are the minimum. Nevertheless, it is interesting to note the apparently higher proportions of rats marked in winter and spring compared to those in summer and autumn. A reduction in ship rat numbers in late winter or early spring following an aerial 1080 operation would provide some relief for those native birds most sensitive to rat predation whilst nesting in spring. Ship rat diet can vary seasonally in New Zealand (Innes 1990) and it may be that there were more alternative foods available during autumn (seeds) and summer (flowers and invertebrates), or the difference was a result of greater competition with possums for the baits in those seasons. The rats caught on the third night of trapping (six nights after the bait was sown) were apparently less likely to be marked than those caught on the previous two nights. In most of the surveys, the baits were no longer observed on the forest floor by three to five nights after they were sown, particularly when there were large numbers of possums poisoned. Those rats trapped on the third night may have been individuals that moved in from outside the treated area and/or represented the more neophobic members of the population. This could also be because the RB marking had worn off, however we suspect this is unlikely because when we did the pilot study for this work we were still able to detect RB in rats caught 2 weeks after the bait drop.

Table 1. Total numbers of ship rats (*Rattus rattus*) caught and proportions (%) of these containing traces of rhodamine B (RB) for each season and for both sexes.

Season/sex	Number of surveys to date	Total number of ship rats caught[a]	Overall % with RB
Spring	2	91	93.7
Summer	3	72	87.5
Autumn	2	51	82.4
Winter	3	86	94.2
Males	All 10 combined	154	89.6
Females	All 10 combined	143	95.1

[a] Three ship rats were scavenged whilst in the trap so could not be correctly autopsied for presence of rhodamine B and the sex of one of these could not be determined.

Mice were not specifically targeted but they were caught incidentally in the rat traps. The proportion of mice trapped in each survey marked with RB varied between 40 and 100%. CHAID exploration of the pooled data collected to date (Table 2) suggested that those mice that were caught following winter and summer operations were more likely to be marked than those caught in autumn and spring (χ^2 = 9.54, df = 1, P = 0.0201). Sex or the year of the survey did not appear to be important predictors of whether a mouse was likely to be marked (χ^2 = 3.19, df = 2, P = 0.203 and χ^2 = 0.6, df = 1, P = 0.4391, respectively). The number of mice caught was quite small, so our results for this rodent should definitely be treated with a high degree of caution. The relatively low bait acceptance (compared to rats) by mice in some surveys, even with this small sample, is nevertheless worth noting and may help explain why mouse populations seem to recover soon after aerial 1080 possum control operations (Innes et al. 1995; Miller and Miller 1995).

Table 2. Total numbers of mice (*Mus musculus*) caught in rat traps and proportions (%) of these containing traces of rhodamine B (RB) for each season and for both sexes.

Season/sex	Number of surveys to date	Total number of mice caught[a]	Overall % with RB
Spring	2	17	47
Summer	3	19	68.4
Autumn	2	31	48.4
Winter	3	31	83.9
Males	All 10 combined	56	69.6
Females	All 10 combined	41	53.7

[a] One mouse was scavenged whilst in the trap so the sex could not be determined.

The main reason that Department of Conservation managers use aerially-sown 1080 is to control possums for forest-canopy protection, not to control rodents. The incidental kill of rodents is usually seen as a beneficial side effect and is occasionally factored into the planning at some conservation sites. The most effective time to control possums using 1080 is when ambient temperatures are lowest and the animals more susceptible to 1080 poisoning (Veltman and Pinder 2001). Our interim results suggest that during winter a high proportion of both rats and mice will eat baits suggesting that this is the season to achieve the greatest knockdown of rodents. So the advantages of doing an aerial 1080 operation in the warmer months when the chances of having predictable periods of fine weather are much higher should be outweighed by the potential for a better knockdown of both possums and rodents in winter.

Interim conclusion

Our interim results indicate that there may be seasonal differences in non-toxic bait acceptance of forest-dwelling ship rats and mice following simulated aerial 1080 operations. Rats trapped in spring and winter were more likely to accept baits than those trapped in autumn and summer and mice trapped in winter and summer were more likely to accept baits than those trapped in autumn and spring. Other factors such as sex or the year of the survey did not seem to be important predictors of whether or not a rat or mouse would take baits, although competition with possums may have influenced what proportion of rats took baits.

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Reproduction and growth in house mice from cold, hot and thermally moderate environments

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Abstract. The house mouse (*Mus domesticus*) is found throughout Australia, and is successful in a wide range of climates. We examined the reproductive success and growth rate of young in differing thermal regimes (13°C, ‘cold’; 22°C, ‘control’; and 30°C, ‘hot’) in a laboratory colony of house mice derived from wild stock from Mudgee, New South Wales. Female mice in all groups did not always have a post-partum litter following the birth of their first litter, although post-partum litters were born in subsequent pairings. Litter sizes did not differ between treatment groups, although more young were born from post-partum matings. Young from the ‘hot’ group were smaller than for other groups, and their growth rates were slower. The observations on post-partum activity, and the differences in growth rates, may be of significance in explaining the sudden plague activities of mice in some parts of Australia.

Introduction

The house mouse (*Mus domesticus*) has been resident in Australia for the past 200 years, and during that time has radiated throughout the continent. While successful throughout Australia, it is less common in desert regions. However, unlike its counterpart in Europe, the Australian house mouse is more widely dispersed in the environment than around farm buildings and houses.

The adaptation of the house mouse to the Australian environment has been a topic of study for at least 30 years, with much of the focus centering on how mice increase their population size at times to plague proportions. Plague activity is found in some North American and European rodents (Bronson 1979), but is not known for the house mouse in Europe (Singleton and Redhead 1990). Australian studies have demonstrated that house mouse populations increase in response to rainfall, although other factors also seem to be important (Singleton 1989; Pech et al. 1999). One important factor may be temperature, and so our aim was to investigate the influence of temperature on some basic reproductive parameters in laboratory-bred house mice that originated from a wild population.

Materials and methods

Ten house mice (6 females, 4 males) were captured at Mudgee, New South Wales (NSW) (32°36'S, 149°35'E) and transported to the laboratory to establish a captive colony. Mudgee was selected because a previous study had demonstrated that mice from this site were ‘average’ for a broad range of morphological parameters (Crowther et al., this volume).

Animal husbandry

Mice were housed in standard cages 300 × 200 × 450 mm and provided with wood shavings, a nest box with nesting material, and a variety of toys or novel objects which were changed weekly. Laboratory mouse cubes and drinking water were available *ad libitum*, and animals were weighed weekly, at which time their cages were also cleaned. The disturbance caused by cleaning days was rewarded with a handful of mixed parrot seeds on the day.

When females were at least 12 weeks old, they were placed with unrelated males for breeding purposes. A second nest box with nesting material was provided at all times. When young were born, the parents were left together for a few days longer to allow the opportunity for post-partum mating to occur, and then males were removed from the cage and housed separately. Females observed to be pregnant at the weekly monitoring session were checked more frequently to determine the date of birth of the young. Females with young were housed together in large cages (450 × 600 × 450 mm), and provided with two nest boxes with nesting material, and, when the young were a few weeks old, toys and novel objects. If a post-partum litter was observed, the young of the first litter were removed and housed together in the larger cages in same sex groups until used for breeding, or for other physiological experiments. Young were weighed weekly for 12 weeks. Post-breeding animals were housed individually. Litter size, survivorship to weaning, evidence of post-partum reproductive activity, and body mass were recorded. All experiments were performed with permission from the University of New England Animal Ethics Committee and NSW National Parks and Wildlife Service.

Temperature treatments

The laboratory colony was established initially under the natural photocycle of Armidale, NSW, and at 22 ± 2°C, in September 2000. When sufficient numbers of mice were available, animals were divided into three treatment groups, with offspring of all founder individuals distributed evenly across the groups. Animals were housed in temperature-controlled rooms at either 13 ± 2°C, 22 ± 2°C, or 30 ± 1°C. All animals were placed under broad-spectrum fluorescent lighting of 250 Lux (mean value at cage lids) for light:dark 13:11 h. During the scotophase, animals were exposed to a dim red light.

Data analysis

Litter sizes between experiments were compared by analysis of variance (ANOVA) followed by Tukey's pairwise tests. Partial and complete losses of litters before weaning were compared between treatments by Chi-squared test. Growth rates were plotted, regression lines calculated for each group, and data were analysed by multiple regression and ANOVA of the Y-intercept and slopes (Zar 1996).

Results and discussion

Mating outcomes

Post-partum matings occurred in approximately half the pairings in all treatment groups (control, 48%; 'hot', 53.4%; 'cold', 47.5%). However, pairings that produced no post-partum litter occurred more often in females that were young, or had not previously had a litter (i.e. it was their first opportunity to have a post-partum oestrus) (control, 71.4%; 'hot', 71.4%; 'cold', 73.3%) compared to pairings which produced a post-partum litter (control, 53.8%; 'hot', 40.1%; 'cold', 57.1%; $\chi^2 = 3.91$, $P < 0.05$).

Litter outcomes

Overall, there were no differences in numbers of young born in each litter for the different treatments (Table 1), although there were differences in the numbers

Table 1. Reproductive success for each of the treatment groups of mice. Data are expressed as means ± se (except for percentages). For mean litter sizes, all treatment effects were not significant.

Groups	Mean litter sizes born (range)	Mean litter sizes weaned (range)	% of litters with all young lost before weaning	% of litters with some young lost before weaning
Control (22 ± 2°C) All litters (*n* = 36)	5.53 ± 0.25 (3–9)	5.17 ± 0.31 (0–8)	2.8	13.8
'Hot' (30 ± 2°C) All litters (*n* = 42)	5.48 ± 0.20 (3–8)	4.72 ± 0.31 (0–8)	9.5	28.6
'Cold' (13 ± 2°C) All litters (*n* = 55)	5.58 ± 0.27 (1–10)	5.00 ± 0.34 (0–10)	12.7	29.1
Control (22 ± 2°C) Litters with no post-partum mating (*n* = 11)	5.36 ± 0.53 (3–9)	5.18 ± 0.48 (3–8)	0	18.2
Control (22 ± 2°C) Litters with a post-partum mating (*n* = 12)	5.33 ± 0.38 (3–7)	5.33 ± 0.38 (3–7)	0	0
Control (22 ± 2°C) Product of post-partum mating (*n* = 13)	5.85 ± 0.71 (3–9)	5.00 ± 0.71 (0–9)	7.7	23.1
'Hot' (30 ± 2°C) Litters with no post-partum mating (*n* = 13)	4.62 ± 0.33 (3–6)	3.84 ± 0.39 (0–5)	7.7	38.5
'Hot' (30 ± 2°C) Litters with a post-partum mating (*n* = 14)	5.67 ± 0.25 (5–8)	5.00 ± 0.43 (0–7)	7.1	21.4
'Hot' (30 ± 2°C) Product of post-partum mating (n = 15)	6.00 ± 0.37 (4–8)	5.19 ± 0.65 (0–9)	13.3	33.3
'Cold' (13 ± 2°C) Litters with no post-partum mating (*n* = 21)	5.16 ± 0.53 (1–9)	4.79 ± 0.61 (0–9)	14.3	23.8
'Cold' (13 ± 2°C) Litters with a post-partum mating (n = 17)	5.65 ± 0.41 (3–9)	4.53 ± 0.63 (3–9)	17.6	41.2
'Cold' (13 ± 2°C) Product of post-partum mating (*n* = 17)	6.00 ± 0.45 (3–10)	5.75 ± 0.50 (0–10)	5.9	29.4

of young produced from different mating activities (no post-partum mating, 5.05 ± 0.28 (n = 45); with post-partum mating, 5.57 ± 0.20 (n = 43); product of post-partum mating, 5.96 ± 0.23 (n = 45); F = 3.25, P < 0.05). All treatment groups lost complete litters before weaning, and all treatment groups had litters that lost some young before weaning (Table 1). Significantly fewer young were lost from the control group (χ^2 = 34.85, P < 0.001). Growth rates were significantly different between groups up to 35 days (immediately post-weaning, Figures 1 and 2). After weaning, the growth rates were also significantly different between groups; young grew at a different rate than before weaning (Figure 2), although the regression r^2 was low, and thus the regression equations are not presented (see Figure 2). The lines of best fit from 0–35 days were control body mass =1.38 + 0.293Days (r^2 = 88.2%, P < 0.001, n = 540); 'hot' body mass (g) =1.26 + 0.266Days (r^2 = 85.0%, P < 0.001, n = 562); and 'cold' body mass (g) 1.52 + 0.276Days (r^2 = 87.4%, P < 0.001, n = 844). The slopes of the regression equations of all treatment groups were significantly different from one another (F = 8.919, P < 0.05).

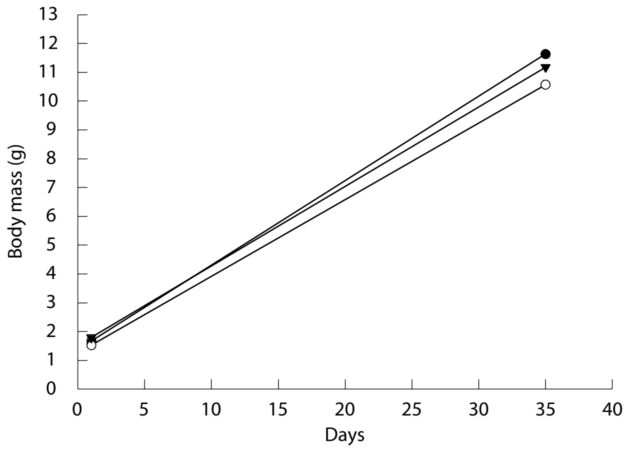

Figure 1. Regression lines for the growth data for the three treatment groups. Closed circles indicate 'control' treatment (22 ± 2°C), open circles indicate 'hot' treatment (30 ± 1°C), and closed triangles indicate 'cold' treatment (13 ± 2°C).

Temperature appears to have an effect on reproductive outcomes for the Australian house mouse. Overall litter sizes were similar between treatment groups, and our data are consistent with other studies (Pelikán 1981; Singleton et al. 2001). However, more young were lost from litters born to females in 'hot' and 'cold' environments, similar to results found in other studies on cold-exposed mice (Barnett and Widdowson 1965; Barnett 1973). A more significant effect of temperature was seen in the growth patterns of the litters. Young from the 'hot' group grew more slowly, and were smaller than young from other groups—this trend continues throughout the post-weaning period (see Figure 2; and Crowther et al., this volume). Young from 'cold' environments also grew more slowly than control young, although their body mass increased after the post-weaning period, again similar to other studies (Barnett and Widdowson 1965; Barnett 1973; Marsteller and Lynch 1987). The differences between 'cold' and control treatments in these parameters are notable because many other studies observed the same differences in cold temperatures of 5°C and –3°C (Barnett and Widdowson 1965; Barnett 1973; Marsteller and Lynch 1987), significantly colder than our study. There are few studies of higher than room temperatures on reproduction and our data suggest that, for the house mouse, hotter temperatures may be more physiologically stressful than colder temperatures.

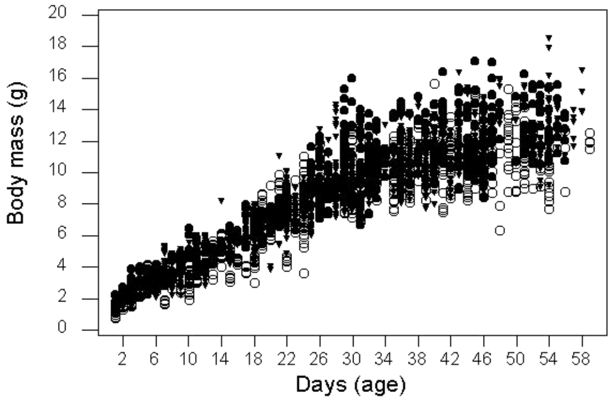

Figure 2. All growth data from 0–60 days for animals from each treatment group. Closed circles represent data points from the 'control' group (22 ± 2°C, n = 767), open circles represent data points from the 'hot' group (30 ± 1°C, n = 828), and closed triangles represent data points from the 'cold' group (13 ± 2°C, n = 1208).

While overall litter sizes were similar between treatment groups, in all groups fewer young were born in litters from females that did not have a post-partum mating and consequent litter. Many of these females were young, first-time mothers, indicating that maturity may influence reproductive outcome in house mice. The larger litter sizes in post-partum litters also may be due to the increasing age of the mothers, and it has been observed that older Australian house mice have larger litters (Singleton et al. 2001). In Australia, plague activity occurs after rainfall and is believed to be closely linked to food availability (Singleton and Redhead 1990). Our study suggests that temperature and the age of the mothers may also have an overall effect on reproductive outcome. Survivorship of older females under more favourable conditions, influenced by both temperature and rainfall, could mean a sudden explosion of young as these older females are producing more young and more post-partum litters. If followed by reproductive recruitment of younger females as suitable conditions continue, the mouse population could rapidly increase.

Conclusion

The thermal environment significantly influences reproductive output, with both 'cold' and 'hot' temperatures affecting litter losses and growth of young. The more deleterious effects of hotter temperatures may explain why mice are sparse in the interior of Australia. The complex interactions between temperature and reproductive success of 'younger' versus 'older' mothers may contribute to the population explosions of house mice seen in Australia.

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Morphological variation within Australian populations of the house mouse: an observational and experimental approach

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Abstract. Morphological variation within Australian populations of the house mouse (*Mus domesticus*) was evaluated using measurements of head–body length and relative tail length. In order to examine the effects of temperature on these characters, and to attempt to experimentally replicate this variation, mice from one of the wild populations were raised under three different temperature regimes in captivity (13 ± 2°C, 22 ± 1°C and 30 ± 1°C). There was considerable variation between wild populations in both head–body length and relative tail length. Comparisons with estimated values of mean annual temperature at study locations found that mice were smaller in cooler climates (opposing Bergmann's Rule), but no real climatic trends were found for tail length. In contrast, mice bred at different temperatures within the laboratory displayed very large differences in morphology, with those raised at the warmest temperature being the smallest in size and having relatively longer tails. These results corresponded with both Bergmann's Rule and Allen's Rule. The differences between the treatments were more apparent in younger mice (6 weeks of age) than those at 12 weeks and 24 weeks. It is apparent that just a few degrees difference in temperature has a major effect on the morphology of house mice. However, comparison with the wild populations shows that many other factors must have a role in shaping mouse morphology. The research presented in this paper and continuing work on internal organ systems has major implications for taxonomy and adaptation of house mice, and could help explain the success of mice in colonising the wide range of habitats within Australia and other parts of the world.

Introduction

House mice (*Mus domesticus*) in Australia have a continent-wide distribution and are found in an extremely wide range of temperature and rainfall zones. This includes arid areas which receive as little as 100 mm of rainfall per year to very mesic areas that receive as much as 8350 mm per year. The life history of house mice is typified by rapid population turnover and small demes, enabling swift colonisation of new areas (Berry 1981). Thus, mice can rapidly diverge from their founder populations (Berry 1981). Since European people probably introduced house mice into Australia a little over 200 years ago (Singleton and Redhead 1990), Australia is the perfect place to study the changes that this species makes in new environments. Studies of Australian *M. domesticus* on limitation to growth, niche invasion and morphological variation in non-Australian mice have been made, but there are very few studies to date on morphological variation within Australian mice.

Morphological characters such as tail length have been used to diagnose and distinguish between species of *Mus*. Short tails are believed to be the preserve of *M. musculus* and long tails of *M. domesticus* (Marshall and Sage 1981). However, in the laboratory, tail length is significantly modified by environmental temperature. When mice are reared at low (–3°C) temperatures, the tail length is shorter by up to 10% than in mice reared at room temperature (22°C) (Barnett 1965; Barnett et al. 1975).

In this study, we examined variation in cranial and dental characteristics, external measurements, coat colour, vertebrae number, and renal and adrenal structure in wild-caught mice. The populations came from a range of climatic and habitat types throughout Australia. To examine for the effects of temperature on morphology and attempt to replicate the variation found in the wild populations, mice from the wild were bred in captivity under different temperature regimes and then the same measurements as from the wild mice were taken. For the purposes of this publication, only relative tail lengths and head–body lengths will be reported.

Materials and methods

Sampling areas

Mice were collected from 18 localities around Australia to represent a variety of habitat and climate types. The populations presented here are Jindabyne (36°24'S, 148°37'E), Emerald (37°53'S, 145°27'E), Broken Hill (31°58'S, 141°27'E), Ouyen (35°4'S, 142°19'E), Mudgee (32°36'S, 149°35'E), Kangaroo Island (35°45'S, 137°37'E), Hattah-Kulkyne (34°42'S, 142°17'E), Millicent (37°35'S, 140°21'E), Mildura (34°11'S, 142°09'E) and Woodcroft (35°06'S, 138°33'E). All mice were collected between April and May 1999 in order to reduce seasonal variation. Further locations covering the breadth of Australia are currently being processed. Animals were judged to be adult based on tooth wear, cranial development and reproductive condition.

Data acquisition and analysis

Head–body (HB), tail (TV), ear, and hind foot lengths were measured with vernier calipers on dead specimens to the nearest 0.05 mm, and body mass with electronic scales to the nearest 0.001 g. Carcasses were then placed in buffered formalin for internal organ measurements and skulls were cleaned for cranial and dental measurements. Skull and dental dimensions were taken with digital calipers to the nearest 0.01 mm on the right side of the skull, except in damaged specimens. Kidneys, adrenal glands and reproductive tracts were dissected out of the mice and weighed using electronic scales to the neared 0.001 g. Localities for each collection were assigned coordinates for latitude, longitude and elevation. The mean annual temperature at each locality was estimated using the program BIOCLIM within the ANUCLIM package (e.g. Crowther 2002). Differences between populations were compared using a one-way analysis of variance (ANOVA) (males and females treated separately), and regressions of the mean of each character (weighted by sample size) versus the estimated mean annual temperature were computed.

Laboratory mice were selected from wild founders from Mudgee, New South Wales (32°36'S, 149°35'E) and placed in different rooms using one photoperiod regime (13:11 h light:dark) and three different temperatures (13 ± 2°C, 22 ± 1°C, 30 ± 1°C). Non-breeding animals were housed individually. When females were 12 weeks old, they were placed with unrelated males for breeding purposes. Refer to McAllan et al. (this volume) for more details of captive protocols. Offspring of these groups of mice were then killed at 6 weeks, 12 weeks or 24 weeks. In order to minimise pseudoreplication, each age class of treatment was replicated over time. Measurements were taken as for the wild-caught mice. Differences between sexes, ages and temperature treatments were compared using a three-way ANOVA.

Results and discussion

Wild caught animals

Thirty to 40 specimens were obtained from each locality. There was large variation in most characters measured between localities, including relative tail length (Figure 1a; $F_{9,201}$ = 8.87, $P < 0.001$) and head–body length (Figure 1b; $F_{9,203}$ = 2.34, $P < 0.001$). There was a significant trend for mice from cooler regions to be smaller (HB = 68.5 + 0.6*Temperature, R^2 = 0.86, $F_{1,8}$ = 50.7, $P < 0.001$), in contrast with the predictions of Bergmann's rule. Relative tail length showed no significant relationship with mean annual temperature (R^2 = 0.35, $F_{1,8}$ = 4.31, P = 0.07).

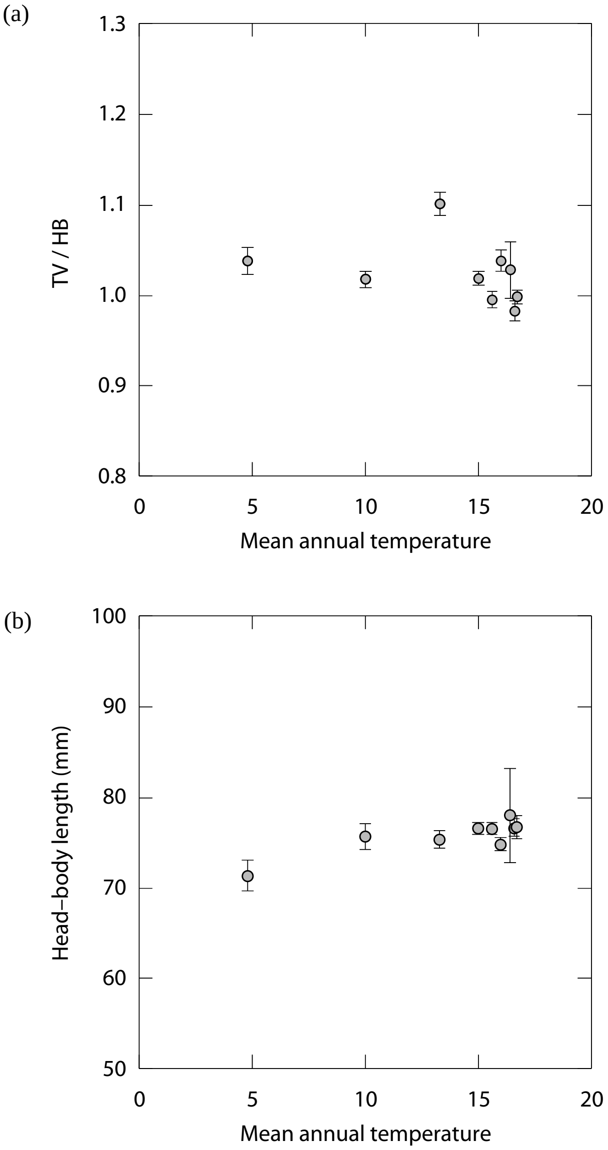

Figure 1. Relative tail (TV/HB) (a) and head–body lengths (b) for Australian populations of house mice versus mean annual temperature (°C) at collection localities (as estimated by BIOCLIM). Means are shown ± standard errors. Only males are shown—while there are sex differences in the data, the patterns of change are the same.

Laboratory trials

There were large differences between the three treatments in both relative tail length and head–body length. Mice raised at warm temperatures (30 ± 1°C) were significantly smaller than those raised at 22 ± 1°C and 13 ± 2°C (Figure 2b, Table 1), and had significantly longer tails (Figure 2a, Table 1). Tail lengths appear to get relatively shorter (compared with the head–body length) as the animals grow older, and the differences between animals raised at different temperatures appear to reduce (hence the significant interactions between age and treatment; Tables 1 and 2). However, the animals raised at 30 ± 1°C still maintain a relatively longer tail than those raised at other temperatures, even after 24 weeks.

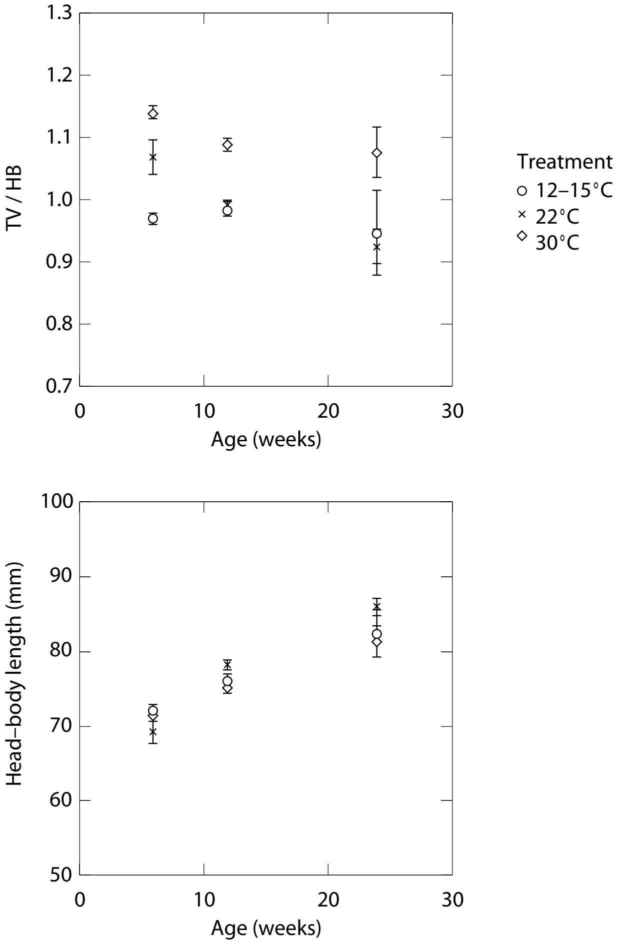

Figure 2. The effects of temperature on relative tail length (TV/HB) (a) and head–body length (b) for mice raised at three different temperatures (means and standard errors). Mice were killed at 6 weeks, 12 weeks or 24 weeks. Only males are shown—while there are sex differences in the data, the patterns of change are the same.

Singleton and Redhead (1990) suggested that the ratio of head–body length to tail length was not variable in Australian mice. They stated that tail length was generally longer than head–body length and also that the difference was rarely greater than 5%. In contrast, this study found much variation in tail length, with some populations having tails much shorter than head–body length (Figure 1). However, most tails were greater than 73 mm, indicating *M. domesticus* rather than *M. musculus* (Marshall and Sage 1981).

Differences between head–body lengths and tail lengths have implications for the thermoregulatory performance of house mice. A smaller body size and relatively longer extremities should assist in heat dissipation. Why the Australian wild mouse populations appear to contradict Bergmann's rule is not easily explained, especially when they appear to follow it under laboratory conditions. Other studies of small mammals, including mice, have found similar trends opposed to Bergmann's rule. Rowe-Rowe and Crafford (1992) found that mice on Gough Island were smaller at higher than lower altitudes. They suggested that the high altitude population was smaller since the mice bred later at higher altitudes. It is also possible that food quality and quantity are a larger determinant of body size than temperature in house mice, although this is yet to be tested. It is also possible that wild mice use behavioural responses to offset the thermoregulatory losses caused by other factors affecting morphology.

Table 1. Results of three-way analysis of variance (ANOVA) for relative tail length of house mice raised at different temperatures.

	SS	df	MS	F	P
Sex	0.033	1	0.033	9.778	0.002
Treatment	0.608	2	0.304	89.277	<0.001
Age	0.103	2	0.052	15.147	<0.001
Sex*Treatment	0.029	2	0.014	4.206	0.016
Sex*Age	0.017	2	0.008	2.484	0.085
Treatment*Age	0.060	4	0.015	4.400	0.002
Sex*Treatment*Age	0.025	4	0.006	1.841	0.121
Error	1.158	340	0.003		

Preliminary work on the skull and dental morphology, and kidney and adrenal size, has shown similarly large degrees of variation between populations of wild house mice. Measurements of these and other organs in the laboratory populations have shown that temperature also appears to have a major effect on their size. Completion of this section of the project promises to produce exciting results for the study of morphological plasticity in house mice and to have major implications for taxonomic

Table 2. Results of three-way ANOVA for head–body length of house mice raised at different temperatures.

	SS	df	MS	F	P
Sex	450.832	1	450.832	29.241	<0.001
Treatment	1.03.608	2	51.801	3.360	0.036
Age	4478.488	2	2239.244	145.239	<0.001
Sex*Treatment	56.305	2	28.152	1.826	0.163
Sex*Age	24.652	2	12.331	0.800	0.450
Treatment*Age	215.770	4	53.943	3.499	0.008
Sex*Treatment*Age	43.812	4	10.953	0.710	0.585
Error	5550.337	360	15.418		

research. For example, characters such as tail length, and cranial and dental characters are often used to diagnose species when in fact they could be just the result of environmental variation within a single plastic species.

Conclusion

Temperature has a dramatic effect on many morphological characteristics of house mice, including size and relative tail length. The differences between mice raised at different temperatures appear to be of different magnitudes at different ages, the largest differences being in the younger animals. Captive-reared mice conform with both Bergmann's rule (mice raised in warmer temperatures are smaller) and Allen's rule (mice raised in warmer temperatures have relatively longer tails). The differences in temperature need to be only a few degrees to produce large changes in the morphology. Morphological variation between wild populations was high, but the effects of temperature on this variation remain uncertain. There was a trend for wild mice to be smaller in cooler localities, contradicting the laboratory results, suggesting that factors other than temperature affect their body size. Current research on other features of Australian populations of house mice (e.g. the kidneys and cranium), both in the field and the laboratory, is producing exciting results and may help unravel the limits of morphological plasticity and adaptation in house mice. Care must also be taken in taxonomic studies, particularly within *Mus*, that morphological differences between taxa are not the result of phenotypic plasticity. The ability for mice to display such high levels of variation and to respond quickly to environmental conditions may help explain their broad distribution within Australia and throughout the world.

Acknowledgments

We thank G. Körtner for assistance in collecting mice, W. Westman for laboratory assistance and the Australian Research Council for funding.

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The impact of age on the breeding performance of female rice-field rats in West Java

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Abstract. The reproductive performance of rodent pest populations is partially determined by the age composition. The rice-field rat (*Rattus argentiventer*) is the major pest rodent in lowland irrigated rice fields in Indonesia. Their populations have pronounced intra-annual fluctuations due to the strong association between female breeding performance and the stage of the rice crop. We collected data from 1995 to 1998 in Sukamandi, West Java and estimated the age of rats based on the dry weight of their eye lenses. The reproductive status of rice-field rats was assessed by necropsy. The age composition fluctuated during the planting seasons. Recruitment of young occurred twice a year—once in the dry season and once in the wet season. The number of embryos per litter in rats 5–8 months old was higher than in younger and older rats. Rat control may be particularly efficient if conducted at the tillering stage of the rice crop—before reproduction commences and when there is a large cohort of medium-aged rats with high reproductive potential.

Introduction

Understanding how animal populations function is fundamental for successful management and conservation. For managing rodent pests, the focus is usually on increasing mortality, and culling is applied with variable success where rodent problems occur (Singleton et al. 2002). In lowland irrigated rice fields in Indonesia, the rice-field rat (*Rattus argentiventer*) is the only mammalian species that causes widespread pre- and post-harvest damage (Singleton and Petch 1994). Most farmers there control rodents by hunting, flooding burrows and trapping (Sudarmaji, Rochman et al., this volume), and by poisoning with alternative pesticides such as endosulfans and organophosphates because legal rodenticides are difficult to find or are too expensive. Another approach for reducing the density of unwanted species is the inhibition of fertility in females, which has been successfully applied in r-selected species (e.g. Twigg and Williams 1999).

Populations of rice-field rats may be particularly prone to the manipulation of female fertility because breeding occurs only in the presence of a rice crop and for only 6–8 weeks per cropping season (Leung et al. 1999). Their reproductive performance is thought to be highest early in the breeding season (Jacob et al. 2002). Two processes may cause a decrease in reproductive performance on the population level during the cropping season: (1) young females, which start reproducing in the same season they are born, may not have the physiological maturity to produce as many embryos as older females; and (2) a higher density of rats and diminishing resources at late stages of the cropping season may be limiting for the production of high litter sizes.

If resources restrict the reproductive performance in rice-field rats, the maintenance of low densities by fertility control could lead to increased reproductive output in young females and partially compensate for the effects of fertility control. If the reproductive performance in rice-field rats is limited by age, compensation may be limited and short-term anti-fertility effects may suffice to prevent high densities of rice-field rats.

We studied populations of rice-field rats in lowland irrigated rice fields in West Java, Indonesia during the wet seasons in 1996/97 and 1997/98 and the dry seasons in 1995–1998 to examine the relationship between the age of female rats and the number of embryos produced per litter.

Material and methods

The study took place in irrigated rice fields at experimental fields of the Research Institute for Rice and the Sang Hyang Seri seed farm in Sukamandi (06°20'S, 107°39'E), West Java in 1995–1998. For a detailed description of the study sites, see Singleton et al. (1998) and Brown et al. (2001). The climate in the region is tropical with an average temperature of 28°C and annual rainfall of 1450 mm. One rice crop is planted in the wet season (November–April) and one in the dry season (May–October).

Rice-field rats were collected by fumigation with sulfur gas and digging and by using multiple-capture wire-cone live-traps (20 × 20 × 50 cm) in rice fields and along the edge of rice fields. The traps were placed along drift fences to maximise trapping success. Traps were set in the evening and checked every morning at sunrise for 3 days in August, September, November and December 1995, January 1996, May–November 1997 and April, May and August 1998. Trapped rats were transferred to the laboratory and killed with CO_2 gas.

For age estimation, we used the weight of the eye lens and the age curves developed by Murakami (1992) for the rice-field rat based on rats collected within 20 km of our study site. Pregnant females were autopsied and the number of live embryos counted.

Results and discussion

We collected 1932 rats for age estimation. Of the 870 female rats caught, 67 were pregnant. Most rats were caught during the fallow stage post-harvest, possibly due to high trappability at that time (Jacob, Sudarmaji and Singleton, this volume). The number of rats was usually low during the tillering and flowering stage of the rice crop.

Age composition

The average age of the rats was 3.8 months (se ± 0.1 month) and the oldest rat collected was 34 months old (Table 1). Young (<2 months old) rice-field rats were present at almost all crop stages, the only exceptions being during ploughing and tillering in the wet season 1995/96 (Table 1). At that time, older rats (5–8 months old) dominated the population. The proportion of young rats in the population tended to be high from after late tillering until harvest but sometimes also during fallow (1997/98).

The predominance of 1–3-month-old rats in August and September 1995 indicated that most births occurred during the booting (June) and heading stage (July) of the previous crop. A high proportion of these rats survived for 5–8 months (Table 1). These animals also bred in January 1996 (1996/97 wet season) and their offspring survived until May 1997; none were recorded in June and thereafter. Interestingly, peak recruitment in the 1997 dry season occurred in June, consisting of young rats (66% were 1–2 months old) that were offspring of the January cohort.

A second bout of recruitment occurred at the end of the dry season (August–September 1997) because all rats caught in October 1997 were 1–2 months old. These rats were probably offspring of rats born earlier in that year (Table 1). Some of the rats born in the dry season 1997 survived until the end of the following wet season but the irregular trapping in 1998 did not allow for further tracking of these cohorts.

In 1995 and 1997, when rats were trapped more frequently, a shift from relatively young rats (1–4 months old) to older rats (5–10 months old) was evident post-harvest. This also indicated that few females bred during the fallow period and that there was no immigration of young rats from other areas where reproduction might have continued.

The presence of young rats at later stages of the rice crops confirmed earlier findings that the breeding of rice-field rats starts about 2 weeks before maximum tillering of the crop (Leung et al. 1999). If the first litter was conceived about then, young rats would enter the trappable population approximately 5 weeks later, which is

Table 1. Age composition of rice-field rats (%) in lowland irrigated rice fields of West Java, Indonesia. Rats were live-trapped in the wet and dry seasons 1995–98 and age estimated from eye lens weight.

Season	Year	Month	Crop stage	*n*	Maximum age (months)										
					2	4	6	8	10	12	14	16	18	20	>20
dry	1995	Aug	fallow	866	53	26	4	7	4	4	4	1	1	0.5	
		Sep	fallow	249	21	59	2	7		2	3	1	0.5		
wet		Nov	ploughing	48		8	54	15	10	4	6	2			
		Dec	tillering	34			50	35	15						
	1996	Jan	booting	73	15		12	26	21	12	3	4	4		3
dry	1997	May	planting	22	27	59	9	5							
		Jun	tillering	47	66	34									
		Jul	tillering	19	47	53									
		Aug	flowering	16	63	31	6								
		Sep	harvest	56	46	54									
		Oct	fallow	30	100										
wet		Nov	ploughing	275	44	46	6	3	0.5	0.5	0.5				
	1998	Apr	ripening	75	84	5		4	4		1			1	
dry		May	fallow	65	97	3									
		Aug	booting	57	75	12		9		2		2			

reflected in the age structure data. The generally low percentage of young rats at transplanting and early tillering confirms earlier reports that the breeding activity of rice-field rats ceases shortly after harvest (Lam 1983; Leung et al. 1999).

Substantial proportions of rats older than 6 months were present in the wet season 1995/96 (Table 1). These rats must have survived the dry season 1995 and some of them also the previous wet season. Almost no rats older than 6 months were caught in the dry season 1997. This was surprising because the relatively long fallow (10 weeks) between dry and wet seasons in the region should have led to low survival rates entering the 1995/96 wet season because of the lack of food and shelter during the extended fallow period. The fallow between wet and dry season in West Java is short (4–6 weeks) and survival should have been higher. Although the data set is incomplete, these results indicate that the length of the fallow seemed to have limited importance for the survival rate of rats. This does not support the recommendation by Leung et al. (1999) that the longer fallow between the dry and wet seasons be maintained to reduce the population size of the rice-field rat. Other factors such as population density and intensity of rat control may have been of greater importance during 1995/96. However, because there was no consistent trapping effort during this period we could not assess density effects. These findings need further study, in particular a detailed study of survival rates of marked rats during the fallow period.

Good survival of rats to the next breeding season results in a large founder population that may create high densities with the potential to cause high levels of crop damage and yield loss. From a management perspective, targeting these rats before they reproduce may lessen their negative impact on the rice crop.

Relationship between age and embryo number

Counts of the number of embryos are closely correlated with litter size at birth because intrauterine mortality is low in rice-field rats (Lam 1983). The breeding history (number of preceding litters) has an effect on litter size in female rice-field rats in laboratory colonies (Lam 1983). Our study showed a parabolic relationship between the age of the mother and the number of young produced per litter (analysis of variance, ANOVA, $F_{6,48}$ = 3.61, p = 0.005) (Figure 1). There was a lower number of embryos in 1–2-month-old rats (7.8, se ± 0.4) than in 5–8-month-old rats (10.8 ± 0.8 – 11.3 ± 0.8) (post-hoc test, t = 3.37, $p \leq 0.001$). Similarly, the number of embryos was lower in rats older than 9 months (6.5 ± 0.5 – 9.0 ± 1) than in 5–8-month-old rats (although sample sizes were small for the older age classes). We could not determine whether there was a parity effect influencing this relationship or whether there was a pure age effect. Either way, if young rats are less likely to produce large litters than older rats, it could be beneficial for the application of anti-fertility agents to manage rats. Fertile offspring of rats not responding to anti-fertility agents had limited potential to compensate for decreased reproductive output of the population. Field trials using or simulating fertility control are desirable to test this further.

In other rodent species, younger females do not have the physiological maturity to have large litters (Ingram et al. 1958). This may be due to physiological constraints. Very young, and therefore small, females may not be able to produce large litters and the effects of senescence in old females may prevent them from having high reproductive output. In addition, the occurrence of medium-aged rats may coincide with low rat density at the beginning of the breeding season and the abundance of food at that time

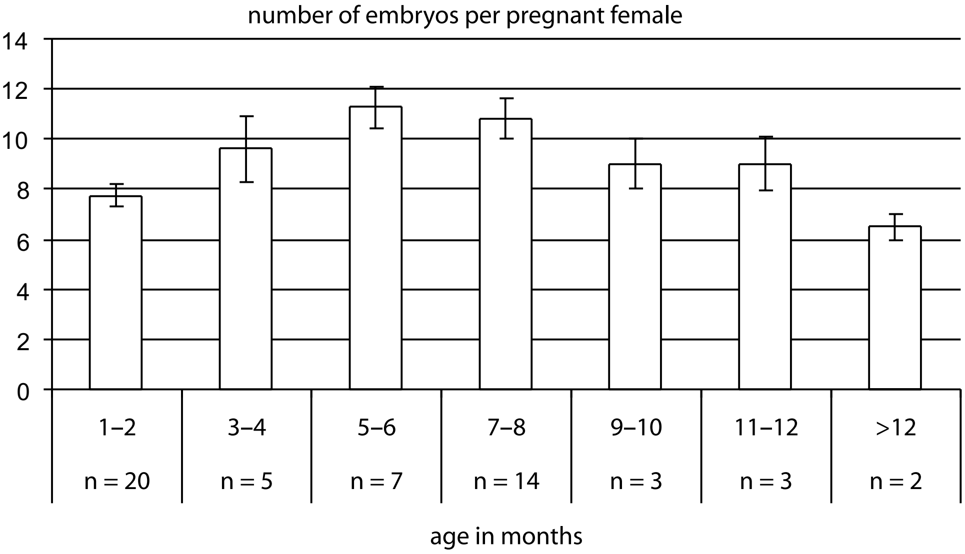

Figure 1. Mean number of embryos for pregnant female rice-field rats of different ages. Rats were sampled in lowland irrigated rice fields of West Java, Indonesia. Rats were live-trapped during the 1995 to 1998 wet and dry seasons and age estimated from eye lens weight. Embryos were counted at necropsy. Error bars are standard errors.

may promote high numbers of embryos. The abundance of 3–5-month-old rats could be high after the 10-week fallow between dry and wet seasons. Larger samples are needed to test whether age, as well as population density, affects litter size in rice-field rats.

Conclusions

The seasonal breeding of rice-field rats with little or no reproduction during the fallow period leads to an accumulation of 3–5-month-old rats at the beginning of the dry season. These rats have a higher reproductive potential compared to younger and older rats. Rat control at the beginning of the cropping season could minimise the size of the founding population and consequently reduce the rate of increase of the population. This may lead to decreased damage to rice crops and thus increased yield. Our results indicate that there was reduced reproductive performance of young rats. Therefore, young rice-field rats may have limited potential for compensation if anti-fertility agents were used to manage rice-field rats. More detailed studies are desirable to validate our data that were pooled over several years and seasons.

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A bioeconomic model for the management of *Mastomys natalensis* mice in maize fields

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Abstract. The existing stochastic population dynamics model for *Mastomys natalensis*, an important field rodent pest in sub-Saharan Africa, is extended with a number of extra components:

- a submodel for maize growth and yield as a function of rainfall and fertiliser;
- functions linking rodent population density to maize damage at planting and harvest;
- simulation of rodent control with poison (simulated by increasing mortality); and
- an economic model expressing costs related to maize growing and poison application and benefits from selling produced maize with net profits for the farmer summed and discounted over a chosen planning horizon.

This bioeconomic model is implemented numerically and used to simulate the effects of different control strategies, not only on the population dynamics of the rodents, but also on a farmer's income. The results show that strategies with only a few months of control, chosen at the appropriate time of the year, are the most economical, even though they have little effect on rodent population dynamics.

This model demonstrates how important it is to combine both ecology and economy when discussing management strategies, with results that are not always intuitive.

Introduction

Field rodents are a very serious concern in agriculture throughout eastern Africa. Farmers consider rodents as the most important pest organism in their staple crops and, after drought and soil fertility, as the biggest impediment to higher yields. Besides the usual annual losses, irregular rodent outbreaks occur during which damage to crops can increase to over 80% (Leirs et al. 1996). Most rodent control is organised in an ad hoc approach, either at a small scale by local farmers, or at a wider geographical level by a government agency (Mwanjabe et al. 2002). Such approaches often come too late, when the damage has already reached high levels. There is a need for better strategies that prevent damage.

Ecological models allow us to investigate which factors contribute to fast population growth, predict outbreaks, or simulate control strategies to evaluate which approach would be most effective in keeping a rodent population at low levels. A number of models for African rodent populations exist (Leirs 1999). Stenseth et al. (2001) used a population dynamics model for *Mastomys natalensis* mice from Tanzania to investigate a number of different control approaches. They showed, for example, that a sustained control strategy, applying poison every month, would be efficient even when the poison was not very toxic (i.e. only had a limited effect on mortality). On the other hand, using highly toxic poisons (i.e. with a strong effect on mortality), but only under high mouse density conditions, was not successful in reducing the mouse population numbers. Interestingly, the latter reactive approach is what most people do in practice.

Ecologically based rodent management should focus on the reduction of damage levels, rather than the mere reduction of population numbers (Leirs et al. 1999). In this paper, we take the argument even further than consideration of damage and include the net economic benefit of damage reduction (i.e. the difference between the reduction of losses due to rodent damage and the cost of the control strategies). We investigate how this affects the strategies that were proposed as useful by Stenseth et al. (2001).

Materials and methods

We used an existing demographic model for the population of *M. natalensis* mice. This model is based on estimates of reproduction, survival and sexual maturation obtained from a capture–mark–recapture (CMR) study in fallow land in Morogoro, Tanzania. Basically, it is a Leslie-matrix type of model in time steps of one month with juvenile, subadult and adult age classes and with demographic processes dependent on rodent population density and on rainfall in the past three months (Leirs et al. 1997). The model's reliability and precision were investigated by Leirs (1999); it is this same model that was used by Stenseth et al. (2001).

We expanded the population dynamics model with a number of new components. They are briefly described here—more details can be obtained from the authors.

- A submodel for maize growth and yield as a function of rainfall and fertiliser, based on data collected in a nearby region in Tanzania (McDonagh et al. 1999). Maize yield increases up to a maximum with better rainfall during the cropping period; the slope of the increase and the level of the maximum are dependent on the application of fertiliser. Although the actual parameter estimates may be different in Morogoro, we assume that the general form of the functions is similar. For the simulations presented here, we simulated fields where 40 kg nitrogen fertiliser per ha was added.
- Functions linking rodent population density to maize damage at planting and harvest. These are based on observations of damage in experimental fields in Morogoro, Tanzania, for which also the rodent population size was calculated, based on closed-model CMR estimates. The relationship between rodent population density and proportional damage at planting is sigmoidal and based on field observations of actual damage and rodent densities in 21 study fields in Tanzania (L.S. Mulungu et al., unpublished data). At harvesting we assume a linear relationship between number of rodents and amount of maize that is actually damaged by the mice during the month preceding harvest (0.270 kg/mouse).
- A simulation of rodent control with rodenticide, increasing the natural mortality up to a maximum of 95% per treatment with poison, depending on the quantity and quality of the applied poison. In this study, a fixed amount of 2 kg of warfarin bait per ha was used for all simulations. We assumed that poison baits remain available to the rodents in a field for a single month after application, after which the bait has disintegrated.
- An economic model expressing costs related to maize growing (for example, preparing fields, buying and sowing seeds, buying harvesting bags) and poison application and benefits from selling produced maize. Net profits for the farmer are summed and discounted over a chosen planning horizon of several years. (See Table 1 for the values used in the model.)

We simulated different control strategies by varying the number of months in which rodenticide was applied. In the present study, we did not compare alternative methods of population reduction, the application of different rodenticides, or the intensity of rodenticide applications. The major variable to change in the model was whether to apply rodenticide in a given month or not. Different strategies included:

- never applying rodenticide;
- applying rodenticide every month;
- applying rodenticide in fixed months only (e.g. every February or every May); and
- applying rodenticide in months matching pre-set conditions of rodent population density.

All simulations were first run for 20 years (240 time steps of one month) to reduce the effect of initial conditions. After that, control strategies were simulated during a period of 10 years and the net benefits to a farmer calculated. The area unit for the model simulations was a maize field of one hectare. In the model, planting always happened in March, replanting was not provided as a possibility, and the maize was harvested in August.

Table 1. Values, prices and costs (in Tanzanian shillings; Tsh) used for the economic part of the model.

Component	Value
Net price of maize	100 Tsh/kg
Price of fertiliser	220 Tsh/kg
Price of poison	6500 Tsh/kg
Fixed costs per ha of maize field	10 000 Tsh/ha
Planning horizon	10 years
Discount rate	0.07

The model was implemented numerically using Stella Research, version 5.1.1 (High Performance Systems, Inc., Hanover, NH, USA). Monthly rainfall in the simulations was bootstrapped from rainfall values measured between 1971 and 1997, adding environmental stochasticity to the model. Every simulation run was repeated 100 times with different rainfall series.

Results and discussion

Figure 1 shows an example of simulations with different control strategies. In this example, all simulations were run with the same rainfall series, i.e. the same environmental conditions. The simulation with no rodent control shows a strongly fluctuating rodent population, an average harvest, and a low income for the farmer. In years with many rodents, the harvest is so poor that it cannot cover the production costs and farmers may have a net loss (negative income). In the scenario with permanent rodent control, the rodent population is completely exterminated. This result was also obtained by Stenseth et al. (2001) who thought this to be the ecologically most rewarding method. Indeed the harvest is very much better and also the farmer's income increases. The third scenario, control under high-density conditions only, corresponds to what is often seen in practice: farmers only perform control actions when they actually perceive high numbers of rodents. Although this strategy does not exterminate the rodent population, and the yield is lower than under the previous control strategy, the farmer's income is considerably higher.

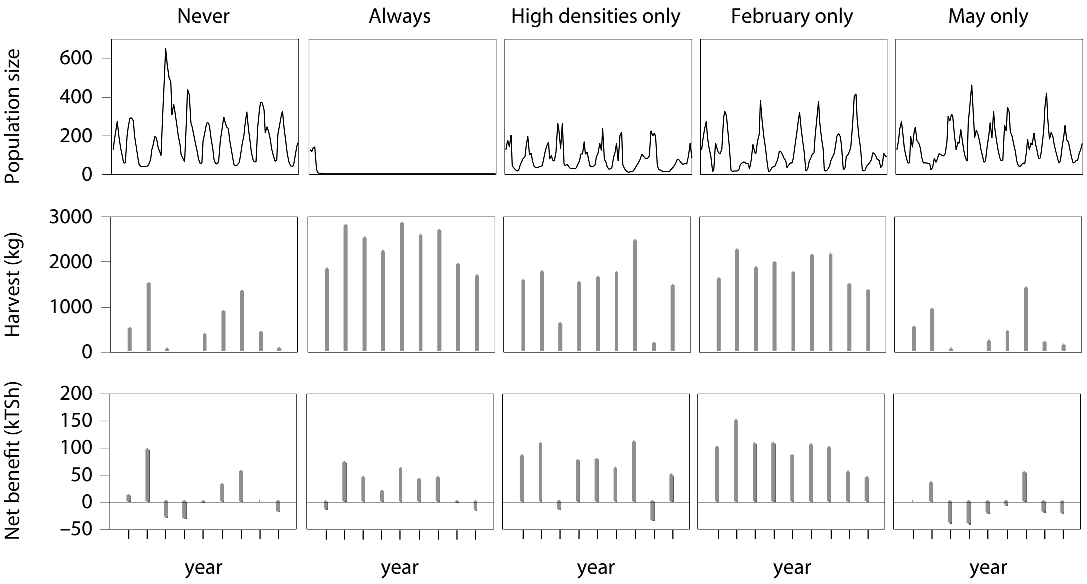

Figure 1. Examples of simulations run with different rodent control strategies for a 1 ha field of maize. From left to right, simulations in which rodenticide was applied: (1) never; (2) every month; (3) in months with a density of over 150 animals/ha; (4) in February every year; and (5) in May every year. The top row of graphs shows the rodent population size per ha over a time period of 10 years, the middle row shows the predicted annual harvest from 1 ha during the simulated period, and the bottom row shows the corresponding net annual benefit to the farmer (in 1000 × Tanzanian shillings per ha), after reduction due to all costs, including those of rodent control. All simulations were run with the same environmental conditions.

The lower harvest is offset by the much lower costs for rodent control, since under this scenario rodent control will be performed in a limited number of months only. The next scenario, controlling every year in February, just before planting, is the most economically rewarding. The population fluctuations of the rodents are not affected very much, but the crop is protected during the most sensitive period of planting and, therefore, the harvest is good. Since only a limited amount of resources must be spent on rodent control (only one month per year), the net income is maximal. In contrast, the last scenario—control in May every year—results in a poor harvest and a very low net income. Money is spent on rodent control at a time when the crop is not at risk, the rodent population is hardly affected and thus the money is basically wasted. It is worth noting that the two latter scenarios have very different results for the farmer's income, although apparently similar outcomes for the rodent population dynamics.

Of course, the results shown in Figure 1 could be due to the specific rainfall series. Repeating the same simulations under different environmental circumstances, however, shows the same pattern (results not shown here). It is interesting that prophylactic rodent control in February corresponds to a certain degree to what some farmers do in Tanzania, but is very different from the government's ad hoc control programs. Comparing more strategies shows that the most rewarding one is a strategy in which control is performed every year in January, February and November regardless of population density of rodents. Changing fertiliser input may affect the relative benefit of different control strategies (results not shown here).

Conclusions

Clearly, a model's output is only as good as the model itself is. The present model does not include movements between fields or flexibility in the rodent management strategies (e.g. replanting, habitat alteration, fertility control). Therefore, the results should be treated with caution and used to guide, but not prescribe, what is done in practice. However, the model allows us to obtain new insights into how the timing of control determines the net benefit to farmers.

Too often, ecologists tend to ignore economics, economists typically have a simplistic understanding of ecology, and pest control managers commonly underrate both. The simulations with the presented bioeconomic model show optimal strategies are sometimes counter-intuitive and rodent population dynamics is not the only factor that must be taken into account.

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Spatial heterogeneity of seed predation on wild apricot by small rodents

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Abstract. In 2000 and 2001, we studied seed predation on wild apricot (*Prunus armeniaca*) by small rodents in three habitat types (forest, shrub and grass) in a mountainous area (40°00'N, 115°30'E) near Beijing, China. Seed predation of wild apricot by small rodents was intense. All the seeds in three habitat plots were removed or consumed within 18 days of seed placement. The seeds disappeared most rapidly from the forest habitat. The number of 'seed remaining days' (SRDs) was negatively correlated with rodent population abundance of the three habitats. Seed predation on wild apricot by small rodents was spatially heterogeneous. This predation affected seed fate and the natural regeneration of wild apricots. Rodent density, predation risk and seed availability may be the key factors affecting seed disappearance of wild apricot. We suggest that grass habitats are more suitable for re-forestation of wild apricot by sowing seeds.

Introduction

Seed predation by animals may affect plant fitness, population structure and dynamics, community structure (Harper 1977; Clark and Clark 1984; Schupp 1988, 1990; Willson and Whelan 1990), natural selection (Janzen 1971) and maintenance of species diversity (Janzen 1970; Connell 1971; Grubb 1977). Previous studies have suggested that rodents ate most seeds and only very few seeds were able to become seedlings (Sork 1984; Miyaki and Kikuzawa 1988; Herrera 1995). On the other hand, rodents are also regarded as an important agent for some types of forest regeneration because they disperse and bury seeds (Jensen and Nielsen 1986). Vander Wall (1994) reported that pine seed predation by vertebrates was helpful to understanding forest regeneration. Some studies have shown that habitat heterogeneity may affect seed removal by animals, especially small mammals (Willson 1992; Burkey 1994). Predation risk may be one important factor influencing the space use and foraging by small mammals (Kotler 1984; Lima and Dill 1990; Gill and Marks 1991; Wada 1993; Schupp 1995). Crawley (1992) reported that post-dispersal seed predation by animals was variable in space and in time. Seed mast years might lead to seed predator satiation (Janzen 1971) since the huge production exceeds the number of seeds that can be consumed by the total predator population.

Wild apricot is one of the common shrubs or low forest species in mountainous areas near Beijing (Chen 1997). Each seed of the wild apricot weighs about 1.5 g and its coat is very hard. Seeds become mature usually in mid-June and sprout into seedlings in the following spring. Apricot seeds are of economic significance, since they are the source of some medicines and are used for a kind of soft drink. Wild apricot can survive in harsh conditions with poor soil quality and low rainfall, and thus is planted in degraded areas to reduce soil erosion. The impact of rodents on seed predation of wild apricot has not been studied and may be critical to understanding plant regeneration. The link between rodents and the regeneration of wild apricots in the study region was first investigated by Zhang and Wang (2001) using tin-tagged seeds. They suggested that rodents were an important factor affecting the natural regeneration of wild apricot. However, the spatial heterogeneity of seed predation has not been studied. The purpose of this study was to investigate how rodent seed predation is influenced by habitat type. The main aim of this series of studies is to propose practical methods for enhancing seeding reforestation of wild apricot.

Methods

Study site

The study site is located at 40°00'N, 115°30'E, about 120 km north-west of Beijing. It is in the Dongling Mountain region, a mountainous area near the Liyuanling, Mentougou district, and has a warm temperate continental monsoon climate. The study area is highly disturbed due to extensive human activities over most of the last century. The common shrubs include oak (*Quercus liaotungensis*), wild walnut (*Juglans mandshurica*), wild apricot (*Prunus armeniaca*), *Vitex negundo* and *Prunus davidiana*. Larch (*Larix principis-rupprechtii*) and Chinese pine (*Pinus tabulaeformis*) are planted in small areas by local forestation farmers. The main rodent species are the field mouse (*Apodemus speciosus*), white-bellied rat (*Rattus confucianus*), striped field mouse (*A. agrarius*), rat-like hamster (*Cricetulus triton*), gray-sided vole (*Clethrionomys rufocanus*), white toothed shrew (*Crocidura lasirua*), striped hamster (*C. barabensis*), long-tailed hamster (*C. longicaudatus*), chipmunk (*Tamias sibiricus*), red-backed vole (*C. rutilus*), house mouse (*Mus musculus*), and gray squirrel (*Sciurotamias davidianus*). In the study area, the rodent density is lowest in spring (usually in May) and reaches a peak in August as a result of summer breeding. Seed production of the wild apricot was normal in 2000 but very low in 2001 due to a spring drought. The mean density of fallen seeds was 13.58 seeds/m^2 in 2000 and 5.26 seeds/m^2 in 2001.

Spatial patterns of rodent population abundance

Wooden snare kill-traps baited with fresh, ripe seeds of wild apricot were used to determine the rodent species removing seeds, as well as the spatial patterns of rodent population abundance. To minimise the effect of trapping on the rodent community in the plot where seeds of wild apricot were released, the trapping plot was placed about 400 m away from the seed-spreading transect, but on the same slope. In each trapping plot, four transects were selected and 25 traps at intervals of 5 m were set along each transect for two consecutive nights. The traps were checked every morning and the rodents captured were recorded. To investigate the spatial pattern of rodent population abundance, trapping was carried out near the three habitat plots (see below) in May 2000 and 2001. Rodent population abundance was measured as the proportion of trap success.

Impact of habitat type on seed disappearance

In May 2000 and 2001, three plots representing three different habitats (forest, shrub and grass) were selected. The forest habitat was a planted larch forest in which *Larix principis-rupprechtii* was the dominant species, with sparse representation of *Q. liaotungensis* and *Ulmus laciniata*. In the shrub habitat, *V. negundo* and *Spiraea pubescens* were the dominant species. In the grass habitat, *Calamagrosis aundinacea* and *Carex rigescens* were dominant species. A transect line was selected in each habitat plot. Five sites were set at intervals of 10 m along each transect line. All sites were located in areas of limited natural seed production. At each site (1 m^2), 20 apricot seeds were placed evenly on the ground surface and then monitored for their loss. Three categories of seed states were defined for seeds or their fragments:

1. intact *in situ*—the seed was intact and remained *in situ*;
2. disappearance, but consumption i*n situ*—in this case, there is a gnawing hole opened by a rodent on the seed coat. The seed coat was left as litter *in situ* and the inside kernel of the seed was removed. The number of seeds consumed in situ was recorded according to the number of seed coats left in the litter; and
3. disappearance with the seed removed to other another location for consumption or burial.

Statistics

The loss rate of intact seeds *in situ* was measured as seed remaining days (SRDs) (one SRD = one intact seed remained *in situ* for one day). Kruskal-Wallis tests were used to identify the difference between SRDs in the three habitats. Pearson correlations were used to identify the relationship between SRDs and rodent abundance in the three habitat types.

Results and discussion

Spatial patterns of rodent population abundance

A total of 99 rodents were captured, and included the field mouse, white-bellied rat, rat-like hamster, striped field mouse and house mouse. The field mouse was the dominant species. Trap success in 2001 (13.5%) was significantly higher than that in 2000 (3%). The average trap success in this study area between 1993 and 1995 was 5.38% (Ma et al. 1999). These results suggest that 2001 was a peak year for rodent populations. The spatial distribution of rodents as revealed by trapping suggested that rodent density was highest in forest habitats (6.0% in 2000, 20.0% in 2001), followed by shrub habitats (2.0% in 2000, 5.5% in 2001) and grass habitats (0.4% in 2000, 2.0% in 2001).

Each of the captured species, with the exception of the house mouse, will consume apricot seeds in the laboratory (unpublished data). Thus, they are likely to be the key species affecting wild apricot seed disappearance. Further, in laboratory feeding trials, the appetite of the field mouse for wild apricot seeds was much greater than that of the white-bellied rat, rat-like hamster and striped field mouse (unpublished data). Previous studies have shown that the field mouse is the dominant species in the rodent community (Zhang et al. 1998). Thus, the field mouse was probably responsible for the disappearance of most of the wild apricot seeds in the study area. In addition, some rodent species such as the Norway rat, gray-sided vole, gray squirrel and chipmunk may be involved in seed removal (Ma et al. 1999) but are not likely to be captured by snare-traps. Some of these species are also rare. Birds were never observed to eat seeds of apricot, probably due to the hardness of the seed coat.

Impact of habitat on seed disappearance

The removal rate of seeds of wild apricot in all three habitats was very high in 2000 and 2001 (Figure 1). Within 18 days after seed placement, all seeds were removed or consumed. The number of SRDs (seed remaining days) of forest habitat was much lower than that of shrub and grass habitats in 2000 ($p = 0.045$) and in 2001 ($p = 0.004$). The number of SRDs was negatively correlated with population abundance of field mouse in three habitats in 2000 ($r = -0.761$, $P = 0.001$) and in 2001 ($r = -0.713$, $P = 0.003$). Nearly all seeds were carried away from the original placement sites. Only one seed was consumed *in situ*—this occurred in the shrub habitat in 2001.

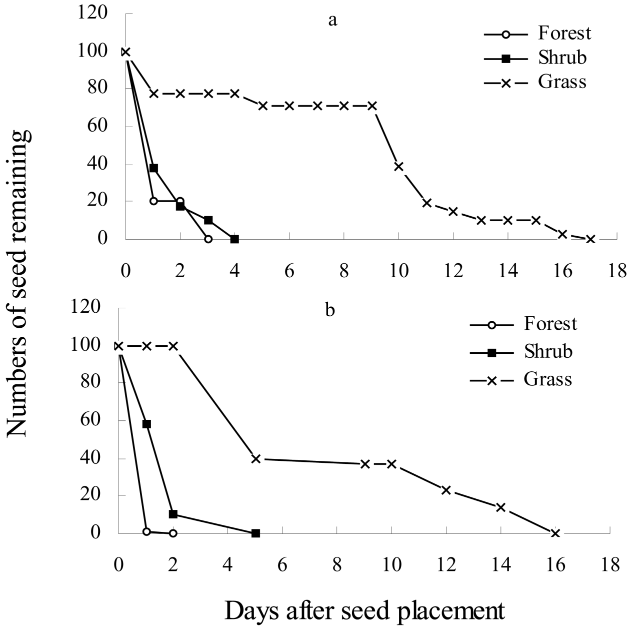

Figure 1. Spatial heterogeneity in the survivorship curves for the seeds of wild apricot (*Prunus armeniaca*) remaining in three habitats (forest, shrub, grass) in (a) 2000 and (b) 2001.

These results indicate that seed predation of apricot by small rodents is very intense in this region. Previous findings have shown that rodents consumed most seeds, with only a few seeds being able to germinate and become seedlings (Sork 1984; Miyaki and Kikuzawa 1988; Herrera 1995). Habitat heterogeneity may also affect seed removal by animals, especially small mammals (Willson 1992; Burkey 1994), and the rates of seed predation by animals are different in different micro-environments (Gill and Marks 1991; Wada 1993; Schupp 1995). In our study, the rate of seed disappearance was also different in the three habitat types, and this showed that seed predation by rodents was spatially heterogeneous. The spatial pattern of seed disappearance showed similar trends in 2000 and 2001, that is, the seeds of wild apricot disappeared most rapidly from the forested sites with a closed canopy. This was probably a consequence of high rodent densities in the forest habitats. The spatial pattern of seed predation by the small rodents was also probably related to the vegetation characteristics of different habitats. In the forest habitat, because of the sparse cover of grass, the ground surface was open—probably making it easier for rodents to find food. In contrast, the dense grass in the grass habitats may limit the ability of rodents to find seeds, as previous studies have suggested that seedling recruitment rates are higher when seeds are planted in the grass habitats (Zhang and Wang 2001). It may therefore be preferable to target reforestation efforts on grassland habitats where seeds will not be at such a great predation risk.

Compared to other seeds (e.g. acorns), very few apricot seeds were consumed *in situ*. This was perhaps related to predation risk. The seed coat of wild apricot is much harder than that of acorns, and a small rodent takes a longer time to open it, so the predation risk will be higher.

Conclusion

We conclude that seed predation by small rodents was spatially heterogeneous. This affected seed fate and consequently the natural regeneration of wild apricots. The rodent population abundance, habitat characteristics and seed availability appear to be the key factors affecting seed disappearance of wild apricot. We suggest that to achieve reforestation of wild apricot, seeds sown in the grass habitats would be more likely to lead to success.

Acknowledgments

We wish to thank Wang F.S. for his assistance in the field. This study was supported by the Key Project of China National Natural Science Foundation (39893360), National Basic Research Program (G2000046802), CAS Innovation Program (KSCX2-SW-103) and Ministry of Science and Technology Project (FS2000-009).

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The role of interspecific competition in determining macrohabitat use by the black rat and brown rat at Bradley's Head, NSW

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Abstract. We investigated macrohabitat use in populations of the black rat (*Rattus rattus)* and the brown rat *(Rattus norvegicus)* at Bradley's Head, New South Wales. The study site included a zoological park and surrounding bushland reserve on a headland of Sydney Harbour. These two environments provided quite different macrohabitat types. The bushland reserve contained a dense mix of native and introduced plant species, while more open and disturbed habitats were located within the zoo. Between December 2000 and June 2001 we found a clear difference in the habitat use patterns of the two species. Only 3 of 30 *R. rattus* trapped were caught within the zoo grounds. For *R. norvegicus*, 51 of 82 individuals were trapped within the zoo grounds, revealing a preference for an area that contained a large food source in the form of a refuse pit. The removal of approximately 73% of *R. norvegicus* from within the zoo grounds by poisoning failed to elicit a change in habitat use by *R. rattus*, as measured by both trapping and radio-tracking. Of the 12 radio-collared *R. rattus* tracked after the removal, none moved into the zoo grounds. Perceived predation risk may play an important role in determining the habitat use patterns of *R. rattus* at Bradley's Head.

Introduction

Both the black rat (*Rattus rattus*) and brown rat (*Rattus norvegicus*) are introduced pest species of the Sydney region. Since European settlement, *R. rattus* has extended its range to cover most of the temperate areas of eastern Australia where the habitat has been disturbed by people (Cronin 2000). *R. rattus* is common to both disturbed bushland and urban areas where it prefers dense understorey vegetation and deep leaf litter in forested areas, and lives a partly arboreal existence (Key and Woods 1996; Cox et al. 2000). In urban areas, black rats will often occupy buildings, nesting in wall cavities and roofs. Both species of rat are omnivorous generalists that are easily able to adapt their feeding habits to the available food types (Macdonald 1984). *R. norvegicus* primarily is found in highly disturbed habitats, such as around the Sydney Harbour foreshore (Cronin 2000). *R. norvegicus* has been found to occupy sewers, drains, and tips and is not noted as a climber, preferring to move between areas through drains and crevices in rocks rather than by climbing through trees (Taylor 1978; Key and Woods 1996).

Interspecific competition can be an important determinant of small mammal macrohabitat use, resulting in restriction or exclusion of the subordinate species from particular habitat types where the dominant species has a competitive advantage (Dickman 1984; Maitz and Dickman 2001). *R. norvegicus* has previously been found to be competitively dominant to *R. rattus* in laboratory experiments (Barnett 1958). In the present study around Bradley's Head in Sydney, we examine interspecific competition between these two commensal rat species. We hypothesise that the Norway rat excludes the black rat from its preferred habitat, so that if the Norway rat is removed from an area, black rats will quickly colonise the empty area.

Materials and methods

During a pilot study in December 2000 and January 2001, 100 traps were spread throughout the Taronga Zoo and surrounding bushland at Bradley's Head. Two trapping sessions were conducted, each for three nights. Wire possum cage traps were used for the capture of rats. The purpose of the trapping conducted at this time was to gauge the abundance and species diversity of small mammals at Bradley's Head. A mixture of oats, wheat grain and fish sauce was used to attract animals to the traps.

We found in these preliminary studies that few *R. rattus* lived on the zoo grounds. On trapping trips in May and June, 2001, we focused on the southern section of the zoo, which allowed more intensive sampling of an area that contained a diverse range of habitats. Sixty traps were set for five consecutive nights in May, and again in June. This smaller study area was broadly divided into two markedly different macrohabitat types: the bushland reserve outside the zoo, and a refuse pit and water treatment works inside the zoo. The bushland reserve extends approximately 500 m between Sydney Harbour and the southern zoo boundary. It is 100 m wide on average and slopes down steeply to the harbour, with the reserve including a headland and small beach 150 m long. The reserve contains many large trees with Moreton Bay figs (*Ficus macrophylla*) and Sydney red gums (*Angophora costata*) the dominant species. The area has a multitude of weeds including blackberry (*Rubus fruticosus*), wandering Jew (*Tradescantia albiflora*) and lantana (*Lantana camara*). Further to the east is a small national park, while to the west is suburbia. The zoo grounds included within the trapping area are largely open. The refuse pit is located approximately 20 m from the zoo boundary and consists of a 25 m diameter concrete floor with a crumbling 4 m high brick wall on its northern side. Hay, chaff, seed, animal waste, and plant clippings are tipped into this area and may remain for a week or more. The northern half of the study site includes treatment ponds, buildings for water treatment, and some small garden beds. North of the refuse pit is a vegetated slope dominated by *T. albiflora*. Beyond the study area to the north are the main animal exhibits.

To test the role of interspecific competition on macrohabitat use, most individuals of the putatively dominant species were removed. In the absence of any suitable replicate sites, individual radio-collared rats were used as replicates. This provides a response of individuals to reduced interspecific competition (Dickman and Woodside 1983). We had planned to remove *R. norvegicus* through extensive trapping. However, in the 6 weeks between trapping sessions, the zoo undertook an extensive baiting campaign around the refuse pit. There was no baiting in the bushland reserve beyond the zoo boundary. This meant that the goal of removal of a large majority of *R. norvegicus* was met at the zoo site. Moreover, if the numbers of *R. rattus* dramatically decreased over this period then it would suggest they had been feeding within the zoo grounds.

During the pre-removal trapping session conducted in May 2001, six *R. rattus* and seven *R. norvegicus* were radio-tracked using single-stage transmitters (Sirtrack NZ). All radio-collared rats weighed over 100 g in order to keep the transmitter weight less than 5% of the animal's body weight. All individuals were still alive and being tracked at the completion of the radio-tracking period on the 9 May 2001. For the post-removal radio-tracking session, 13 new individuals were radio-collared of which eight were *R. rattus* and five were *R. norvegicus*. Two *R. rattus* were unable to be tracked for a sufficient time to allow their home ranges to be calculated. This session was completed on the 28 June 2001.

Results and discussion

Fifty-five rats were live-trapped at Bradley's Head between December 2000, and June 2002 (Table 1). Of these, 82 were *R. norvegicus* and 30 were *R. rattus*. Twenty-seven of these *R. rattus* were caught in the bushland reserve, beyond the zoo walls. The three trapped inside the zoo were caught amongst thick vegetation in the aviaries and gardens located centrally within the zoo. This contrasts strongly with *R. norvegicus*, of which 62% of individuals were trapped within the zoo grounds. *R. norvegicus* was trapped over a range of habitat types including open areas, such as along paths and in animal enclosures. They were observed to congregate in large numbers at food sources, such as around the refuse pit, in animal enclosures where food had been spilt, as well as around kiosks and bins where zoo patrons had discarded food. The observations of this species suggested that *R. norvegicus* may be excluding its smaller congener from an area rich in food. The restriction of *R. rattus* within the zoo grounds to thick vegetation suggests that they may be able to persist in the presence of *R. norvegicus* only where there is ample cover. This is consistent with observations that *R. norvegicus* is competitively dominant to *R. rattus* (Barnett 1958). The arboreal habit of *R. rattus* in dense bushland (Cox 2000) indicates that they may be able to partition their use of the landscape to avoid *R. norvegicus*.

Table 1. Total number of captures from four trapping trips conducted between December 2000 and June 2001. The zoo fence is the boundary that divides the two macrohabitat types. Only three male *R. rattus* were trapped inside the zoo grounds during this period.

	Rattus rattus		*Rattus norvegicus*		Total captures
	Zoo	Bush	Zoo	Bush	
Males	3	12	24	19	58
Females	0	15	27	12	54
Total	3	27	51	31	112

The trapping during May and June revealed an even clearer pattern of habitat use by *R. rattus*. Of the 40 rats trapped, 10 were *R. rattus* and all of these were trapped outside the zoo grounds within the bushland reserve. *R. norvegicus* was found in approximately equal numbers inside and outside the zoo. The refuse pit was a key feature of the southern section of the zoo and it contained a wide range of suitable rodent food. Large numbers of *R. norvegicus*, up to 20 in 10 m^2, were observed to feed from the refuse pit each night. We expected an area containing such a varied and ample food supply would be frequented by both rodent species. Yet trapping suggested that *R. rattus* avoided this area. The area is relatively open and *R. rattus* may avoid it because of a greater perceived risk of predation. This area is fenced to minimise access by cats, dogs, and foxes, hence the emphasis on perceived predation risk. We know of no other study that has reported similar habitat partitioning by these two rat species in an urban landscape dominated by vegetation and open access to food waste.

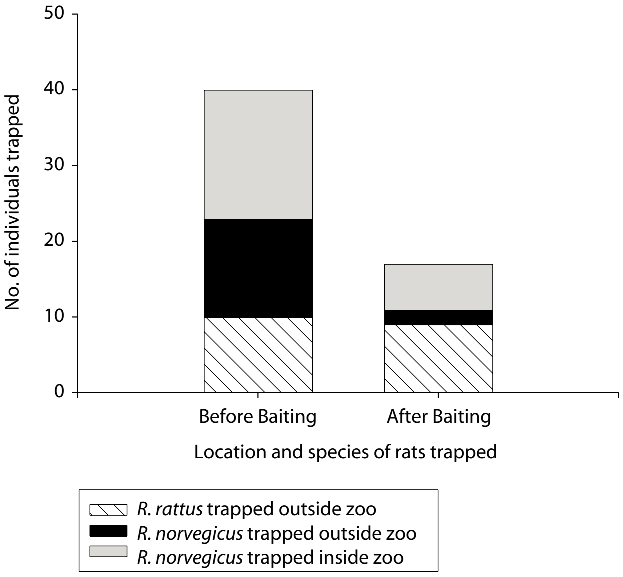

Figure 1. Response of both *Rattus rattus* and *Rattus norvegicus* to baiting conducted around the refuse tip within the grounds of Taronga Zoo between 9 May and 20 June 2001. A reduction of 73% in *R. norvegicus* numbers was observed, with numbers reduced both inside and outside the zoo. No *R. rattus* were trapped within the zoo grounds. The absence of a significant reduction in the number of *R. rattus* further supports the hypothesis that *R. rattus* does not venture into the zoo grounds to feed.

The baiting of *R. norvegicus* from around the refuse pit reduced the population by 73% in 6 weeks (Figure 1). The amount of bait laid out by zoo staff around the refuse tip increased five-fold during this period. The dramatic reduction in *R. norvegicus* numbers and the apparent lack of an effect on the numbers of *R. rattus* suggests that few, if any, *R. rattus* consumed bait. While this may reflect an aversion to bait stations, this finding, combined with the trapping data, suggests that *R. rattus* rarely venture from the bushland reserve into the adjacent zoo grounds.

Immigration into the study area over the 6-week period during which the numbers of *R. norvegicus* decreased appeared to be low. Few *R. norvegicus* were observed feeding from the refuse pit at night during the final trapping session. This is despite the observation that *R. norvegicus* numbers remained high in other parts of the zoo. This may be due to an abundance of food in animal enclosures in other parts of the zoo. With such resources available elsewhere, there may have been no incentive for migration to take place. Dickman (1991) found that subordinate species of small mammal might respond within hours to the removal of a dominant species, so the possibility of a delayed response to the removal of the majority of *R. norvegicus* is unlikely. The large decline in *R. norvegicus* numbers was most likely due to the change in baiting regime rather than intrinsic demographic factors because it occurred when the rats were still breeding and high rodent densities were observed elsewhere in the zoo.

In May and June, radio-tracking of 12 *R. rattus* yielded a total of 373 location fixes, with each of these rats having their position recorded not less than 28 times. No difference was found in habitat use patterns following the removal of *R. norvegicus*. On no occasion was any *R. rattus* observed to occur on zoo grounds (Table 2). By contrast, approximately two-thirds of all locations recorded for *R. norvegicus* were within the zoo grounds. The 12 radio-tracked *R. norvegicus* were all documented entering the bushland reserve and all visited the refuse pit. Therefore, *R. rattus* appeared to be restricted to areas of dense vegetation, whereas *R. norvegicus* moved freely between the two habitat types and fed from the refuse pit.

Table 2. Total number of fixes recorded in the two macrohabitats for 24 radio-collared rats between May and June 2001. No *Rattus rattus* was found to enter the zoo grounds, while *Rattus norvegicus* moved freely between the two macrohabitat types.

Rattus rattus				*Rattus norvegicus*			
Sex	Fixes in zoo	Fixes outside	Total	Sex	Fixes in zoo	Fixes outside	Total
Male (M)	0	32	32	M	31	1	32
M	0	32	32	M	29	3	32
M	0	31	31	M	24	8	32
M	0	33	33	M	11	21	32
M	0	34	34	M	9	25	34
M	0	28	28	M	9	25	34
Female (F)	0	32	32	M	11	20	31
F	0	31	31	F	31	1	32
F	0	30	30	F	30	2	32
F	0	31	31	F	7	22	29
F	0	31	31	F	29	2	31
F	0	28	28	F	25	3	28
6M, 6F	0	373	373	7M, 5F	246	133	379

Conclusion

The two commensal rodent species showed markedly different patterns of habitat use at Bradley's Head. *R. rattus* strongly favoured areas of dense bush, whereas *R. norvegicus* occurred in both the zoo grounds and in the bush adjacent to the zoo. We suggest that more marked predator avoidance behaviour by *R. rattus*, rather than interspecific competition, is responsible for the perceived difference in habitat preference. There is mounting evidence that predators can strongly influence the habitat use of rodents (Banks 1998; Ylönen et al. 2002; Arthur and Pech, this volume). The strength of this effect on habitat use by *R. rattus* in urban settings requires further investigation, as does the apparently weak effect that it may have on *R. norvegicus*. A practical recommendation from this study is that pest control at the zoo should be focused on *R. norvegicus*, with invasion by *R. rattus* appearing unlikely even in the absence of its larger congener. Control methods at the zoo should initially address the problems of food spillage, animal waste, and the storage of these in a location that is not open and easily accessible for *R. norvegicus*.

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SYMPOSIUM 6: SOCIOLOGY AND ECONOMICS OF RODENT MANAGEMENT

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Modelling the structure of non-linear and non-additive climatic forces in small rodent population dynamics

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Abstract. Understanding the role of interactions between intrinsic feedback loops and external climatic forces is one of the central challenges within the field of population ecology. For rodent dynamics, the seasonal structure of the environment involves changes between two stages: reproductive and non-reproductive. Nevertheless, the interaction between seasonality, climate, density-dependence, and predators has been generally ignored. In this study, we analysed the combined effects of non-linear feedback and non-linear, non-additive climatic forces on population dynamics of small rodents. We studied population time series of several small rodent species inhabiting different continents: (i) southern temperate forests of Chile, (ii) a desert in south-western United States of America (USA) and (iii) a deciduous forest in eastern USA. We analysed the numerical fluctuations exhibited by these small rodents using theoretically based models of population dynamics. Recent climatic changes seem to account for dramatic perturbations of the rodents' dynamics. Direct and indirect climatic effects and their non-linear structure are likely to have important effects on rodent dynamics. Assuming such interactions to be typical of ecological systems, we conclude that appropriate predictions of the ecological consequences of climate and global change on small rodent populations will depend on having an in-depth understanding of the community–weather system.

Introduction

The numerical fluctuations exhibited by small rodent populations have fascinated ecologists during the last 80 years. Since Elton (1924), the study of regular cyclic oscillations of arvicoline rodents (lemmings and voles) has been influential for understanding animal population dynamics (Hanski et al. 1993; Stenseth 1999). The emphasis of these studies has been the search for the underlying feedback structure (first- and second-order) representing the individual interactions (within- and between-level trophic interactions). By contrast, the population dynamics of non-cyclic small rodents have been less studied. While studies focusing on cyclic rodent dynamics have emphasised the role of direct and delayed density-dependent feedback and seasonality as the important factors driving numerical oscillations, the influence of climatic forces on fluctuations of small rodent populations has received less attention.

For decades, the role of exogenous and endogenous factors in determining population dynamics has been hotly debated in population ecology (Nicholson 1933; Andrewartha and Birch 1954). Today, there is a growing body of empirical evidence supporting the joint effects of endogenous and exogenous forces on the dynamics of natural populations (Leirs et al. 1997; Forchhammer et al. 1998; Grenfell et al. 1998; Lima et al. 1999). However, in most of the studies, it had been assumed that the endogenous and exogenous effects are linear and additive. As a consequence, the existence of non-linear and non-additive climatic effects has been much less studied (but see Sæther et al. 2000; Mysterud et al. 2001; Stenseth et al. 2002).

The inclusion of climatic forces in population dynamic models represents an interesting challenge for small rodent ecologists (Stenseth et al. 2002). Two factors contribute to this challenge: first, because the signature of the climatic forces on population dynamics depends on the underlying feedback structure (Royama 1992); and second, because there are complex interactions between the feedback structure and climate. For example, climate can affect the maximum per capita growth rate, or the food supply, or even the intra- and inter-specific interactions. In this case, climate affects the system in a non-additive manner because the feedback structure parameters are a function of climate (Stenseth et al. 2002). In this study, we analysed the combined effects of non-linear feedback and non-linear, non-additive climatic forces on the population dynamics of small rodents. We studied population time series of several small rodent species inhabiting different continents: (i) southern temperate forests of Chile, (ii) a desert in south-western United States of America (USA) and (iii) a deciduous forest in eastern USA. We analysed the numerical fluctuations exhibited by these small rodents using theoretically based models of population dynamics.

Material and methods

Small rodent data

We used time series data of three small rodents from Chile, six species of small rodents from eastern deciduous forests in Pennsylvania, USA, and 12 species of small rodents from south-western semi-arid USA.

Climatic data

For characterising the climate in Chile, we used the annual rainfall from Illapel station (31°30'S, 71°06'W) and Valdivia town (39°38'S, 73°07'W) (NCDC 2002) the Southern Oscillation Index (SOI) (DNRM 2002) and the Antarctic Oscillation Index (AAOI) (Climate Prediction Center 2002).

For characterising the climate in Pennsylvania, USA, we used different climatic variables to represent environmental conditions: the North Atlantic Oscillation (NAO) index, the yearly rainfall, the average winter and summer temperatures and the average snow depth for Powdermill Biological Station (40°10'N, 79°16'W).

For characterising the climate in south-western USA, we used data for the summer and winter rainfall from the Portal study site.

Statistical models of population dynamics

Population dynamics of small rodents are the result of the feedback structure and climatic (also stochastic) influences. To understand how these factors determine population fluctuations, we consider the scenario of Figure 1. The arrows define the potential ecological interactions between rodents, plants, predators and climate: the first-order intraspecific feedback within the rodent population is defined by the partial derivative, ($\partial f_N/\partial N$). The trophic interactions between rodents and plants are given by the partial derivatives, $\partial g_N/\partial P$ and $\partial g_P/\partial N$, respectively, and the trophic interactions between rodents and predators by the partial derivatives $\partial \mathrm{j}_N/\partial \mathrm{Y}$ and $\partial \mathrm{j}_Y/\partial N$ and the direct climatic effects are given by $\partial h_N/\partial C$ and $\partial h_P/\partial C$ (Figure 1).

One way to simplify the system is when rodents have no effects on plant dynamics (i.e. $\partial g_P/\partial N = 0$) and there are no effects of predators on rodent dynamics (i.e. $\partial j_N/\partial Y = 0$) Under this scheme, we can represent these ecological relationships from the small rodent perspective using a very general model in terms of reproduction and survival of individuals (Berryman 1999), which represents a variant of the Ricker (1954) discrete-time logistic model influenced by climate and stochastic forces.

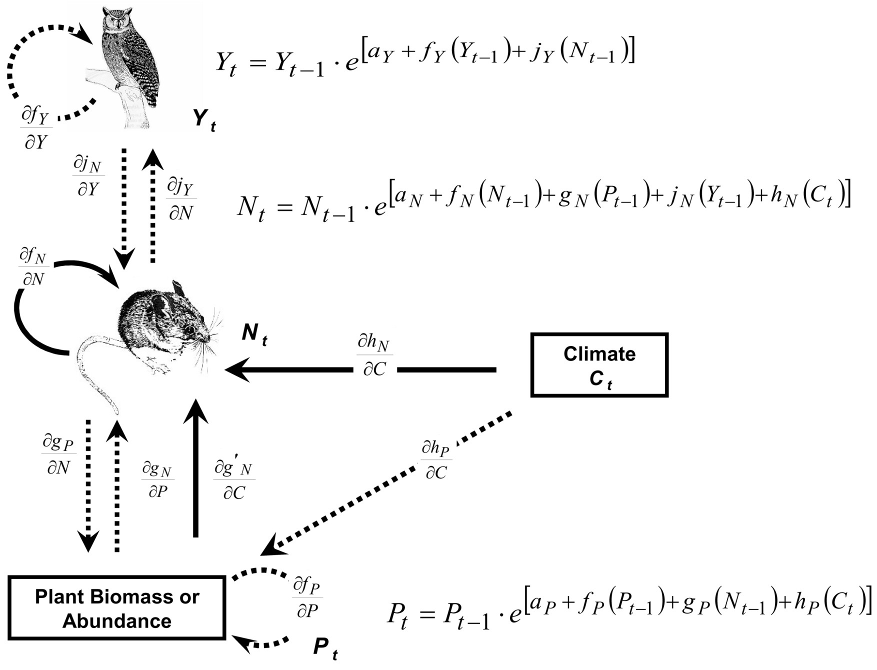


Figure 1. A schematic model illustrating the potential interactions between plants, small rodents, predators and climate. Y_t, N_t and P_t give abundance of predators, small rodents and plants respectively, while climate denoted by C_t. The ecological functions $f_Y(\bullet)$ and $j_Y(\bullet)$ in Y_t, $f_N(\bullet)$, $g_N(\bullet)$, and $h_N(\bullet)$ in N_t and $f_P(\bullet)$, $g_P(\bullet)$, and $h_P(\bullet)$ in P_t describe the changes in predator, rodent and plant populations following the ecological interactions given by the arrows and defined by the partial derivatives. The dotted arrows indicate the relationships that were not explicitly considered in our modelling of the population dynamics. See text for details.

$$N_t = N_{t-1} \cdot e^{\left[A_N + f_N(N_{t-1}) + g_N(P_{t-1}) + h_N(C_t) + \varepsilon_t\right]} \tag{1}$$

where N_t and P_t are the small rodent and plant abundances at time t, C_t is the variable representing the climate state. The term A_N is the maximum per capita growth rate and the functions $f_N(N_{t-1})$, $g_N(C_{t-1})$, and $h_N(C_t)$ represent the effects of rodent abundance, plant abundance and climate on rodent population dynamics and ε_t represents normally distributed stochastic perturbations. Direct effects of climate on rodent population dynamics may be produced by mortality due to freezing temperatures or snow depth, and also by flooding. On the other hand, plant abundance is directly influenced by climate. In consequence, from model 1 and in the absence of data about plant biomass or abundance, we can represent the small rodent population dynamics as a single equation with lagged climatic effects (see Royama 1992; Forchhammer et al. 1998):

$$N_t = N_{t-1} \cdot e^{\left[A_n + f_N(N_{t-1}) + g'_N(C_{t-1}) + h_N(C_t) + \varepsilon_t\right]} \tag{2}$$

(where N_t denotes the small mammal abundance at time t, C_{t-1} is the lagged climatic effect due to delays in interactions with the lower trophic level (plants biomass) (see Forchhammer et al. 1998), C_t is the direct effect of climate (for example, snow, freezing temperatures, rainfall and floods) and $f_N(N_{t-1})$, $g'_N(C_{t-1})$, and $h_N(C_t)$ are unknown functions which have to be estimated from the data. The lagged climatic effect ($g'_N(C_{t-1})$) is a compound function of three ecological processes—the direct effects of climate on plants ($\partial h_P/\partial C$), the self-regulation term of plants ($\partial f_P/\partial P$), and the positive effects of plants on rodent dynamics ($\partial g_N/\partial P$) (Figure 1). An alternative way to express equation 2 is in terms of the instantaneous *per capita* population growth rates, which represent the processes of individual survival and reproduction that drive population dynamics. This is the *R*-function (sensu Berryman 1999). Defining $R_t = \log(N_t) - \log(N_{t-1})$ equation 1 can be expressed as:

$$R_t = A_n + f_N(N_{t-1}) + g'_N(C_{t-1}) + h_N(C_t) + \varepsilon_t \tag{3}$$

This model represents the basic feedback structure, without explicit representation of the plant trophic level, and includes the climatic and stochastic forces that drive population dynamics in nature.

On the other hand, climatic effects can be non-additive. The non-additive effects of climatic variables can be modelled in different ways. For example, the climatic effects on plant dynamics may have a logistic demand/supply structure where C_{t-1} is an index of the effect of food availability on rodent population dynamics:

$$R_t = A_n + f_N\left(\frac{N_{t-1}}{C_{t-1}}\right) + h_N(C_t) + \varepsilon_t \tag{4}$$

or the climatic effect may be a factor of the feedback structure, that is, the feedback function depends on climate:

$$R_t = A_n + f_N(N_{t-1} \cdot C_{t-1}) + h_N(C_t) + \varepsilon_t \tag{5}$$

The basic idea for population analysis is to choose a family of functional forms to fit time series data. This treats equations 3, 4 and 5 as non-parametric non-linear models (see Bjørnstad et al. 1998 for an ecological example). The choice of the functional forms for *f*, *g* and *h* can be approximated using natural cubic splines (Bjørnstad et al. 1998). The complexity of the curve (the number of degree of freedom) was 3 and the number of terms was tested by using the Schwarz's Bayesian criterion (SBC) (S-PLUS 2000). The SBC is obtained as the –2*log-likelihood + npar*log(nobs), where npar represents the number of parameters and nobs the number of observations in the fitted model.

Results and discussion

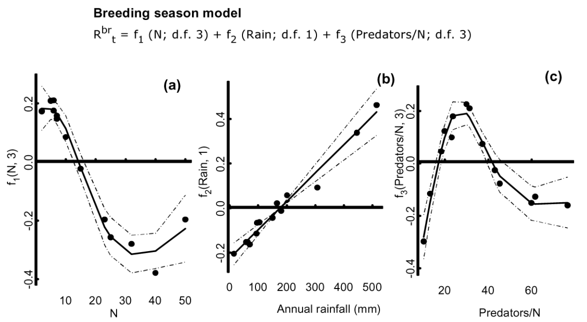
The numerical fluctuations observed in these small rodent species appear to be the result of strong non-linear climatic effects combined with negative first-order feedback, which were strongly non-linear in some species. In addition, some species showed non-additive climatic effects.

For example, in northern Chile, population growth rates of the leaf-eared mouse (*Phyllotis darwini*) exhibit a clear seasonal structure, i.e. factors influencing population growth rates are clearly different between breeding and non-breeding seasons. In addition, we detected non-linear density-dependence. The seasonal structure and the factors influencing population growth rates were able to capture the observed temporal variation in these rates, including their structural variation over time (Figure 2).

The long-haired field mouse (*Abrothrix longipilis*) in southern temperate forests of Chile was characterised by a second-order feedback (N_{t-1} and N_{t-2}) and a non-linear effect of SOI on the per capita growth rates. This climatic effect can be a proxy for the influences of climate on food (fungus in autumn and winter, and fruits and plants during summer) (Figure 3).

Long-tailed rice rats (*Oligoryzomys longicaudatus*) were characterised by first-order dynamics and a negative non-linear effect of SOI on per capita growth rates, that means that El Niño years have a negative impact on the population dynamics of rice rats. This negative impact may be associated with the relationship between SOI and summer rainfall in southern Chile. Also, the non-linear and negative effects of rainy winters may be the effect of high over-winter mortality produced during very rainy winters due to cold weather or flooding. The non-linear effects of rainfall and SOI on population growth rates represent a new and interesting finding for understanding population dynamics of this rodent (Figure 4).

Strong non-linear and non-additive effects of winter weather were observed in the population dynamics of small rodents from Pennsylvania (USA) (Figure 5) and Chihuahuan desert in Airzona, USA (Figure 6). This finding emphasises the importance of interactions between climate and feedback structure for understanding the population dynamics of small mammals. Although several studies have shown effects of climate in different ecological systems (see Ottersen et al. 2001 for a review), in this study we describe for the first time effects of the NAO on small rodent populations inhabiting North America and non-linear effects of rainfall on kangaroo rats. The NAO is primarily a winter phenomenon influencing air temperatures, winds, and precipitation over the North Atlantic areas. In the same vein, strong non-linear and non-monotonic effects of winter and summer rainfall on small rodent population growth rates were observed in time series from south-western USA.



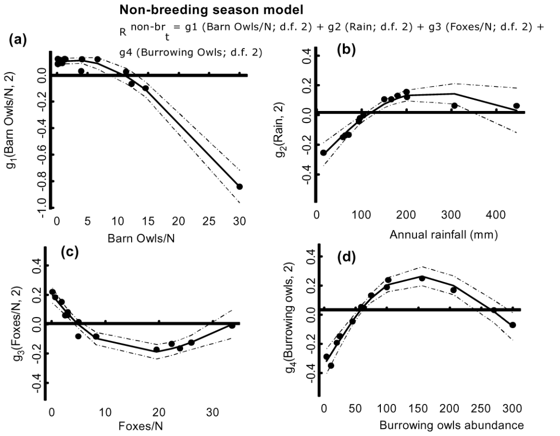


Figure 2. Best generalised additive model (GAM) representing the breeding *R*-function for leaf-eared mouse dynamics (breeding season model): (a) partial non-parametric regression line for the population density (N_t–1); (b) partial non-parametric regression line for annual rainfall; and (c) partial non-parametric regression line for the ratio (total predator abundance index)/(leaf-eared mouse abundance). The model was fitted by using natural cubic splines with 3 df. Dashed lines are 95% confidence intervals; $R^2 = 0.97$.

Best GAM model representing the non-breeding *R*-function for leaf-eared mouse dynamics (non-breeding season model: (a) partial non-parametric regression line for the ratio (barn owl abundance index)/(leaf-eared mouse abundance); (b) partial non-parametric regression line for annual rainfall effect; (c) partial non-parametric regression line for the ratio (culpeo fox abundance index (foxes))/(leaf-eared mouse abundance); and (d) partial non-parametric regression line for the effect of burrowing owl abundance index (burrowing owls). The model was fitted by using natural cubic splines with 2 df. Dashed lines are 95% confidence intervals; $R^2 = 0.98$.

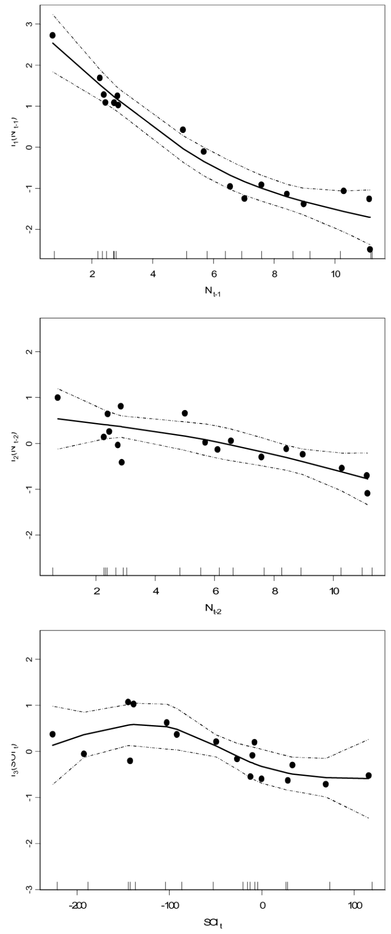


Figure 3. Statistical population dynamic model representing the per capita population growth rates [(R_t = Log (N_t/N_{t-1}) or *R*-function] for long-haired field mice (*Abrothix longipilis*). (a) Partial non-parametric regression line for first-order feedback (N_{t-1}). (b) Partial non-parametric regression line for the second-order feedback (N_{t-2}). (c) Partial non-parametric regression line for Antarctic Oscillation Index (AAOI). The model was fitted by using natural cubic splines with 3 df. Dashed lines are 95% confidence intervals and explain 94% of the variance.

Consequently, we suggest that the interactions between direct and indirect climate effects, and non-linear density-dependence, are the key elements in understanding the dynamics of many small rodent populations. The principle that emerges from this study is that predicting responses to global change of natural populations may be confounded if non-linearity and non-additive effects are not clearly assessed. The existence of both non-linearity and non-additivity has profound implications for understanding natural population dynamics and food web structure. We contend that one cannot predict the responses of natural systems (populations and communities) to climate changes unless the particular non-linear structure of these systems is fully understood.

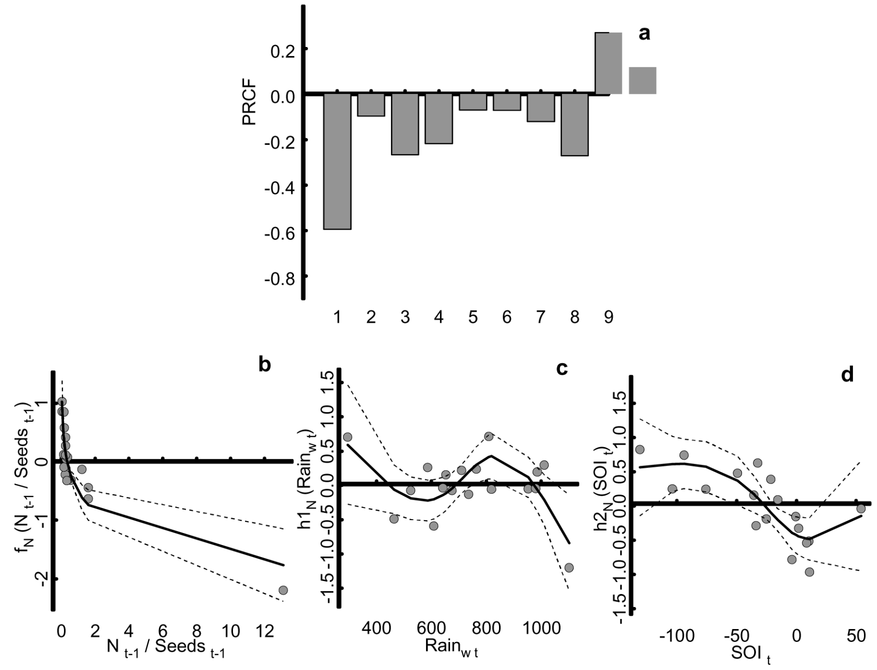


Figure 4. (a) Partial rate correlation function (PRCF) for the rice rat time series. (b) Best model representing the *R*-function and the climatic co-variables for rice rats (*Oligoryzomys longicaudatus*). Partial non-parametric regression line for the ratio between population density and seed density (N_{t-1}/Seeds$_{t-1}$); partial non-parametric regression line for winter rainfall (c) and partial non-parametric regression line for Southern Oscillation Index (SOI) (d). The model was fitted by using natural cubic splines with 3 df. Dashed lines are 95% confidence intervals.

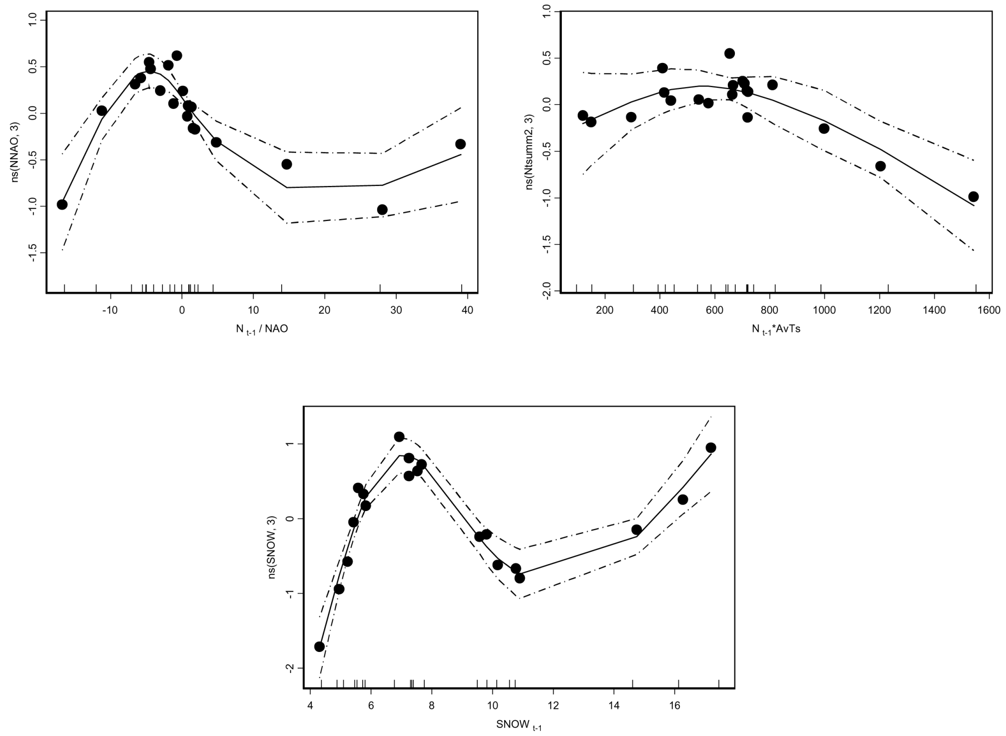


Figure 5. Best model representing the *R*-function and the climatic co-variables for southern flying squirrels (*Glaucomys volans*) at Powdermill Biological Station, Pennsylvania, USA. Partial non-parametric regression line for population density (N_{t-1})/North Atlantic Oscillation (NAO); partial non-parametric regression line for population density (N_{t-1}) * Average summer temperature (*AvTs*); and partial non-parametric regression line for direct snow depth effects. The model was fitted by using natural cubic splines with 3 df. Dashed lines are 95% confidence intervals.

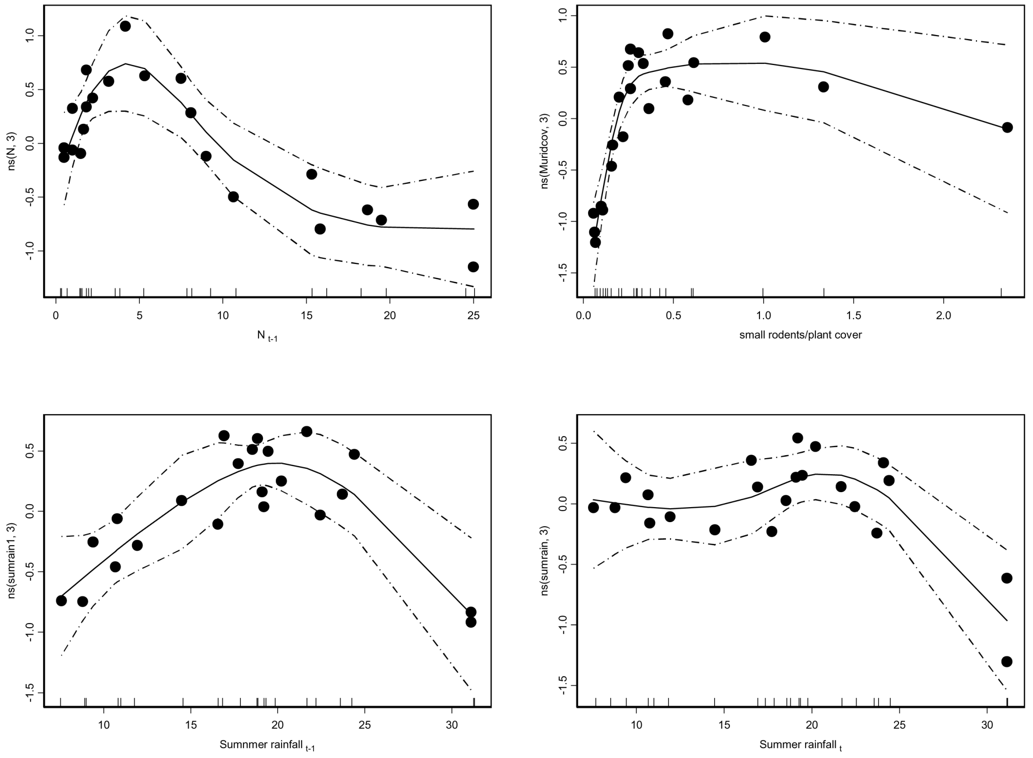


Figure 6. Best model representing the *R*-function and the climatic co-variables for Banner kangaroo rats (*Glaucomys volans*) at Portal, Arizona, USA. Partial non-parametric regression line for population density (N_{t-1}); partial non-parametric regression line for the interation between small rodent abundance/plant cover; and partial non-parametric regression line for lagged and direct summer rainfall. The model was fitted by using natural cubic splines with 3 df. Dashed lines are 95% confidence intervals.

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A sociological perspective on the community-based trap–barrier system

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Abstract. The community-based trap–barrier system (CTBS) is a relatively new technology for the non-chemical control of rodent pests in rice fields. There has been substantial biological work conducted on the CTBS but relatively little anthropological work. This paper develops a framework for understanding the CTBS by redefining the CTBS as a common property resource (CPR) and thus subject to many of the same constraints and opportunities as other CPRs. The paper shows that many of the documented threats that other CPRs have are also present in the CTBS, principal among these are the free rider, issues of transparency and equity, and the use of existing institutional structures for resource management. We begin by applying a typical CPR framework to the CTBS—demonstrating the links between the two systems. This is followed by an analysis of a set of threats to CTBS derived from our understanding of CPRs. We conclude with a set of testable hypotheses for those interested in applying this framework to other CTBSs or CPRs in general.

Introduction

The community trap–barrier system (CTBS) is a relatively new technology for the management of rodents in rice fields (see Singleton et al. 1999 for review). We have made an effort to define the CTBS in sociological terms to better understand the social dynamics of management. This in turn allows us to make better recommendations regarding how to improve the overall effectiveness of the system.

In this paper we draw on our experiences of the adoption of the CTBS in the Mekong Delta to present a theoretical framework for understand the sociological component of the CTBS, followed by a selection of threats to the sustainability of the CTBS, considering only sociological aspects. Based on these threats, a set of mechanisms for improving the likelihood of the sustainability of CTBS is suggested. Finally, we identify a set of hypotheses that can be used to test the CTBS in different cropping systems.

Technical background to the CTBS

A CTBS for rodent control in rice fields has an early planted 'trap crop' within the CTBS, which lures rodents to the traps. Ideally, the trap crop should be planted about 20 days before the surrounding rice fields. The trap crop has a plastic barrier around it, placed along the margin of a rice crop, and small holes are made in the fence just above the irrigation water. Adjacent to each hole is a multiple-capture trap suspended on bamboo above the water level (on the crop side of the fence). A mud mound provides access to the hole and thence to the trap. Rats are attracted from an area beyond the field of one farmer. This area is referred to as the 'halo', or the area of effectiveness, and may cover an area of 10–15 ha (Singleton et al. 1999). One distinct advantage to the CTBS is that no poisons are used, although management and labour costs may be higher than in typical baiting systems.

Theory

Frames of reference

There are at least two analytical frames possible in a CTBS. First, the CTBS is a common property resource (CPR), created with the establishment of the system by community labour and shared cash inputs. Second, the CTBS is a private resource, where the outputs of the CTBS, e.g. low rat damage, is considered a positive externality of individual behaviour.

Property rights are understood as the "*sanctioned behavioural relations* among men that arise from the existence of goods and pertain to their use" (Furubotn and Pejovich 1974). Theorists typically recognise four sanctioned behavioural relations: private, communal, state, and open access (Feeny et al. 1990). State control of resources and open access rights regimes will not be considered here since they are not generally relevant to the management of a CTBS. Of interest here are the various costs, benefits, and general utility of private and common property in the management of rodents.

A rice field is typically owned privately by the farming household. This means that the right to manage, sell, or lease the property is determined by the household itself, without any undue encumbrances laid upon it by either the government or other households. Common property exists where a group of users cooperate in the management and disbursement of the resource, and thus share in the benefits 'stream'. Users share the 'rights' of resource use and 'duties' of resource management (Bromley and Cernea 1989).

Typically, no common property exists in a rice field since rice is the sole property of the owner. But when a CTBS is established using shared resources, such as materials and labour, a common property is created. In this case, the shared resources are reduced rodent damage to rice, any consumable rodents, and other consumable animals caught in the trap. The shared costs include the cost of the fence, and the labour to erect it, and any costs incurred related to early establishment of the rice crop and daily monitoring of the traps and the fence.

In some cases, the TBS may operate as a private property system with a stream of positive externalities. In this case, a family may decide to establish TBS on their own. They receive the full benefits of reduced rat damage and the control of all the live animals caught in the traps. Those farmers outside the immediate family yet still within the halo of protection are the beneficiaries of what is referred to as a positive externality—they receive benefits at no cost.

The difference between the private and common theoretical frames can be described according to two dimensions: the number of participating households within the closed system and the degree to which participating members feel burdened by non-participants who benefit. In the pure case of the common CTBS, all members pay equal costs and receive equal benefits. For all practical purposes, this can never be achieved due to the complex nature of the transactions and the importance of perceptions of equity in the allocation of resources.

In farming communities where the average farm size (most are <2.5 ha in Southeast Asia and South Asia) is at least a quarter of the halo of protection (10–15 ha), it is unlikely that many farmers will willingly establish a TBS alone (the private option). This is because the trap–barrier system is costly, and usually beyond the means of individual farmers. The main costs for Mekong farmers are draining the field before direct seeding, especially in the wet season, and purchasing the poles and plastic of the fence. A farmer may, on the other hand, build a CTBS with their own funds for the benefit of their neighbours, particularly where these neighbours are relatives. However, since exchange in extended households often changes form, e.g. weeding labour may be exchanged at a later date for a cash loan, the establishment of a CTBS would be considered a common good for his extended family. The main difference here is the degree to which these decisions turn on the expectation of return. Within a household, all members contribute resources and receive benefits according to some culturally determined set of principles.

For a typical common property resource (CPR), the attributes are important in determining the management strategy employed for optimum use (McCay and Acheson 1987). There are four important aspect of a CPR: (1) the technical attributes; (2) the decision-making arrangements; (3) the patterns of management interaction; and (4) the outcomes of various management decisions and options (Oakerson 1986).

Technical attributes

One important technical attribute is subtractability, which is the degree to which one resource user limits the use of another (Oakerson 1986). This is important because most resources are limited in time and space, thus too many users would mean both higher costs to obtain resources and the potential for degradation of the resource over time. Neither of these are problems necessarily, because the main benefit of a CTBS is actually the *absence* of a problem (rat damage), creating a *presence* of a resource in the form of a public good (improved rice yield within the halo). Sharing the trapped rats can be dealt with through institutional cooperation. One community group came up with the idea that those who check the traps also receive the rats inside ("check the traps, keep the rats").

Excludability, the degree to which entitled users can keep out other potential users is another important technical issue. Like subtractability, this is important because the benefits of the resource are limited, so the presence of unentitled users would mean less benefit for all entitled users. Excludability in a CTBS is very low—all entitled users (paying and within the halo) of the CTBS would receive the full value of their investments. Others outside the halo, who are not required to pay, may also receive benefit. However, if this causes no concern on the part of the entitled users, then no problem exists. On the other hand, if the halo is determined not theoretically, as in "200 metres in every direction from the trap crop", but practically by assuming that all those who have no rat damage are within the halo, then subtractability may be an important issue. This view redefines those outside the halo as free riders, and thus makes them problematic for the community group.

Finally, divisibility, the ability of users to divide common property into private sub-units, is indeed a threat to the CTBS. The process of privatisation of the CTBS could involve either an individual voluntarily constructs a TBS and others benefit from that, or a small group of local users could develop their own CTBS, whereby only those individuals in this smaller group benefit. In the former case, a private property system has emerged, while in the latter case it is simply a selective form of CTBS.

Decision-making arrangements

Decision-making arrangements are as important as the technical attributes in determining the sustainability and effectiveness of a CTBS. These arrangements are typically made up of a set of rules or guidelines to structure the behaviour of members. The majority of the rules are unwritten, and they govern how decisions are made, and the content of these decisions. In addition to rules, other management tools include incentives for cooperation, structures for the dispersal of benefits, and allocation of labour among households.

Group decisions in resource management are based on individual understanding of the dynamics of resource use. In the case of the CTBS, this includes an understanding of the fundamental link between the creation of a CTBS and a reduction of rodent damage. If this understanding is limited, participation will also likely be limited because the link between individual costs and benefits are not understood.

Patterns of interaction

A third important element is the patterns of interaction or interrelationships between actors, in relation to the resource. These include the behavioural outcomes of the rules and technical attributes of the resource (Figure 1). For instance, if one farmer opts out and becomes a free rider, others will see this and it will cause friction within the group. This will give members a negative expectation of the behaviour of the group as a whole, thus reducing the amount and enthusiasm of their own investment. Alternatively, if reciprocity is the norm, the CTBS is more viable and transaction costs are lowered. Transaction cost in this case is the time, effort, and other resources needed to search out, negotiate, and carry out the operations of management.

In 1968, Garrett Hardin proposed the concept of the “tragedy of the commons” (Hardin 1968), which has since become a standard feature of any discussion on common property resource management. The tragedy of the commons refers to the destruction of a common resource due to individual pursuit of resources to the maximum, in spite of obvious resource degradation. This individual pursuit is characterised as the free rider (Hardin 1968). Hardin’s analysis has been often cited as a reason to privatise the commons, thus linking the maintenance of resources with the benefits derived from them.

Ostrom (1990) has shown that successful CPR systems are usually the result of “factors internal to the given group” Unsuccessful CPRs may be marred by the inability of members to communicate with each other or to develop trust in the institutions. Also, factors “outside the domain of those affected”, e.g. lack of local autonomy to change the given institutional framework, can also have detrimental effects on the effectiveness of CPRs (Ostrom 1990).

Internal factors are important for successful CPRs because they determine how members of a given group interact with one another. The size of the governing group is critical in determining the likelihood of successful cooperation in achieving group aims (Olson 1971), and group size is not determined by the number of actors, but the relative degree of their transparency of action (Ostrom 1990). Moreover, the actual patterns of interaction among members cannot be dictated from outside, nor should criteria for success be presumed at the outset.

Reducing costs and increasing benefits to individual members or the group as a whole will increase the likelihood of maintenance of the institutions responsible for continuation of the CTBS. Alternatively, holding meetings and talking with neighbours about the CTBS can be presumed to be a (transaction) cost, regardless of how small. Therefore, the relative ease with which people can meet and discuss the CTBS will determine the likelihood of success. We recommend that the CTBS group be made up of people who will generally talk to each other often anyway, e.g. kin, to reduce transaction costs.

This begs the question: what (or who) is the community in community trap–barrier system? Generally, the community is a default set of individuals who happen to share fields within a halo. The community in a CTBS can either be created, by vested local leaders (e.g. village head, or extension worker), or through the adoption of an existing community for a CTBS, such as a kin group described earlier. Our research shows that both types of communities exist: the communities in a CTBS may be a community in other terms, either through integrated pest management or farmers’ club, or related by kin in some way.

These are important considerations, because farmers’ commitment to the community relates directly to feelings

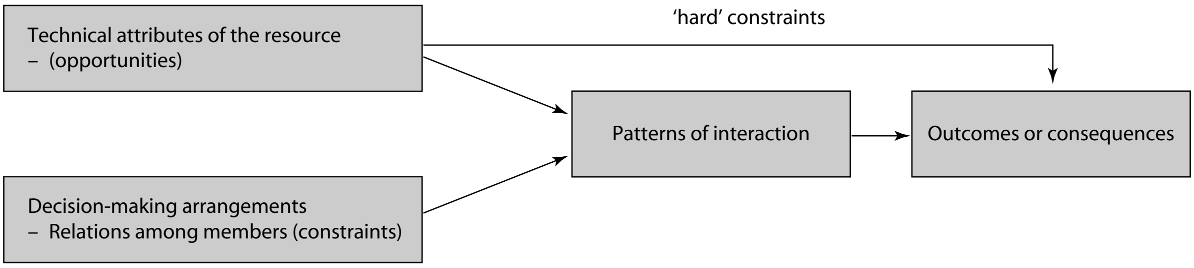

Figure 1. Model of common property resource interactions.

of obligation and the likelihood of active participation in maintenance of the CTBS. The anthropological CPR literature is replete with examples of how the problem of free riders has been avoided through active, vital community involvement in resource management (Netting 1976; McCay and Acheson 1987; McCabe 1990; Ostrom 1990). The basic thrust of this work is to demonstrate that the tragedy of the commons is avoidable through historically relevant institutional arrangements and local culture.

Outcomes of the community resource management system: equity and efficiency

There are two important considerations regarding the outcomes of a community resource management system: whether the system efficiently allocates resources for optimal gains to users and whether these allocations are made equitably. Both equity and efficiency can be understood at the group and individual level. Group efficiency arises from an overall reduction in the damage due to rats within the entire halo area, and whether total CTBS costs are less than those of rodenticides and other control measures. Individual efficiency may be understood as a function of individual costs of the CTBS (including labour) in relation to other control methods. For instance, some farm households may have excess labour, but less capital, therefore preferring to contribute more labour than cash to the CTBS.

Equitable individual division of the benefits of CPRs and CTBS are especially difficult to implement and monitor. Because costs and benefits must be defined both internally, i.e. within the household, and externally, the precise benefits to the individual user could vary widely in an otherwise successful rodent control program. This is exacerbated by the inexact size and shape of halos, which are presumed to be more or less circular, although factors may exist (e.g. rat breeding hot spots: heterogeneity of source and sink habitats for rats in the landscape), which would skew this distribution pattern. Indicators of inequity include variable rat damage between farms, lower yields within the trap crop, and absence from the construction teams.

If inequity is too great, farmers will be less likely to continue working with the CTBS. Whether the inequity is real or imagined, it is important in regards to methods for mitigating the inequity. Transparency and communication can solve the problem but technical solutions would be ineffectual. For real problems of inequity, such as random rat damage in a rice field, technical solutions are possible and should be pursued. These may include a change in the location, size or design of the trap crop or associated management actions to reduce the number of breeding hot spots. It is important to determine whether inequities are borne out by demonstrable facts or due to improper perceptions of the on-the-ground case.

Equity is very difficult to manage because it is based on many factors. Most importantly perhaps is the unpredictability of rodent damage and the effect this will have on farmers' perception of CTBS equity and effectiveness Farmers know that rat damage can be very heavy one year and light the next, but they do not know what effect CTBS will have on this annual variability. Farmers must be able to properly assess the causes of damage to determine whether they can modify social and physical mechanisms. Therefore some understanding of rodent ecology is critically important. A technical or sociological solution needs to be found if inequity in equity exists.

The shape that a halo takes has important implications for the equitable distribution of benefits in a CTBS (Figures 2 and 3). In Figure 2, the halo is well defined for the 10 farmers. All five CTBS members are within the halo and all five non-members are outside. The relationship between benefits and costs is well defined, and reality (i.e. damage) will support this understanding of the distribution of goods. Figure 3 illustrates a poorly defined halo. Two non-participating farmers are found within the halo, and thus defined as free riders, and three participating farmers are outside the halo, giving a total of five people who are not properly described by the halo concept.

This membership by benefit scenario, which will be indicative of the likelihood of the sustainability of the CTBS, suggests that members who receive benefits will remain within the CTBS. Non-members who receive benefits are likely to encourage the members to continue the system, since they are free riders. Members who do not receive benefits are likely to quit.

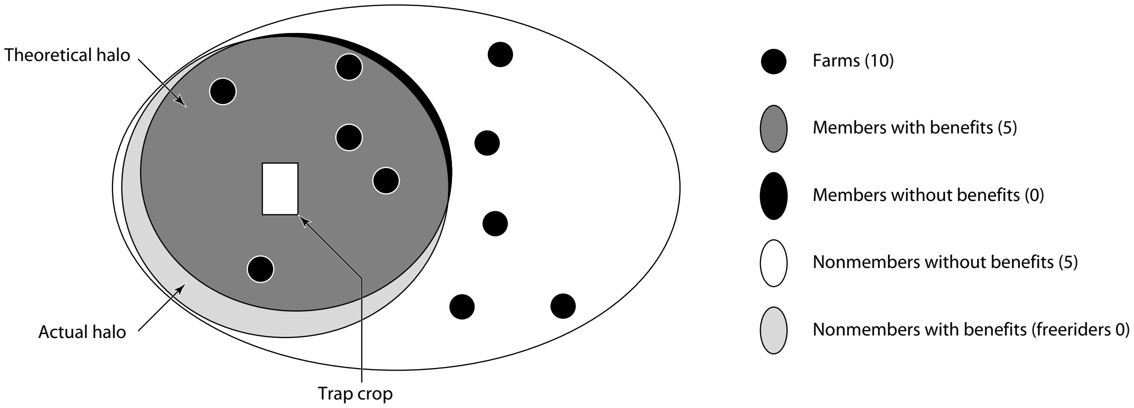

Figure 2. Equity: actors in a well-defined community-based trap–barrier system.

Benefit–cost in technology assessment

In economics, everything used in the productive process has calculable value, including family labour. However, because family labour is not sold, it has an imputed value based on the concept of opportunity costs. Opportunity cost is defined as the value of any resource when put to its best alternative use (Doll and Orazem 1984). Let us consider the opportunity cost of the farmer's time. If they have a job off the farm which they have to give up temporarily to check if there are rats caught in the rat traps, then we say that the opportunity cost of their time in checking rat traps is the wage which they would have been earning if they had stayed in the job instead. Normally, and in our case, the imputed wage for family labour is the average agricultural wage.

One measure of assessing the viability of the CTBS is through the marginal benefit–cost ratio (MBCR). This is the ratio of additional benefit due to adoption of the TBS and additional costs due to adoption of the CTBS.

The potential benefits of the CTBS are:

1. reduction in the cost of rodent control other than TBS, i.e. rodenticide, labour;
2. value of the incremental yield due to less rodent damage; and
3. value of rats caught (in this case, there is a market price for live rats caught).

There is also the environmental benefit from reduced chemical use, but this is difficult to valuate.

The potential costs of the TBS are:

4. materials and labour to build the fence;
5. material cost of rat traps;
6. labour to check the traps daily, remove rats from the traps and maintain the fence;
7. reduction in the trap-crop yield;
8. reduction in field size due to the creation of a buffer around the trap crop; and
9. increased crop protection costs in the trap crop from other pest infestation.

The result of our benefit–cost analysis is presented in Table 1.

Case study: threats to the sustainability of the CTBS

Based on research with previous CPRs, two threats to the sustainability of a CPR are transaction costs and costs associated with maintenance of the institutional and physical infrastructure. Private property regimes improve resource management systems in these two areas. Considering that privatisation is not yet an option for the CTBS, we must consider ways to improve the efficiency within the CPR. This can be achieved by considering two of the main costs of the CTBS: the labour associated with daily maintenance of the traps and fence; and the transaction costs associated with establishing and running the CTBS.

In October 2001, an informal survey was conducted examining the characteristics of members of the trial CTBS in the Mekong Delta, Vietnam. The leaders of the CTBS were asked to list the members of the CTBS, their relationship to other members, and the distance from the trap crop to the members’ residences. We found that there was a dense network of interrelationships among members of the CTBS, shown in Table 2, in which all but one of the farmers were related by affinity (marriage) or consanguinity (blood) to someone else within the CTBS (defined as the area presumed to be protected by a CTBS). According to the CTBS leader[1], this pattern resulted from the historical sharing of plots among extended kin. The inheritance preference among Vietnamese parents is for the youngest son to have first rights because he will help his parents as they get older. The youngest son will also bring a wife into the family. If the youngest son cannot inherit, preference is given to any son, and lastly to a daughter. The daughter is not preferred because she will marry and give part of her inheritance to the family she marries into, thus reducing the landholding of the corporate group. This also illustrates why so few women landholders are part of this study (Table 2).

This means that the CTBS has a good prospect of being successful in Vietnam because there is a large group

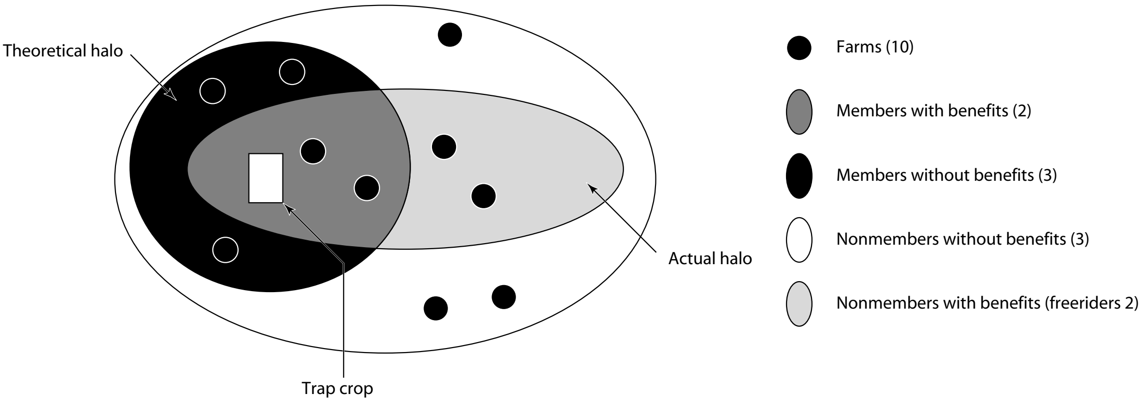

Figure 3. Inequity: different actors in a poorly-defined community-based trap–barrier system.

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[1] The CTBS leader, unless otherwise noted, is the same person who owns and maintains the trap crop.

of potential workers who are related and have neighbouring fields. As kin, they share labour and other resources on a routine basis, particularly among and between men. In the CTBS illustrated in Table 2, the trap-crop owner said he relied mostly on two of his nephews, or junior male kin (farmers represented by numbers 12 and 15), to help him build the CTBS fence. This reduces transaction costs, helps to ensure equity in the distribution of resources, increases transparency, and it increases the perception of equity, i.e. participants are less likely to assume a relative is a free rider than a neighbour, and a relative would be less likely to cheat on transactions such as sharing of benefits.

A number of trap-crop owners said they will continue to operate their CTBS, at some cost to themselves, because it serves a useful purpose that they can share. As we can see from the list of relationships in Table 2, the goods described in this case are, to some degree, private goods, with sharing occurring within a defined kin group. This conceptualisation, however, blurs the distinction between private and common property. Nearly everyone in Table 2 is related to someone else within the CTBS.

A final threat to the sustainability of CTBS is low cash flow. Many farmers commented that they are just too poor to actually pull together the cash at the right time to effectively use the CTBS. This may imply that there is not

Table 1. Marginal benefit–cost ratio (MBCR) from taking part in a community-based trap–barrier system (CTBS) for individual calculation. (The exchange rate at the time of the survey was approximately Vietnamese dong (VND)14,500 to US$1.)

Factor	Cost (VND)	Benefit (VND)	MCBR
Additional cost due to TBS			
TBS materials and labour (VND1.35 million/10 farmers)	135,000		
Additional benefit due to TBS			
Rats caught 100/4 (rats/kg) * 6000 (VND/kg)		150,000	
Yield due to TBS 500 kg/ha * 1500 (VND/kg)		750,000	
Reduced/eliminated rodenticide expenditure		16,000	
Total cost	135,000		
Total benefit		916,000	
MCBR			6 (916,000/135,000)

Table 2. Relationships of community-based trap–barrier system (CTBS) members and their household distances from the trap crop, Thuan Hung village, My Tu district.

Number	Family name of farmer	Relationship 1	Relationship 2	Relationship 3	Distance to trap (m)
1	Nguyen	Leader	Related throughout		150
2	Nguyen	Cousin of leader	Younger brother of 3		Other village
3	Nguyen	Elder brother of 2	Cousin of leader		Other village
4	Nguyen	Brother-in-law of leader			700
5	Truong	Cousin of leader			700
6	Trinh				700
7	Nguyen	Son of 8	Cousin of leader	Brother of 10	700
8	Nguyen	Uncle of leader			700
9	Nguyen	Son of leader			300
10	Nguyen	Son of 8	Cousin of leader	Brother of 7	700
11	Quach	Nephew of leader			500
12	Truong	Son of 5	Nephew of leader		300
13	Quach[a]	Cousin-in-law of leader			300
14	Huynh	Son-in-law of leader			5000
15	Truong	Son of 5	Nephew of leader		300

[a] Denotes a female farmer, otherwise all are male.

sufficient interest in it to make it work, because farmers can usually bring resources together when there is need and determination. It is also possible that there is competition for cash—farmers generally believe in the CTBS but do not, at the time of trap construction, have the necessary cash for purchasing the fence, stakes, and fuel to pump the water of an area for transplanting the early trap crop.

Mechanisms for improving the sustainability of the CTBS

The threat of privatisation, abandonment, or simply disintegration of social networks are significant hurdles to the widespread adoption of CTBSs in Southeast Asia. Therefore, it is important to address these threats in the design of the system to minimise or to eliminate them. We have identified eight decision factors that should be taken into consideration when establishing a CTBS.

Factor 1: keep the social relationships among participants within the halo as 'dear' as possible

Typically, the topography of the rice field is the main criterion in where to establish a CTBS, with preference given to open, mostly flat areas. This assumes that the social grouping that constitutes the membership within the halo is of secondary importance. Our contention is that topography is important, but not as important as the people running the CTBS. It is our belief that the social grouping should be given an equal weight when considering where to locate a CTBS. Ideally, the CTBS should be located where both topography is adequate and social relationships close.

We first must assume that, as a general rule, kin will work for other kin more than they will for non-kin. With this assumption, we can make the statement that the density of kin relations within the group is positively associated with level of altruistic behaviour. Where many kin relationships exist, there will be a greater sense of altruism and actions consistent with the survival of the group over individual benefit. Where these kin relations are lacking, the degree of cooperation will be reduced, although never absent.

There are other ways to ensure that members act in ways that are group rather than individual oriented. Among them are strict agreements at the outset regarding behaviour, high levels of transparency, and strict allocation of costs and benefits. The advantage of using the density of kin networks is that many of these mechanisms are already present and do not need to be legislated or explicitly stated. Principal among these unstated rules is the capacity to allocate rights and duties within the CTBS. In many CPRs, the eldest, or the most respected in the group, will allocate labour and the nature of the benefit stream.

There are ways to ensure greater density of relations, kin or otherwise. One is to use it as a basis for selection of the CTBS in the first place. Halos of various sizes and shapes, and trap crops of various configurations, have to be explored. It is our belief that slight losses in the efficiency of the system to capture rats can be exchanged for a greater likelihood in creating a socially sustainable system. Using existing institutions, such as integrated pest management (IPM) clubs, is another way to ensure greater internal cohesion. This saves the CTBS organisers from building new institutions, which can be very difficult and time-consuming and are likely to fail.

Factor 2: determine as accurately as possible the size and shape of the halo

It is important to know the shape of the effective halo because this represents the good being distributed. This has practical benefits because it will suggest how the costs should be shared and it is a theoretical question because, at present, it is presumed that halos are generally circular (in the absence of a hot spot). The shape of halo also will show who is a free rider and who is not, within the effective halo. This is especially important in rodent control, considering that damage is spatially and temporally variable.

Factor 3: keep the trap crop close to the homes of the people who are required to check it

Checking traps is a simple, necessary activity. Unfortunately, it must be done every day. The labour costs associated with checking traps increased proportionally to the distance needed to travel to the trap crop. In our informal survey, we found that average distances ranged from around 200 to over 1500 m from home to the trap crop. In such cases, the trap-crop owner has no choice but to allow those living a long distance from the trap to check it less often. This places a greater burden on those close to the traps for contributions to labour.

Factor 4: use the CTBS in seasons or areas known to have high rat populations

The CTBS, like most agricultural technologies, will not work in every place for every season. Therefore, identifying where and when it will work enhances the positive image farmers will maintain of it. If it is used too often in the wrong places or seasons, farmers will begin to distrust it. Therefore, CTBSs ought to be implemented in places where rodent damage is a major constraint to rice production.

Factor 5: choose farmers whose labour and cash availability are not severely limited

If farmers are overburdened with the labour requirements of rice farming, the addition of another labour-intensive technology will not be well received. In addition, low-income farmers would prefer to use their available cash for food rather than investment in a CTBS, where the probability of success is uncertain and the payoff is not immediate.

Factor 6: choose locations where post-capture markets or consumption habits make rat collection a profitable chore

Farmers in Vietnam and elsewhere eat rice-field rats. Although their market value per rat may be low, there is an emerging rat-meat market in southern Vietnam (Khiem et al. 2002). This creates an incentive for farmers to capture and sell clean, live rats. Farmers refuse to eat rats killed by rodenticides, so the CTBS offers an alternative income source. Elsewhere, rats are cooked and then used as a source of protein for fish or livestock.

Factor 7: select large landholders to achieve an economy of scale

An alternative approach to the CTBS is to target large landholders, whose decision-making processes, institutional frameworks, and capital needs are much less complicated than the community's. Indeed, in West Java, Indonesia, a company that produces certified rice seed for sale to farmers has been using the CTBS successfully on its 2000 ha farm since 1998. The annual schedule for construction and management of the CTBS has varied little during the period 1998–2002.

Factor 8: determine, and make known to farmers and extension workers, the profitability of the CTBS

The CTBS is likely to be adopted if the benefit is greater than the cost. Table 1 shows marginal benefit–cost ratio (MBCR) for individual participants in a CTBS in southern Vietnam. The MBCR was 6, which suggests that for every one Vietnamese dong (VND) additional investment, a farmer in that village or region gets VND6 additional return. The high profitability of participating in the CTBS is encouraging for farmer adoption. However, this individual calculation of MBCR assumes that all participating farmers will bear the costs and that the benefits will be equally distributed (or randomly over time).

A high MBCR is not always returned (Palis et al., this volume); benefits depending on a number of local conditions.

Hypotheses for research

Hypothesis 1

The social distance between halo members is closely associated with the likelihood of continuation with the CTBS as a system of rodent control (assuming equal efficacy of the system to control rodents).

This hypothesis requires measurement of the social distance between members and some measure of the likelihood of continuation of the CTBS. One important ranking criterion would be the likelihood of cooperation in labour activities. For instance, a brother–brother relationship would be ranked closer than a brother–cousin. Father–son or brother–brother relationships may have the highest ranks, whereas 'uncle–niece-in-law' may be lowest. In the latter case, the relationship crosses three recognised social boundaries: gender, generational/age, and marriage. The lowest-ranked case would be non-relatives. The assumption that non-kin have the lowest rank may have to be tested in its own right.

Hypothesis 2

A more tightly integrated CTBS organisation will demonstrate generally less transparency.

Oftentimes, the methods of sharing resources in families, and their inherent equity, are not immediately clear. This is because family members usually have a shared understanding of the meaning of given behaviours, and thus these need not be explicitly stated. Therefore, within families, the concept of transparency is not a good measure of the degree of openness in institutional decision-making or power. To test this, a measure of integration must be compared to some notion of transparency, perhaps through knowledge tests.

Hypothesis 3

In situations where there are wide divergences in labour investments in the CTBS, there will also be greater likelihood of the free rider.

If free riders openly flaunt the system, they can be quite disruptive. However, in those cases where the free rider has no choice in deciding whether to be a free rider, e.g. if they live a great distance from the trap crop and cannot easily check the traps, the degree to which this is perceived as negative will change. They are still a free rider, however. In order to test this hypothesis, interviews can be conducted which evaluate members of the CTBS in terms of both their contribution to the group and the overall evaluation of that person's role in it.

Hypothesis 4

The severity of a rodent problem is directly related to the likelihood of CTBS acceptability and sustainability.

In situations where rodents are a highly significant constraint to production, farmers would be more likely to adopt a CTBS. This may happen regardless of the existing social relationships in the community, particularly in the farm neighbourhood. One measure of this is whether a CTBS is adopted for each of the rice crops in a year or only for the crop or crops that typically have greater losses to rats.

Conclusion

The CTBS is an effective means for controlling rodents in rice fields. It shows a high rate of return on investment and individual labour costs remain relatively low. It is sustainable in both the short and long term. Farmers appreciate the ingenuity and complexity of the system and have suggested effective alternatives to the system to fit their local conditions.

Farmers will determine the success of CTBS for their particular farming systems. We have suggested eight factors that will generally encourage success in the application of the CTBS. Gone are the days when a single technology will solve the same problem for all rice farmers; there is just too much between-farm diversity for this ever to occur. This is why it is imperative that the CTBS be applied judiciously where it has the greatest likelihood of success. The CTBS will not work everywhere, but we have found that it does work in the Mekong Delta region of Vietnam. There are certainly other locations where it will work.

Like many technologies, the CTBS will work best where farmers understand the technology and have the social and institutional background to effectively apply it. Scientists, particularly biologists, can help in this process by explaining to farmers the biological details necessary to effectively apply the technology (such as the link between the birthing cycle of rats and the rice crop).

Defining the CTBS as a common resource is a productive and effective analytical tool for understanding the social relations of CTBSs. We have uncovered important sociological constraints and opportunities to CTBSs and suggested means to overcome them. We have also made suggestions for future researchers should they wish to apply the same analytical framework to their CTBS or CPR.

Acknowledgments

This project was partially funded by the Australian Agency for International Aid (AusAID) under their Vietnam Capacity-building for Agriculture and Rural Development (CARD) program.

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Farmers' perceptions and practices in rat management in West Java, Indonesia

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Abstract. Pests are one of the major constraints to rice production in Indonesia. We examined the perceptions, knowledge and current rat control practices of 120 farmers, 40 from each of three villages (Pasirukem, Sukatani, and Tegalurung) in the Cilamaya subdistrict, of Karawang district in West Java. The survey was conducted in November 1999. The respondents were aged 20 to 70 years, and most had only 1 to 6 years of schooling, a mean of 18.9 years in rice farming, and a mean farm size of 2.13 ha. Rats were reported as the most important pest to manage in this region. Controlling rats was important for 98.3% of farmers. There was divided opinion as to when it was best to conduct rodent control: approximately 60% thought it should be done during land preparation and 40% thought only during the rice-growing seasons. However, early rat control was conducted by 87.2% of farmers, with most effort during the land preparation–seedling stage. Most respondents (80.7%) agreed that by controlling rats they could increase rice yields, and 83.3% of respondents believed that rats could be controlled successfully. Cooperation between farmers was identified by 76.7% of farmers as important for successful rat control, although 13.8% of farmers prefer to do rat control by themselves because they were more satisfied with the results. Usually, local government officers coordinated group activities. Individual expenditure on rodent control per hectare ranged from US$0.3 to US$45. The common rat control methods were plastic barriers to protect rice seedlings (100%), rodenticides (98.3%), mass hunting (79.7%) and flooding rat burrows or fumigation/digging (44.1%). Most farmers used alternative pesticides such as temik (aldocarb; carbamate) (78.5%), akodan (endosulfan) (77.6%) and azodrin/guzadrin (monocrotophos; organophosphate) (12.9%), because legal rodenticides were difficult to find and/or were more expensive. These are all broad-spectrum poisons and some were mixed with oil before applying to the flooded crop. Although these poisons are of major environmental concern, a majority of farmers did not consider these to be environmentally unsafe.

Introduction

Important constraints to increasing rice production in Indonesia are the losses caused by pests and diseases, which occur every season. One of these pests is the rice-field rat, *Rattus argentiventer.* This pest causes the largest pre-harvest damage to rice crops (Geddes 1992; Priyono 1992; Singleton and Petch 1994). There are chronic low levels or rat damage (5–10%) in the rice fields of Java, with some villages experiencing high damage in most years. During the decade 1989–1998, a mean of 93,908 ha per year was identified as having severe rat problems, with a mean damage intensity of 19.3%. The largest losses were in 1998, with severe damage reported over 159,057 ha and a mean damage intensity of 24.8% (unpublished report from Direktorat Perlindungan Tanaman Pangan, 1999).

The rice-field rat is a pest of various agriculture commodities, such as food crops, horticulture and plantations, and it causes significant losses across a wide range of agro-ecosystems (e.g. lowland irrigated rice, rainfed rice in elevated areas, tidal swamp area). This rat species is also a vector for a number of human and animal diseases (Singleton and Petch 1994). Farmers in Southeast Asia use several rodent control methods, such as mechanical/physical control, chemical control and biological agents (see Fall 1979 and Singleton et al. 1999 for reviews). In many cases, the rodent control efforts by farmers in Indonesia and elsewhere in Southeast Asia have not given satisfactory results (Singleton and Petch 1994). The socioeconomic conditions and culture of farmers are thought to influence the success of pest management practices compared to other factors, such as the technology availability to manage the problem (Untung 1992). Information therefore needs to be collected on farmer beliefs, perceptions and practices associated with pest management (Heong and Escalada 1999). This study reports on information on rodent pest management gathered through farmer surveys conducted in the Karawang District in West Java, Indonesia.

Materials and methods

In November 1999, a farmer survey was undertaken at three villages (Pasirukem, Sukatani and Tegalurung) in Cilamaya subdistrict, Karawang district, West Java province, Indonesia. A structured questionnaire was developed and then pre-tested through field interviews. One hundred and twenty farmers (40 per village) were interviewed on their knowledge, perceptions and practices of rat control. The questionnaire consisted of 43 questions, which were divided into three sections and focused on the previous 1999 dry-season crop. The first section summarised demographic and farming information. The second section began with a general question on the main pests of rice during the previous crops and then considered rat control only. Farmers were asked what methods they used to control rats, how often, when and where they were applied, the time spent on control and its cost. The structure of rodent control activities (individual, groups, how groups were organised and their structure) was recorded also. The third section considered beliefs associated with rodent control with 13 questions that each had five descriptors from which the farmers chose the one that best described their belief. In this overview paper, the five categories were collapsed to three. The data were coded and are presented as percentages. Respondents were chosen at random from a list of farmers in each village provided by local extension agencies. Six people, with each conducting three or four interviews per day, conducted the surveys.

The villages were selected as part of a larger study on ecologically based management of rats using a farmer participatory approach that was imposed in two of the villages for the 1999/2000 wet season. All respondents are to be re-interviewed after the rodent management project has been operating for three years.

Results and discussion

Farmer characteristics

The age of respondents ranged from 20 to 70 years: 14.7% were 20–30 years old, 23.3% were 31–40 years old, 29.3% were 41–50 years old, 20.7% were 51–60 years old, and 12.0% were 61–70 years old. Only two of the respondents were female.

The formal educational background of the farmers varied considerably: 18.6% had not attended school, 61.2% had attended elementary school (1–6 years of schooling), 8.5% had attended junior high school (7–9 years of schooling), 10.2% had attended senior high school (10–12 years of schooling), and 1.7% had more than 12 years of education.

Farming was the main occupation for the people living in these villages in Cilamaya (92.1%). The farmers had a mean of 18.9 years of farming experience (range 2 to 59). The mean farm size was 2.13 ha. (range 0.3 to 15 ha). The respondents either owned their farm (60.2%), had a fixed rental (4.2%), were share-tenants (22.9%), or had another arrangement (2.5%). A high proportion of respondents had additional jobs (42.4%) such as trader of goods, local government officer or a driver. This often led to responses such as “we have no time” or “we do not only work in the field”, when questioned on their field activities for controlling rats.

Farmer knowledge

During the 1999 dry-season rice crop, the common pests and diseases were rats, golden apple snails, brown planthoppers, stemborers, worms and ragged stunt. The most important pest for that season was brown planthopper (46.4%), followed by the rice-field rat (29.5%) and the golden apple snail (15.2%). A few farmers (1.8 to 3.6%) also identified stemborer, worms, and ragged stunt damage as their most important pest. Although the brown planthopper was identified as causing the largest amount of damage during the 1999 dry-season crop, farmers ranked rats as the most important pest to be controlled. The farmers indicated that insect pests were relatively easy to control by using available insecticide, whereas rodenticide use was not sufficient to control rodent pests. Rodent management also required technical and mechanical control. Moreover, brown planthopper damage was mainly restricted to the generative stage of the crop, whereas rat damaged occurred during the whole growing season.

Farmer perceptions

Perceptions of farmers were determined from their agreement or disagreement to a series of specific questions. There was an interesting spread of responses regarding the timing of rodent control: 54.3% were strongly of the opinion that the control should be done before transplanting, whist 39.1% thought that control should only be implemented when the crop is growing. Almost all of the respondents agreed that rat control is important (98.3%), can increase rice yields (80.7%), and that it is important to increase yields by controlling rats (94.9%). Most farmers believe that rats can be controlled (83.9%) and that it is important to do so (94.9%) (Table 1).

The respondents realised that cooperation among farmers on rat control is required (76.72%) and important (92.3%), although some farmers were not sure and disagreed. Half of the respondents (55.5%) agreed that the rat control should be done after harvest and it was considered to be an important activity (75.99%).

Rat control was important for the farmers, although there was variation as to the best time for control and the preferred methods of control. Some farmers had the opinion that early rat control was not important. The success of rat control was identified as requiring cooperation among the farmers. Nevertheless, some farmers prefer to do rat control by themselves.

Rat control practices

During the 1999 dry season, farmers in Ciliamaya adopted many methods for rodent control (Table 2). The main physical methods of control were mass hunting

(79.7% of respondents), flooding rat burrows (44.1%), fumigation (using sulfur dioxide) and digging of burrows (44.1%), and plastic fences around rice nurseries (100%). Fumigation and digging were usually conducted individually or in small groups of farmers. Mass hunting is less expensive and is conducted in large groups, usually coordinated by local government extension staff as a control activity at the village scale. The paternalistic hierarchy of farmer groups influences coordination of rodent control; some farmers delay control until activities are coordinated by the head of a farmer group or by local government officials (Untung 1992).

Almost all of the farmers used rodenticide (98.3%), however, no farmers used anticoagulant rodenticides, which are readily available in the stores in Cilmamya subdistrict and are the only rodenticides registered for use in rice fields

Table 1. Perceptions of farmers on rodent control in Cilamaya subdistrict, West Java.

Perceptions	Agree		Do not know		Not agree	
	Number	%	Number	%	Number	%
Rat control must be done once rice is growing	41	39.05	7	6.67	57	54.28
Controlling rats is important	116	98.30	0	0.0	2	1.69
By controlling rats, a farmer can increase his rice yields	92	80.70	10	8.77	12	10.53
The yield losses caused by rats is important	112	94.91	4	3.39	3	1.70
Rats can be controlled	99	83.90	11	9.32	8	6.78
Rat control is important	111	94.86	4	3.42	2	1.71
Rats can cause severe yield losses	109	93.97	2	1.72	5	4.31
These severe yield losses are important	96	82.05	1	0.08	20	17.09
Rats can only be controlled if farmers work together with other farmers	89	76.72	11	9.48	16	13.79
It is important for farmers to work together to control rats	108	92.30	6	5.13	3	2.56
Rats should be controlled after harvest	65	55.55	22	18.80	30	25.64
To control rats after harvest is important	89	75.99	3	2.56	25	21.36

Table 2. Methods of rat control, and frequency of application, by farmers in Cilamaya subdistrict, during the 1999 dry-season rice crop.

Rat control method	Farmers		Mean number of times action is applied per season (range)
	Number	%	
Physical/mechanical (*n* = 118*)*			
Mass hunting	94	79.7	3.57 (1–16)
Flooding rat burrows	52	44.1	3.33 (1–8)
Fumigation/digging	52	44.1	4.1 (1–12)
Fencing for seedlings	118	100	1
Rodenticide (*n* = 116)			4 (1–6)
Temix (acute poison)[a]	91	78.5	
Phosphit (zinc phosphide; acute poison)	10	8.6	
Klerat (anticoagulant poison)	0	0	
Other pesticides[b]			
Azodrin, Gusadrin (monocrotophos)	15	12.9	
Akodan (endosulfan)	90	77.6	
Bait used (*n* = 105)			
Broken rice	79	75.2	
Unhulled rice	11	10.5	
Crab	12	11.4	
Fish	1	1.0	
Dedak	2	1.9	
Biological method/Predator	0	0	0

[a] A nematocide that is not registered for use in Indonesia as a rodenticide.

[b] Insecticides not registered for use in Indonesia as rodenticides.

in Indonesia. Temix, a nematocide, was widely used and is available in small plastic satchets without instructions for its use (e.g. concentration for its application). Temix is a potent aldocarb that has been banned in the United States of America since the 1940s. Of particular concern is the high use of the organophosphate 'azodrin' (monocrotophos) and the endosulfan 'akodan' because they are mixed with vehicle oil and spread on the flooded rice paddies. Rats that enter the paddies get the chemical on their fur and die when they ingest the chemical through preening themselves. Both chemicals affect the central nervous system and are broad-spectrum poisons. Although monocrotophos is rapidly degraded and does not persist in the environment, water birds (White et al. 1983; Flickinger et al. 1984), aquatic invertebrates, bees, fish, and mammals are particularly susceptible to monocrotophos and it is moderately toxic to fish and earthworms (WHO 1993). The World Health Organization states that this is a highly toxic chemical and care should be taken to avoid contamination of soil, water and the atmosphere. Endosulfans usually break down in crops over a period of a few weeks, however they stick to soil particles and may take years to completely break down. Endosulfans can also accumulate in animals that live in contaminated water (Agency for Toxic Substances and Disease Registry 2001). Farmers used these 'alternative' rodenticides because they are considered easy to use and are cheap to purchase.

Therefore, the usage pattern by farmers in Ciliamaya of these chemicals is a major environmental concern. The respondents used akodan because they believed it was very effective (3.6%) or effective (60.9%). Only 33.3% of farmers considered akodan not to be environmental safe to use (Table 3). It is clear that these farmers do not know the harmful effects of these pesticides on the environment. Interestingly, the respondents who considered akodan not to be safe reported dead chickens, ducks and fish around the rice plots treated with the akodan and oil mixture.

Farmers generally conducted rat control from land preparation through until harvest (Figure 1). Most of respondents conducted rat control during land preparation–seedling (87.3%), and there was also a concentration of effort at this time of the crop cycle with control activities conducted an average of 13.1 times (range 1 to 27). Rodent control activity decreased during the panicle stage and during ripening–harvest (Figure 1). After harvest, the farmers did not conduct rat control. Therefore, most of the farmers in Cilamaya conduct early rat control and realise the importance of early management action. Farmers also reported that after the vegetative (tillering) stage, rat damage seemed to be lower and so they reduced their rat control activities accordingly.

The time of application of rat control methods varied among farmers (Figure 2). Farmers used rodenticide from land preparation until the panicle initiation of the rice crop, with high usage during the seedling, transplanting, and tillering stages. Mass hunting started from land preparation until the booting stage, and the focus was especially on seedlings and recently transplanted rice. Night hunting of rats with torches was only conducted around the rice

Table 3. Opinions of farmers on the environmental safety of using akodan (an endosulfan) plus oil and its effectiveness in controlling rodent populations.

Opinion	*Is it effective?*		*Is it safe?*	
	Number of respondents	%	Number of respondents	%
Very effective/safe	4	3.6	2	1.9
Effective/safe	67	60.9	50	46.3
Not sure	19	17.3	20	18.5
Not effective/not safe	20	18.2	36	33.3
Highly ineffective/not safe	0	0.0	0	0.0

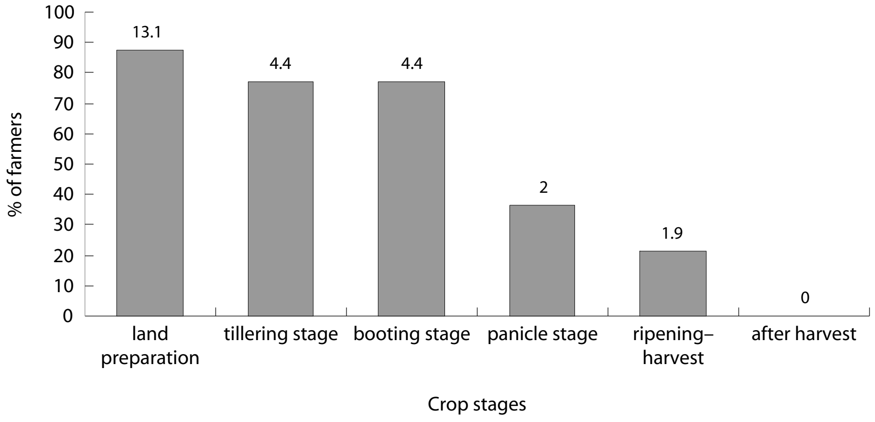

Figure 1. Percentage of farmers who conducted rat control at different crop stages in Cilamaya during the 1999 dry season. The mean number of rodent control activities for each crop stage is shown above each bar.

nurseries. Flooding of rat burrows was conducted on large banks or irrigation channel banks, with the sanitation or clearing of these banks conducted from land preparation until the booting stage. During land preparation until the ripening stage, the farmers fumigated rat burrows using sulfur dioxide. Plastic fences were only used to protect seedbeds of rice.

Table 4. Profile of rat control activities and access to tools to conduct rodent control in Cilamaya subdistrict, West Java.

Details	Number of farmers	% of farmers
Implementation of rat control		
Alone	14	12.07
Group	18	15.52
Combination (individually and group)	79	68.10
Hired labour	5	4.31
Coordinator		
Village/local government officer	87	81.31
Farmer group	10	9.34
Extension officer	10	9.34
Farmer themselves (neighbours)	10	9.34
Ownership of rat control tools		
Yes	47	40.52
No	69	59.48
Reason for no rat control tools		
Expensive	15	23.81
Not required	22	34.92
Could borrow/hire	24	38.09
Difficult to find	2	3.17

The farmers from the three villages owned land in one of four cropping areas where rice is grown as a monoculture. For the 1999 dry season, the mean cost per hectare of rodent control for these four areas was US$6 (*n* = 27), US$6 (*n* = 22), US$4 (*n* = 26) and US$4 (*n* = 26), respectively. However, there was a high amount of variation between farmers, with individual expenditure per hectare ranging from US$0.3 to US$45. This variation confirms the patchy nature of rodent damage that is often reported for rice cropping systems in Southeast Asia (Fall 1979; Buckle 1988; Singleton and Petch 1994).

Cooperation among farmers played an important role for rat control: 12.1% prefer to work alone, 15.5% only in groups, and 68.1% used a combination of both. Only a few farmer hired labourers to control rats (Table 4). Village or local government officers generally coordinated mass control actions and were an important source of information on rat control practices. Access to tools such as a fumigator and nets also influenced rat control activities (Table 4). Only 40.5% of farmers owned their fumigator or net.

None of the farmers used the trap–barrier system with an early-planted crop to manage their rat problem.

Conclusion

In the Cilmaya subdistrict, West Java, farmers identified rodents as a major pre-harvest pest, which is consistent with previous reports on the important impacts of rodents in rice agricultural systems in Indonesia (Geddes 1992; Singleton and Petch 1994). A wide range of physical and chemical methods of rodent management was adopted and farmers used a combination of these methods. Most effort in rodent management occurred during the land preparation–seedling stage, which is consistent with our understanding of the ecology and biology of the rice-field rat in West Java (Leung et al. 1999).

Most farmers agreed that by controlling rats they could increase rice yields, and believed that rats could be controlled successfully. Cooperation between farmers was identified as important for successful rat control, although 13.8% of farmers preferred to do rat control by themselves because they were more satisfied with the results.

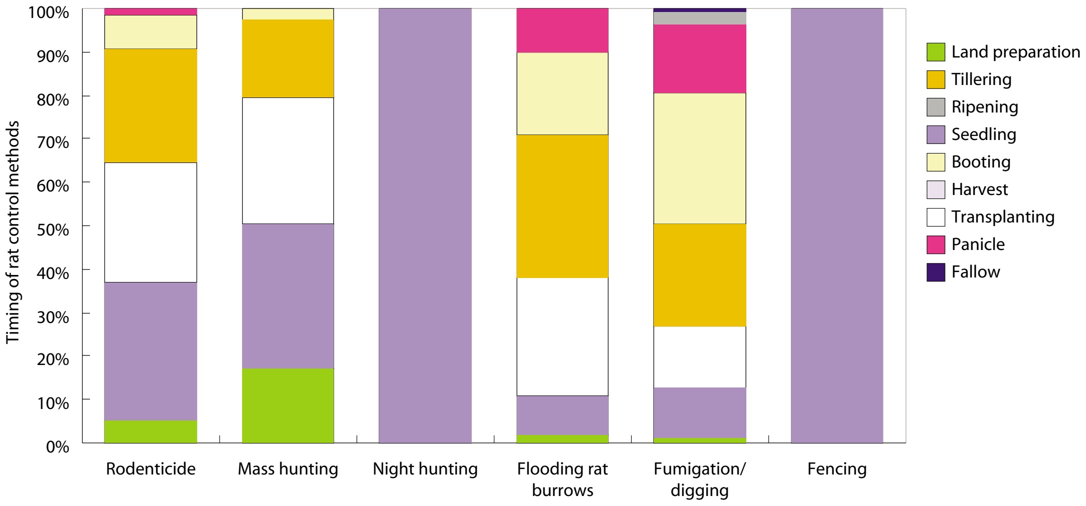

Figure 2. Rat control methods in different rice crop stages in the 1999 dry season in Cilamaya.

A major environmental issue emerged from the survey; over 75% of farmers used broad-spectrum poisons that are not registered for use against rats. Some were mixed with oil before applying to the flooded crop—an environmental disaster. A majority of farmers did not consider these to be environmentally unsafe. This is an area of education that needs to be urgently addressed.

None of the farmers had used the environmentally friendly trap–barrier system (TBS) to control their rodent populations. This simple technology is new to West Java (Singleton et al. 1998) and was implemented in two of the three villages, beginning with the 1999/2000 wet season crop. A follow-up survey will be conducted in late 2002 to examine the impact of this technology on chemical usage and whether the farmers are likely to continue with the use of the TBS technology.

Acknowledgments

We thank Jumanta, Tedi Purnawan and Elon Rasdan for their expert technical assistance with this study. Dr K.L. Heong and Dr Moni Esclada provided feedback on a draft of the questionnaire. The project was supported by funds from the Australian Centre for International Agricultural Research (AS1/98/36), the International Rice Research Institute (Rodent Ecology Work Group) and the Indonesian Institute for Rice Research.

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Community costs and benefits of rodent control in Cambodia: a first-round analysis of adaptive management

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Abstract. This case study examines the first round of experience from the Farmer-based Adaptive Rodent Management, Extension and Research System (FARMERS) Project. The project involved the introduction of a trap–barrier system (TBS) for rodent pest management across 11 villages in Samrong Commune in Kampong Cham province in Cambodia. This system has been trialled with some success in other countries and elsewhere in Cambodia. Participatory research methods were employed in the FARMERS Project, engaging the farming community in planning, managing, monitoring and evaluating the TBS. This article describes the process and outcomes of the first round of research, conducted in association with the dry-season crop in the early part of 2002. Farmer groups operated the TBS under social agreements that recorded the details of group responsibilities, entitlements and obligations.

After trialling the system on the dry-season crop in 2002, the farmers were firmly committed to the second-round establishment of the TBS for the wet-season crop. This indicated that TBSs were perceived as an improvement to rodent control strategies, although the test for sustainability was yet to occur.

There was a tendency for free-riding behaviour in the community, placing the burden of the cost of the TBS on the persons who owned the lure crop for the TBS. Nonetheless, the processes embodied in the social agreements for the TBS have been shown to be an effective mechanism for community education and the evolution of arrangements to counter free-riding behaviour.

Introduction

This case study is based on work conducted at Samrong Commune in Kampong Cham province in Cambodia. The work was a component of the Farmer-based Adaptive Rodent Management, Extension and Research System (FARMERS) Project; jointly undertaken by the community of Samrong, the Kampong Cham Office of Agricultural Extension (OAE), the Cambodian Agricultural Research and Development Institute (CARDI) and researchers from the University of Queensland. The FARMERS Project was aimed at developing and implementing rodent pest management strategies consistent with the ecological, technical and socioeconomic constraints faced by the community.

Rodents are considered a major pest of rice in Cambodia, particularly for dry-season crops (Jahn et al. 1999). The FARMERS Project introduced a trap–barrier system (TBS) for rodent pest management that has been trialled with some success in other countries and elsewhere in Cambodia (Jahn et al. 1999; Singleton et al. 1999). The TBS requires community cooperation and coordination to achieve a broad pattern of rodent control. The FARMERS Project sought to create the conditions for cooperation and coordination in the 11 villages of Samrong Commune. Monitoring work was also conducted in the neighbouring L'vea Commune, as a prelude to further involvement by that community.

The study of the socioeconomic conditions under which the project operates requires an assessment of both costs and benefits borne by farm households and a framework for the analysis of social costs and benefits. The TBS provide a limited *public good* in the form of relative freedom from rodent damage. The public good is limited in geographical extent by the ranging nature of the rodents, their reproductive patterns and ecology. A public good has attributes of *non-exclusivity* and *non-rival consumption*. These characteristics are commonly associated with *free-riding* behaviour. The characteristics of public goods and the consequences of free riding are widely discussed in the literature of environmental economics (Tietenberg 1996).

Participatory research methods (Martin and Sherrington 1997) were employed in the FARMERS Project, engaging the farming community in planning, managing, monitoring and evaluating the TBS. This paper describes the process and outcomes of the first round of research, conducted in association with the dry-season crop in the early part of 2002. CARDI's growing involvement in participatory research has previously been discussed by Cox and Mak (1999) and Lyons (2001).

This paper does not report results in the format of a scientific field trial. It was a trial conducted with the farming community and involved the dynamics of the agro-ecosystem of the commune. It was an action research project rather than a scientific experiment. There was no replication and no control. There was considerable variation in the timing of implementation, the surrounding landscape, and construction, management and monitoring of the TBS in the rice fields.

The economic impact of rodent pests in rice production in Cambodia is not well known. However, farmers and researchers alike confirm that rodents are a major pest and can be particularly damaging under certain conditions leading to population explosion. Singleton et al. (1999) report on cost–benefit analysis of the TBS in controlled studies in West Java and Vietnam. They found that the TBS generally enjoyed positive cost–benefit ratios and this was particularly apparent when rodent densities and crop losses in surrounding areas were high. Singleton et al. (1999) identified a challenge in transferring this technology readily and effectively to farmers. They observed that the small size of the rice fields in Southeast Asia would lead to neighbours enjoying the benefits of the 'halo of protection' of the TBS, without the need for bearing any of the costs. Thus, they concluded that the TBS would be most effective if implemented as part of a community-based approach to rodent pest management.

Earlier work by CARDI (Cambodia–IRRI–Australia Project 1998) in Svay Rieng province in Cambodia found that the TBS was not an effective mechanism for rodent control due to the need to monitor traps regularly, the high cost of the materials involved, the danger of theft of the traps, and the capture of non-target species. They observed that the major limitation of the TBS appeared to be the high cost of materials relative to the value of the losses associated with rodent damage.

Methods and results

Participatory planning processes

The initial introduction of the ideas for the FARMERS Project involved participatory methods of information collection and planning. Seasonal calendars were used to gather information to assess the significance of rodent pests in rice production. With the assistance of project staff, the farmers from the 11 villages in Samrong Commune formed 20 groups, each of approximately 10 farmers, to implement a commune-wide system using the TBS to protect the dry-season crop early in 2002. Social agreements were used to record the group membership and to formalise the social arrangements for the groups, their responsibilities, shared benefits and costs, and expectations of others. The agreements revealed that the majority of the farmers who intended to establish the TBS on their rice plots were also the group leaders. This pointed to likely farmer perceptions that the TBS would bring material benefit to the person who sited it in their own field.

Rice production budgets

The irrigated dry-season crop in Samrong Commune is grown mainly for sale and is exclusively IR66—a high-yielding, short-duration variety. Samrong has a total of 573 ha of dry-season rice (Powell 2002). A survey was conducted to develop a detailed rice production budget using in-depth interviews of key informants. This approach is based on Powell (2002) who estimated a return of US$199 per ha from dry-season rice production after all costs, including family labour, were deducted. In this study, 16 farmers from 4 villages in Samrong Commune were interviewed to gather detailed information on their rice production budgets. All farmers owned land and their dry-season fields varied from 2.3 ha down to 0.13 ha, with an average of 0.82 ha. Rice yields were in the order of 2.5 t/ha on average, returning an average gross income from rice of approximately US$160 per ha. Costs and returns were highly variable, with one of the farmers interviewed suffering a complete crop failure due to water shortage.

The training and materials for construction of the TBS in Samrong were provided by CARDI and OAE, and the labour for construction was provided by the farming community. Demonstration TBSs were constructed at the CARDI research station and cost US$40 for labour and materials. The farmers at Samrong received approximately $30 worth of materials for each 25 × 25 m TBS. They contributed labour and used local materials for the bamboo supports for the plastic sheeting.

Although 20 TBSs were planned and groups formed for each TBS, two TBSs were reported not functional, principally for lack of water for the crop. Assuming a 200 m radius of protection around each TBS (Singleton et al. 1999), the TBS in Samrong offered the potential to protect approximately 226 ha of rice. However, the TBSs were dispersed according to a complex of both physical and social conditions, rather than a simple grid system. Some of the TBSs were separated from the commune by a broad stream, where farmers owned fields located in an adjacent district. These conditions might significantly influence the area protected by the TBS.

Social and environmental costs and benefits

There was no anecdotal evidence of yield loss in the TBS lure crop beyond the levels experienced in adjacent crops and the farmers with lure crops made no claims for compensation for yield loss. The detailed monitoring of yield loss through cut tiller counts, visual estimates and calculations of grain dry weights produced highly variable results that limited bio-physical and economic analysis. The project team reviewed data collection techniques in an effort to learn from the problems encountered in the first round. The first round of yield loss measurements was based on the differential between an estimate of the yield from an undamaged crop and the actual yield. The estimate of potential yield was based on a calculation of the yield from undamaged hills, multiplied by the number of hills per square metre. The choice of undamaged hills allowed for subjectivity in sampling and the amount of variability in the results was unsatisfactory. This technique had been devised to eliminate the need for the construction of rat barriers and exclusion plots.

Farmers raised both intra-group and inter-group issues relating to the cost of the TBS. Intra-group issues primarily concerned the elimination of free riding. Many group leaders (who also tended to be TBS 'owners') complained that the commitment of group members tended to fall away after TBS construction. They also felt that the location of the TBS on their field exposed them to higher risk through the early planting of the lure crop. The group leaders felt that they bore a burden of labour in monitoring traps and in packing up and storing the TBS materials. Their major concern before commencement of the second round was for access to a secure water supply to prepare the field for transplanting the lure crop and for raising seedlings. The cost of crop failure was highly significant for the individuals concerned. Some villagers considered the conditions so difficult in their locality that they asked for cooperation from other villages to provide seedbeds or seedlings.

After their first experience with the TBS, it was reported by farmer representatives that other farmers were reluctant to work on the TBS because they perceived that the benefits of the TBS were enjoyed by the TBS 'owner'. This indicated that they believed that the benefits of the TBS were associated with the physical protection provided by the barrier, as opposed to the wider-scale protection the research team envisaged would accompany reduced rodent numbers. This indicated a need for more information on the function of the TBS to be provided to the community.

The farmers identified a number of factors that would show whether the project was successful. These included: reducing the number of rodents and yield losses; improved standard of living; adoption of the techniques by other communities; the ability to buy the materials for the traps and to set them up themselves; and the generation and sharing of new ideas for rodent management. Cost-effective management for rodents was considered a critical indication of success by all other elements of the project team.

Farmers at Samrong Commune rated the effectiveness of various rat control methods using a scoring matrix under the guidance of farmer facilitators from the project team. The results of the farmers' ratings in Samrong Commune are presented in Table 1. The matrix shows the TBS scores poorly (☹) in terms of the requirement for labour, monetary outlays and materials. It was rated very highly (☺) on environmental friendliness and effectiveness. Despite the perception that the TBS was environmentally friendly, it was apparent that some farmers continued to use rodenticides, even around the paddies containing a TBS.

In the first round of trapping during the 2002 dry-season crop, 349 rodents, comprised predominantly of two forms of *Rattus rattus* and *Rattus argentiventer* (K. Aplin, pers. comm., August 2002), were caught in the 18 functional TBSs in the fields farmed by Samrong Commune farmers. Project team members considered this number indicated a relatively low population of rodents in the dry-season crop. Farmers agreed that rat problems were relatively low for that particular crop and understood that the number of rodents caught would fluctuate in accordance with seasonal variations.

Gender issues

Although there has been wide interest in the field activities associated with the project on the part of men, women and children, all of the TBS group leaders are men, and women had minimal representation in the groups and at formal meetings concerning the project. A few women were listed in the social agreements as group members, but other women involved in work were described as the wives of group members. A workshop evaluation before the first-round implementation of the TBS specifically identified the involvement of women farmers as an issue for improvement for further workshops. However, the CARDI field facilitator reported that the women farmers considered the TBS to be the work of the men.

Estimates of the division of labour were gathered on several separate occasions using different techniques, from both men and women in Samrong Commune. Powell's initial (2002) findings were verified by focus groups involving women in Samrong and by the construction of

Table 1. Matrix scoring table for the evaluation of various rat control methods in Samrong Commune (rating by farmers from low favourability = 1, ☹; to high favourability = 5, ☺).

Methods	Chemical control	Trap	Hoe	Community rat hunt	Dogs	Trap–barrier system
Evaluation criteria						
Labour	5	4	4	1	5	1
Money	1	3	2	5	4	1
Materials	4	3	3	4	5	1
Environment	1	5	5	5	5	5
Effectiveness	5	3	3	5	3	5

division of labour pie diagrams by the project team and the predominantly male farmer representatives during workshop sessions at CARDI and in Samrong. The breakdown of labour inputs (Table 2) reflects other research into the traditional division of labour for rice production in Cambodia (Catalla et al. 2001) and is representative of the other opinions collected in this study.

Table 2. Breakdown of labour inputs for rice production by gender (% contribution).

Activity	Male	Female
Land preparation	90	10
Seedbed	70	30
Seedlings and transplanting	30	70
Crop management	50	50
Harvest	30	70

Discussion and conclusions

The commitment of the farming community to the second-round establishment of the TBS for the wet-season crop indicates that TBSs are perceived as an improvement, although the test for sustainability is yet to occur. This will be evident when the community action is self-funded and directed. The continued adoption or adaptation of the TBS is the critical test for each round of cropping in the project area. The initial provision of materials from project funds and the assistance from the project team at that stage limits any judgement of the sustainability of the TBS.

The first-round experience showed that the social agreements had not fulfilled the role that they might have done in curbing free-riding behaviour. The groups were encouraged to review their social contract on the basis of new knowledge and experience, rather than to abandon the tool. The guidelines for forging the social agreements for the second round were modified to account for inter-group obligations and more definitive contractual arrangements for the intra-group arrangements. Plans for better communication with the wider farming community were also devised.

It was clear from the results of the first round that a better flow of information was required. A notice board was subsequently erected at the commune centre for information and photographs to stimulate community interest in the TBS. Regular meetings with TBS groups were planned, along with educational activities in the four commune schools to coincide with the second round of TBS activity.

The TBS did not appear to impose a major change in the division of labour by gender. The increase in workload appears to have been borne mainly by men. The main implication for labour was that the burden of work associated with the TBS fell unevenly between households. There was a tendency for free-riding behaviour in the community to place the burden of the cost on the person whose field contained the TBS. Nonetheless, the processes embodied in the social agreements have been shown to be an effective mechanism for community education and the evolution of arrangements to counter free-riding behaviour. More information on the benefits of the TBS will consolidate this process. There is considerable scope for improving the research process, particularly through the development of a better flow of information, in successive cycles of investigation.

The intention of the OAE to extend the TBS technology and social organisation to another district is a promising sign of their confidence in the system. The relative success of the system in the new environment and under the sponsorship of the Provincial Government staff will provide valuable information for the evaluation of sustainability.

Acknowledgments

This project was made possible by funding from the Australian Centre for International Agricultural Research (ACIAR).

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Farmers' perceptions and practices in rat management in Vinh Phuc province, northern Vietnam

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Abstract. A survey of farmers was conducted in Vinh Phuc province, Vietnam, to examine the knowledge, attitudes and practices for rodent management near the beginning of a village-level study to examine the impacts of a range of rodent management practices. Thirty farmers were interviewed from four study sites. There are three main crop seasons during the year, two rice crops and a winter crop. Over 20 different vegetable crops were grown throughout the year. Most farmers believed that rats caused the most damage to their crops and that rats were the most important pest species to control. Most farmers identified kohlrabi then rice as the crops that suffered most damage. Most farmers identified crop damage through damage to plants and fruits rather than tracks, droppings or burrows. Trapping was the most common method used to control rats in the fields, followed by use of chemicals and plastic barrier fences. An average of 16 days labour was spent controlling rats in the previous season, and Vietnamese dong (VND)16,000–18,000 (~US$1.2) was spent per day of labour. On average, farmers spent VND130,000–170,000 (~UD$10) in the previous season on controlling rats. The farmers estimated a loss of about 40% of their rice yield if they were not to implement any rat control practice. Nearly all farmers stated that rat control must be carried out and that it is very important. Many farmers believed rats can severely reduce their rice yield and that rats can be controlled if all farmers work together and throughout all stages of the growing season. A follow-up survey will be conducted towards the end of the project to examine changes in farmers' perceptions and practices.

Introduction

An important constraint to rice production in Vietnam is significant yield loss by pests and diseases both in the field during growth and in post-harvest storage. Rodent pests have been identified as causing severe damage to rice plants in the field and rice grain in storage (Singleton and Petch 1994; Brown et al. 1999), and have been described as one of the three most important pests of rice crops (Huynh 1987). The rice-field rat (*Rattus argentiventer*) and the lesser rice-field rat (*Rattus losea*) are the two major species found in rice fields in Vietnam (Brown et al. 1999; Brown, Tuan et al., this volume).

There is a range of management practices available for farmers to control rodents, but the level of damage suffered by farmers can still be significant. An experimental study is being conducted to test a range of rodent management techniques within a village scale in Vinh Phuc province, Vietnam (for details, see Brown, Tuan et al., this volume). Among the practices being tested are the community trap–barrier system (CTBS) (for details, see Singleton et al. 1998, 1999), field sanitation, synchronising of planting and harvesting, reducing the size of bunds within fields, and conducting bounty systems at certain times during the crop (Brown, Tuan et al., this volume). It is valuable to learn what other methods are used by farmers for rat control, not only to learn new methods, but to establish some basis for an analysis of the success of the CTBS and other methods. Furthermore, information on the amount of time and money used by farmers for controlling rats would enable an analysis of the benefits and costs.

In an effort to determine the success of rodent management at the village-level, a preliminary survey of the knowledge, attitudes and practices of the farmers in four villages was conducted. Similar surveys have been used to assess changes in rice farmers' pest management in the Mekong Delta (Huan et al. 1999), for quantifying farmers' decision-making for stem borer control (Heong and Escalada 1999), and on farmers' practices and perceptions for rodent control in Indonesia (Sudarmaji, Singleton et al., this volume). The initial survey was conducted 18 months after the commencement of the project, which was 9 months after implementation of the treatments. A follow-up survey will be conducted towards the end of the four-year project. This paper reports on the initial survey.

Materials and methods

A questionnaire was developed specifically for farmers in the Vinh Phuc province, 40 km north of Hanoi in the Red River Delta. The questionnaire was modelled on several other questionnaires that have been conducted in the Mekong Delta, southern Vietnam (Sang et al., this volume), the Nakuru district, Kenya, West Africa (N. Oguge, 2000 unpublished data) and West Java, Indonesia (Sudarmaji, Singleton et al., this volume). It was designed to gather information on general farming practices and farm characteristics and, more specifically, rodent pest problems, management and farmer attitudes.

Four sub-villages (sites) within the Vinh Phuc province, which are currently being managed for a study on ecologically based rodent management, were used in this study. Farmers within these sites were surveyed to gain information on their knowledge, attitudes and practices for rodent management. Surveys were conducted in October 2000. Thirty farmers were interviewed from each site and were chosen at random from the field at the time of the survey, including some important members of the farming cooperative. A cooperative is set up in each sub-village (~150 families) and consists of a few smaller 'groups', each having leaders and various management positions held by farmers. The cooperative is responsible for major village farming decisions.

Results and discussion

Of the 120 farmers interviewed, 47% were female and 53% male, and the average age of farmers interviewed was 36 years old. The average overall level of education was 8 years and on average the farmers had 17 years of rice-growing experience. The average farm size was 0.3 ha (8.4 sao; 1 soa = 360 m^2), and rice was normally grown on 0.19 ha (5.2 sao) and vegetables on 0.13 ha (3.6 sao). The average rice yield for the area was 5.17 tonnes/ha (±0.18 se).

Crops and pests

The farmers surveyed at four sites in Vinh Phuc grew over 20 different crop types. Rice was the most commonly grown crop in the spring and summer seasons at all four sites. Tomato, squash and melons were grown commonly in the summer and spring seasons. Kohlrabi, onion, tomato and beans were the most frequently grown crops, respectively, in the winter season, at all sites.

Most farmers at each site believed rats caused the most damage to their crops (Figure 1). Farmers across the four sites identified 17 different pest types and pest categories; rats, insects and fungi being the three main pests identified. Stem rot, plant disease and a range of insects also were identified by a few farmers as important pests and some farmers indicated that climate or ‘nature’ was their biggest crop enemy.

The majority of farmers at all sites identified rats as the most important pests to control and the pests that caused most damage to crops (Figure 1). Most farmers at sites 1, 2 and 3 identified kohlrabi, then rice, to be the crops most damaged by rats. Farmers at site 4 believed the crops most damaged by rats to be green beans, then onion and kohlrabi (Table 1).

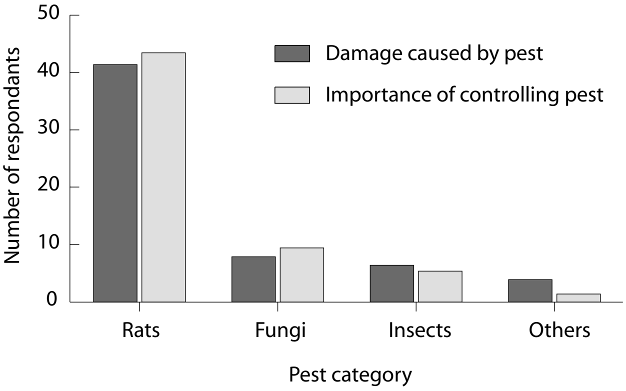

Figure 1. Responses by farmers to questions about which factors cause the most damage to their crops (black bars), and which pests they should control (white bars).

Table 1. Crops suffering the most rat damage (% respondents) (*n* ≈ 30).

Crop	Site 1	Site 2	Site 3	Site 4
Rice	31	21	17	16
Green beans	0	0	0	40
Tomato	0	7	0	4
Onion	0	3	0	20
Kohlrabi	69	69	83	20
Others	0	0	0	0

Farmers at each site had similar methods of assessing crop damage. The farmers looked at plant and fruit damage more often than the direct evidence of rat presence such as tracks, droppings and burrows. Many farmers detected rats in their vegetable plots through evidence of chewing and biting marks on their growing fruits and tubers. The damage to vegetables was more commonly mentioned than damaged rice plants.

Nearly all farmers at all sites said that rat damage was ‘regular’, occurring every season. This corresponds with their belief that rats are a major pest animal and one that is important to control.

For rodent management in the fields, trapping was the most popular method of rat control at all sites (Table 2). Chemicals were the second most popular control method at sites 1 and 4 while plastic barrier systems were the second most popular control methods in sites 2 and 3. Digging was carried out frequently at all sites, then to a lesser degree hunting, cat predators, trap–barrier systems, fumigation, flooding and some other methods used very infrequently at all sites (Table 2).

Farmers were aware of safety in their control methods, many believing chemicals to be unsafe. This did not deter widespread use of a variety of chemicals, most commonly an unknown Chinese chemical believed to be highly toxic. It was commonly used because it is effective, cheap and easily obtained.

Physical control methods were highly favoured and trapping was the most commonly employed method with a few different traps being used. The most popular traps used were kill-traps (metal and wood mechanical traps) and sticky-traps (sheets of sticky substance that physically trap rats). Sticky-traps were favoured for use in the house and kill-traps for use in the field.

A barrier system (BS) was commonly used in all sites except site 4 where only 50% of surveyed farmers used a BS (Table 2). Many farmers incorporated traps with their BS or would hunt around its borders at night. Most other activities were quite similar across sites, with similar methods and timing of application.

Families were primarily responsible for their own rodent and pest management but the farming cooperative organised some pest control activities. Leaders from site 4 told us that their cooperative has provided funding for a rat bounty system in the past, with most farmers using digging and hunting. They would put aside money to pay local people in a concentrated rat-hunting effort.

In all sites, an estimated 16 days labour was spent controlling rats in the previous season and on average between Vietnamese dong (VND)16,000 and 18,000 (~US$1.2) was spent per day of labour. Overall, farmers at all four sites claimed to have spent between VND130,000 and 170,000 (~US $10) in the previous season on controlling rats. The farmers estimated a loss of about 40% of their rice yield if they did not implement rat control practices.

Farmers at all sites believed that controlling rats was most effective at the booting and tillering stages of rice growth (Figure 2). This belief corresponds with research carried out at the National Institute of Plant Protection, indicating that rats are most attracted to rice seedlings at these stages of development. This means that for physical control practices, there will be high densities of rats to control at these times.

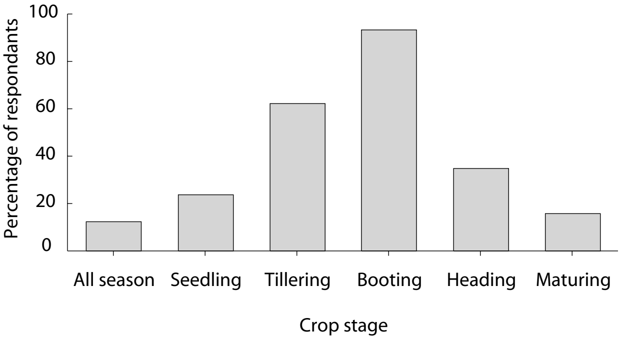

Figure 2. Responses by farmers concerning the best time for rat control throughout a rice-growing season (*n* ≈ 120 due to incomplete surveys).

Rats in the Red River Delta have a breeding cycle which follows the availability of food, and this is cued to specific times in the rice-growing season (Brown et al. 1999). Some farmers indicated that it is important to control rats at the time that vegetable plants develop fruits and tubers. Some farmers said they control rats when they see damage to their crops or rats in their fields, or in particular seasons, while some practised rat control continuously all year.

Nearly all farmers stated that rat control must be carried out and that it is very important (Table 3). Many farmers believed rats can severely reduce their rice yield and that rats can be controlled if all farmers work together and throughout all stages of the growing season. Some farmers were less convinced that rats could be controlled and seemed indecisive about when and how to control them (Table 3).

Most farmers believed that rat numbers had increased over the past 10 years to high numbers of rats in the past 2 years. This corresponds with national data for rodent damage, which indicate a steady increase in rodent

Table 2. Summary of all rat control methods used at four sites in Vinh Phuc province, indicating their rank order of use (rank) and the percentage of farmers (%) that use each method.

Control method	Site 1		Site 2		Site 3		Site 4	
	rank	%	rank	%	rank	%	rank	%
Chemical	2	87	3	77	3	77	2	83
Trapping	1	100	1	96	1	100	1	97
Hunting	4	47	4	47	4	59	4	57
Digging	3	76	3	77	2	79	3	80
Flooding	–	0	6	3	6	0	6	20
Trap–barrier system	6	10	6	3	5	3	6	20
Barrier system	1	100	2	80	1	100	5	50
Fumigation	7	3	6	3	6	0	8	7
Cats	5	33	5	13	5	3	7	10
Other	–	0	6	3	–	0	–	0

damage to rice crops over the past decade (Ministry of Agriculture and Rural Development 2000).

Table 3. Farmer responses (%) to a series of statements about rat control (average for all sites).

Question	Always true	Maybe true	Definitely not true
Rat control must be carried out	100	0	0
Controlling rats is important	98	2	0
Rat damage can severely decrease rice yield	58.5	39.5	2
Rats can be controlled	16	78	6
Rats can only be controlled if farmers work together with other farmers	73	24.5	2.5
Rats should be controlled at all stages of the growing season	46.5	51.5	2

Conclusions

The study site at Vinh Phuc supports a complex cropping area, with over 20 different crops being grown across three distinct growing seasons, experiencing quite different climatic characteristics. Farmers in the area primarily grow rice, but nearly all of them grow other vegetable crops concurrently. This mixed cropping structure can create difficulties for crop management, especially pest management. Farmers at Vinh Phuc identified nearly 20 different crop pests they considered important to control. Rats were considered as an important crop pest, not only for rice, but for some vegetable crops. Farmers use a variety of control methods including chemicals and plastic barrier fences.

With three growing seasons overlapping, there is always a food source for pests, especially for opportunistic pests such as rats. Farmers seemed more concerned about protecting their vegetable crops than their rice crops. They often built barrier systems around vegetable crops, especially when plants developed fruits and tubers and especially around kohlrabi crops, and used large amounts of chemicals to control rats.

Farmers in the Vinh Phuc province have a broad understanding of the pest management issues in their complex, mixed cropping farms. Most farmers believe that pest management, especially of rodent pests, is extremely important for the viability of their crops and that a range of different pest control methods implemented throughout the growing season is required for effective pest management.

Acknowledgments

This project was funded by the Australian Centre for International Agricultural Research (As1/98/36). Susan Williams was supported through the Australian Agency for International Development (AusAID) Australian Youth Ambassador for Development scheme. We sincerely thank the farmers for their time and sharing their knowledge of farming and rat control. We thank Prof. M. Escalada and Dr K.L. Heong for their advice and encouragement.

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Adaptive management: a methodology for ecosystem and community-based rodent management in Cambodia

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Abstract. There appears to be no easy solution to reducing crop damage caused by rodents in Cambodia and other parts of Southeast Asia. Agricultural and pest management scientists focusing on technological improvements have expressed frustration with the apparent slow uptake of management options produced from an 80-year history of research. In Cambodia, rats destroy an estimated average 0.1% of the total rice production area annually. This may sound barely perceptible, but damage is often very patchy and locally severe. An outbreak in 1996 was reported to have destroyed rice sufficient to feed over 50,000 people for one year. Typically, farmers' rat management efforts have had poor success. There is an increasing awareness that traditional research, development and extension (RD&E) approaches have frequently led to inappropriate, irrelevant and unequally distributed technologies and unrepresentative decision-making. This paper provides an overview of one approach, adaptive management (AM), which aims to overcome these problems. An example of the application of AM to improve Cambodian RD&E in rodent management is also presented. We propose that the management of rodent problems in lowland rice could improve dramatically if approaches are community-based and if the concept of uncertainty is incorporated as an integral part of the decision-making process.

Introduction

Although traditional research has advanced the understanding of rodent ecology, the predominant extension model has been the transfer of technology (ToT) approach. After decades of using the ToT model, extension theorists and practitioners began to notice that the ToT approach proved successful only under certain conditions. These conditions are described by Jiggins (1993) as "homogenous production environments, for larger commercial farming units, wherever field conditions and interactions can be replicated in the laboratory and research station, and where innovation is driven by strong market forces which signal demand for tightly specified, discrete and specialised products". Where the approach had been inadequate, however, had been in more complex situations, particularly heterogeneous environments (e.g. varied soil types, unpredictable seasonal distribution, mixed cropping systems) and where social and cultural factors (e.g. division of labour, market forces, individual preferences) influenced and were influenced by changes in farming practices. In this light, it is easy to see why the ToT approach has not been successful to the small-scale, often unpredictable (due to poor food distribution, rat outbreaks and food shortages), and subsistence nature of Cambodian rice-farming systems.

In the 1970s, to deal with the inadequacies of ToT, the importance of developing technologies within the context in which they were to be used (both environmental and social) made its way into the research, development and extension (RD&E) agenda under the label of 'farming systems research' (FSR). This approach was seen as a more holistic approach to prior reductionist research approaches and had researchers conducting experiments and developing technologies in farmers' fields. However, FSR (in its early forms) still retained many of the assumptions of ToT, in that scientists still retained control over the research agenda. That is, FSR seemed a subsidiary of ToT, albeit a more effective way of doing it.

The 1980s saw a new approach in the RD&E arena referred to as 'participatory technology development'. In this setting, the extension agencies, particularly non-government organisations (NGOs) began to focus on issues of power and equity, introducing the notion of social justice into their framework for thinking about agricultural development. In the social justice agenda, participation was not only seen as a way of developing better technologies in relation to context, but also a right of individuals and communities in shaping and determining their own destiny. Extension theorists and practitioners began to pose questions such as "Whose knowledge for whom?" and "Who are the beneficiaries of development projects?"

Community-based approaches and participatory methods were developed accordingly.

By the 1990s, extension science (if not extension practice) had become concerned increasingly with rural people's sense-making activities (i.e. how people make sense of the activities in which they are engaged) and extension agents took on the role of facilitators and coordinators of these multi-stakeholder forums. However, the notion that farming systems (as we might view them) are embedded in larger systems that provide context and meaning for decision-making was often neglected in RD&E efforts. This caused projects to expand their focus toward multi-disciplinary and inter-disciplinary research. Mak (1998; see also Cox and Mak 1999) advocates, in the context of rodent management, that unless research on rodent ecology is matched by parallel research in the social sciences, gains in understanding rodent ecology will not be transformed into development outcomes.

In conjunction with this change, RD&E approaches that could also allow for the recognised complexity of and uncertainty within systems were being sought. What were needed were new approaches that would allow knowledge and understanding to emerge from the process. This led to the application of learning and action based participatory approaches, such as action learning, action research, participatory action research, soft systems methodology, and adaptive management. The success of these in agriculture and resource management is well documented through the 1990s (Hamilton 1995; King 1997, 2000; King et al. 1999). Success factors include strengthening community capacity, generating innovation and communication, enhancing organisational and research capacities, and developing and adapting technologies to local agro-ecological and socioeconomic conditions.

Today, the current trend in agricultural and resource management extension is for practitioners to facilitate multi-stakeholder participatory methodologies that allow for uncertainty and surprise (Röling and Wagemakers 1998). This may be at the 'soft', as well as 'hard' system level, as King (2000, p. 269) explains:

> There are a variety of reasons why a participatory learning process does not flow according to a blueprint plan or is not as effective as one might imagine. Issues of power, hidden agendas, expectations, past experiences, different world views and the fact that people are intentional beings, makes group learning processes and outcomes unpredictable at the level of praxis. Facilitating participatory learning processes is inherently complex, requires a wide range of skills and has many implications. It is not as simple as following a 'recipe' but requires an alternative, responsive approach to the flux of process.

This paper provides an overview of *one* particular approach, adaptive management (AM), which aims to allow for uncertainty and surprise. An example of the application of AM to improving Cambodian RD&E in rodent management is also illustrated. We propose that the management of lowland rice could improve dramatically if uncertainty were not only acknowledged, but also incorporated as an integral part of the decision-making process.

Adaptive management: what is it?

Adaptive management has a 25-year history in the natural resources literature. It was first introduced by Hilborn and Walters in 1976 in a fisheries paper that discussed how scientific research conducted separately from management was not producing useful predictions for fisheries managers (Walters 1995). The term itself was coined in 1978 by an inter-disciplinary team of biologists and systems analysts under the leadership of the Canadian ecologist Clarence Holling (Lee 1993). Walters (1986) and Lee (1995) further expanded ideas on AM, treating natural resource management as deliberate experimentation as well as advocating the methodology as a means of conducting better habitat management over time. Jiggins and Röling (2000, p. 3–4) illustrate the impetus for AM:

> AM has been gaining ground in response to a widely perceived sense of societal crisis. This perception is essentially concerned with the relations between people and their physical and biological environment, and the ways in which those relations are changing the function and capacity of the ecological processes on which human existence depends. The nature of change is seen as generating fundamentally new kinds of irreducible uncertainty. The conventional tools of risk assessment, planning and design, and the methodological and explanatory reductionism of conventional science are held to constitute an incomplete, inadequate, and an inappropriate toolbox for the construction of the future in situations in which surprise becomes increasingly determinant of outcome.

The formulation of AM was based on detailed studies of complex ecosystems such as the Florida Everglades, the Columbia River, the New Brunswick spruce forests, the Baltic Sea and others in which humans play a dominating role. Jiggins and Röling (2000) acknowledge the work of Gunderson et al. (1995), Holling and Sanderson (1996), Walters (1986), and Birkes and Folke (1998) in bringing together the concepts of AM in relation to these studies.

Definitions of adaptive management

There are now many definitions of adaptive management. To illustrate a few:

- AM is a heuristic process coupling science and social values to promote the sustainable management of natural systems (Holling 1978).
- AM aims to base management decisions on site-specific information gained through experimentation with management. Experimentation with management serves to combine information collection and policy design into a single process, in which policy is both informed by, and designed to yield, information (Blumenthal and Jannink 2000)
- A key aspect of AM is acknowledgment of uncertainty about what policy or practice is 'best' for the particular management issue, noting that AM has a sequence of steps including (1) problem assessment, (2) project design, (3) implementation, (4) monitoring, (5) evalua-

tion, and (6) adjustment of future decisions (Nyberg 1998).

- AM entails identifying areas of scientific uncertainty, devising field management activities and real-world experiments to test that uncertainty, learning from the outcome of such experiments, and recrafting management guidelines based on the knowledge gained (Walters 1995).
- AM is 'learning by doing' (Walters and Holling 1990).

While there are several approaches, Farr (2000) suggests that the following are key attributes of an AM approach:

1. Decision-makers, scientists, and other stakeholders work together and seek to enhance the understanding of the system that they manage
2. Identification of:
   - indicators (i.e. quantitative measures of the state or dynamics of the system that are relevant in the analysis of trade-offs among management alternatives);
   - actions (management activities or policies that will affect the system); and
   - ecological processes (that link actions to changes in the indicators).
3. Explicit predictions of outcomes of potential management actions on a suite of indicators, using simulation models or other projection tools. Exploration of trade-offs among alternative approaches.
4. Identification of key uncertainties and knowledge gaps. These are prioritised based on how reducing these uncertainties will help in the trade-off analysis (i.e. if we know X, would it help us to choose among management alternatives A and B?).
5. Active AM typically involves (management) experiments implemented at an operational scale, designed to test hypotheses or qualitative relationships between management actions and changes in indicators.
6. Monitoring of indicators.
7. Evaluation of observed and predicted changes, diagnosis of reasons for differences, and assessment of whether newly acquired knowledge justifies modification of the management plan, e.g. based on new projections of consequences of proposed actions with new relationships between actions and indicators. Other reasons for changes in plans include new objectives of stakeholders.

Two points raised by Holling (1978) that illustrate the difference between AM and traditional research are that at least as much effort must go into communication as goes into the analysis, and that there exists a serious trade-off between designs aimed at preventing failure and designs that respond and survive when that failure does occur. Taylor et al. (1997) suggest that AM differs from traditional research in three important ways:

1. managers play an integral and often lead role;
2. polices are implemented at an operational scale, in an operational setting; and
3. monitoring is less detailed, and the focus is on understanding the response of the system as a whole (rather that on detailed understanding of parts of the system).

Challenges to implementing adaptive management

Halbert (1993), Walters (1997) and Jiggins and Röling (2000) analyse the constraints to the effective implementation of adaptive management from a sociological and institutional perspective as follow:

- Under the experiential learning-based AM model, data are generated, analysed and interpreted over time periods that often exceed project time frames and political tenure. The process of learning is the primary objective rather than reaching an anticipated goal or output.
- As a methodology, AM has been questioned as to whether it is applied to the appropriate situation. It has been suggested that AM is most useful in situations in which environmental change is driven by high human activity, which threatens to undermine essential ecological functions and capacity.
- Computer-supported simulation models, although seen as an important tool for AM, are typically too complex to be easily understood by the stakeholders themselves. In addition, the overall objective of learning is often traded-off when scientists are focused on establishing 'true' models.
- Temporal scale is difficult to address, particularly where there are inter-generational differences in future equity stakes and differences in the articulation of action among different scale levels. Solving problems at one level does not automatically add up to solving problems at another system level with different emergent properties.
- A key assumption of AM is that social learning will lead to concerted action at the scale of the ecosystem being managed. In the case of large ecosystems, it has so far been difficult to establish effective management regimes (as opposed to the scale at which common property regimes have been successfully established).

Halbert (1993) suggests that although formal adoption and institutionalisation of AM is critical, this alone is insufficient to ensure successful implementation, which further requires that:

- management takes risk-prone actions while providing institutional patience and stability;
- managers and politicians redefine success so that learning from errors becomes an acceptable part of the learning process;
- managers set clearly established goals and decision-making criteria that will allow for accountability and effective evaluation;
- the goals must be compatible with natural processes, existing or achievable technology, and social norms; and
- the definition of adaptive management itself needs to be negotiated and agreed upon.

The application of adaptive management to Cambodia's rat problems

Rice production is the basis of food security in Cambodia. In some areas, rodent pests cause chronic and acute damage to rice crops and jeopardise food security for subsistence farmers and their families (Jahn et al. 1997, 1999). For example, Jahn et al. (1999) reported an outbreak in 1996 that destroyed rice sufficient to feed over 50,000 people for one year. The Cambodian government recognises the seriousness of the rodent problem and has in the past instituted bounties for rats, free distribution of rodenticide, and rodent pest awareness campaigns. Leung (1998, 1999) evaluated the Cambodian government campaigns for rodent pests and found that they were ineffective for crisis management or involved poorly timed routine activities without a sound ecological or socioeconomic basis. Leung (1999) also concluded that, while farmers had some knowledge of local rat populations, their ability to transform this knowledge into better management actions was limited by:

- a lack of community-based learning and actions;
- a lack of understanding of the ecological and socio-economic issues; and
- some technical problems of rodent control methods.

The trap–barrier system (TBS) is a novel technological solution that holds considerable potential to control rodent problems in lowland rice systems (Leung 1999). While much has been learned of the *ecological* properties of the TBS, the *economic and social aspects* of this technology are poorly understood. However, what is clear is that the use of the TBS will be less than socially optimal if managed by individual decision-makers acting in isolation. Management of the TBS as a common property resource (i.e. at a community level) may provide a means to overcome this problem. This also means that the technical aspects of the technology and the social arrangements that support it have to be melded together.

'FARMERS' (Farmer-based Adaptive Rodent Management, Extension and Research System) is a collaborative project between farmers of Somrong Village, the Office of Agricultural Extension (OAE), the Cambodian Agricultural Research and Development Institute (CARDI) and The University of Queensland (UQ), funded by the Australian Centre for International Agricultural Research (ACIAR). Figures 1–6 illustrate aspects of the project. The project is based in Kampong Cham province, Cambodia, and has been in operation since July 2001. Details of the study location and TBS implementation are provided by Russell et al. (this volume).

Figure 1. The Australian Centre for International Agricultural Research (ACIAR) project team.

Figure 2. Rat damage to a rice field.

Figure 3. Rats, rat traps and a trap–barrier system.

Figure 4. Map of common property resources and trap–barrier system locations.

Figure 5. Participatory matrix for exploring gender and seasonal labour.

Figure 6. Participatory pie chart for assessing different control options.

The benefits expected from the project include:

- greater understanding of the technical, economic and social aspects of rodent management;
- development of appropriate social institutions for managing the TBS technology as a common property resource at a village level; and
- greater familiarity of community-based technology development approaches at CARDI.

The definition of adaptive management within the context of the FARMERS project is based on an action research model and is *an integrated, problem-solving approach, which operates on continuous learning and action cycles, with community participation in all phases of the planning, implementing, monitoring, interpretation and evaluation of the research*. Key aspects to the facilitation of AM in this project have been:

- The AM cycles coincide with cropping seasons to better link learning with ecological processes and the project includes social, economic and biophysical aspects to optimise learning about ecosystems management.
- Participatory planning has included farmers, scientists, extension agents and managers at the whole project level. This in itself is innovative, as farmers are typically involved in activity-level decision-making but excluded from decisions made at the whole project level.
- Research is carried out on-farm and involves the facilitation and coordination of a number of stakeholders that have formed their own ‘research’ community to explore more effective strategies together.
- Interactive participatory tools are used to bring out the stakeholders’ different perceptions of reality.
- AM is seen as an overarching approach, but the emphasis in planning meetings has been on foundation concepts such as systems thinking, participation and action research.
- Spatial-scale issues are being addressed through mixes of processes allowing stakeholders to conceptualise and ‘vision’ their environment in a systemic way and to become aware how their own context fits into a larger picture.
- Monitoring and evaluation (M&E) is participatory, and the core project team (including farmers) uses, critiques and adapts the M&E methods before using them with farmers in the community. These tools can also be reframed as projection tools for future planning. Social aspects are incorporated into these methods, thereby surfacing and acknowledging the complex nature of introducing different management strategies.
- Indicators have been developed that reflect anticipated changes at both the farming systems level and the project team and management level. Indicators also reflect biophysical, economic and social phenomena.
- The AM approach is being used also to develop the learning and understanding of the project team itself. That is, the team is also facilitated through the process of planning, implementing, monitoring, interpretation and evaluation; and then reflects on this process.
- Negotiations and agreements are seen as dynamic rather than static, allowing for re-negotiation as learning by all participants increases.
- The inclusion of management in the core team aids in linking understanding to policy and redefining learning as a valid project outcome. The inclusion of farmers in the core team moves a step closer to ensuring the sustainability of the learning process in communities. It also acknowledges the value of farmer process knowledge as well as farmer technical knowledge.
- The learning focus and reflective nature of the team and community activities aim to sustain the learning process itself (beyond project time frames). Facilitated learning about learning also anticipates an increased understanding about the process of learning and its relationship to uncertainty and surprise.

Conclusions

Traditional RD&E approaches have frequently led to inappropriate, irrelevant and unequally distributed technologies and unrepresentative decision-making. Adaptive management is one methodology that may overcome many of these problems in complex ecosystems management. It is community-based, allows for the inherent uncertainty and surprise associated with complex systems, has a strategic learning focus, and links policy to practice change. Although further understanding of the complexities in facilitating such a process is needed, the application of AM to managing the lowland rice rats in Cambodia is showing promise.

Acknowledgments

The authors would like to acknowledge those participating in this project, with special thanks to the farmers of Somrong and the project team: CARDI—Ms Chan Phaloeun, Ms El Sotheary, Mr Uy Sokco, Mr Ung Sopheap, Mr Seth Sopheap, Mr Pol Chanthy and Mr Ny Vuthy; OAE—Mr Tea Rithyvong and Mr Chheng Nareth; and Somrong farmers—Mr Kao Lim Pon, Mr Mak Pha, Mr Hem Chhoeung, Mr Long Seng Hau, Mr Boeur Kok and Mr Meuk Kom Ain.

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Gathering indigenous knowledge as a tool for rural research, development and extension: case study on rodent management in Cambodia

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Abstract. Many researchers and facilitators acknowledge the value of farmer participation in rural research, development and extension (RD&E), both for problem recognition and for problem solving. Although the intention to include farmers in the RD&E process may be genuine, implementation is often complicated by the fact that researchers, facilitators and farmers have very different perceptions of the natural and human environments and the complex interactions between them. This can lead to fundamental misunderstandings and act as a barrier to effective exchange of knowledge and ideas between project partners. This paper emphasises the need for researchers and facilitators to first explore the knowledge and beliefs of the farmers with whom they are working. It reports on research carried out to gather indigenous farmer knowledge and perspectives on rodent management in a rice-growing community in Cambodia.

Introduction

The population of Cambodia is over 85% rural, with most people involved in lowland rice production. Rodents are reported as a major cause of crop losses in many parts of Cambodia (Jahn et al. 1999) and farmers typically use rodenticide at times when rat damage is observed. This method is rarely, if ever, cost-effective, and may be harmful to the farmers' water supply and the environment. Since the end of 2001, researchers and extension agents have been introducing farmers of Somrong commune in Kampong Cham province to alternative, ecologically sustainable methods of rodent control, based primarily on the use of a trap–barrier system (TBS; Singleton et al. 1999). In brief, the TBS uses a lure crop (usually a rice crop planted 3 weeks ahead of surrounding fields) to attract and trap rodents before the surrounding fields reach booting stage. In theory, this leads to a reduction in rodent populations before the onset of breeding activity. The TBS method is best applied in a coordinated fashion across large cropping areas, but this requires a high level of community involvement and cooperation. In Cambodia, the willingness to work as a community was eroded during the Khmer Rouge time and consequently it is perhaps more than usually difficult to raise a community effort (Meas Nee 1995).

For the introduction of any new agricultural method to be successful, farmers must genuinely *believe* that it works and that it is cost-effective. In the case of the TBS method, this poses a considerable challenge, as the method works through subtle manipulation of ecological processes and, unlike the current practice of rodenticide use, does not result in large numbers of dead rats. Adoption and future cost-effective application of the TBS method is thus likely to hinge on farmers acquiring quite a high level of understanding of rodent ecology, including aspects of breeding biology, population cycles and seasonal movements, as well as a firm grasp of the way in which TBS acts to mitigate rodent population growth and crop damage.

Adult learning and indigenous knowledge

Adults tend to learn more effectively when the knowledge is problem-oriented (Rogers 1992), i.e. when they can relate the new information to real life situations. A study on adult learning involving farmers in Queensland, Australia, showed that the learning process is enhanced when the facilitator can relate the new knowledge to the individual experience of the farmer (King 2000). Other important points in relation to adult learning include those suggested by Malouf (1994), that learners must: set their own learning goals; participate actively; build upon their own experiences and knowledge; and see learning as desirable. In addition, the learning environment needs to be perceived as a mentally and socially safe space, and must allow effective, interactive communication. An understanding of the dynamics of adult learning is particularly relevant to farmer participatory research, where scientists and farmers come together (typically in farmers' fields) to collectively learn about and address problem situations.

Where cultural backgrounds differ substantially, the dynamics of adult learning may take on a new dimension. Farmers may have a fundamentally different world view that is difficult to reconcile with the Western scientific paradigm held by researchers or trainers, with different concepts of causality and contrasting modes of explanation. Such differences can lead to fundamental misunderstandings and may act as a barrier to effective exchange of knowledge and ideas between the project partners. In such situations, it is imperative that researchers and facilitators take time to explore the knowledge and belief systems of the farmers with whom they are working.

The idea that indigenous knowledge and scientific knowledge can be complementary in the research process is not new. Parallels between indigenous knowledge and sustainable development within particular situations are well documented (Agrawal 1994; Scoones and Thompson 1994). Indigenous knowledge has been introduced into development projects primarily in recognition that (i) it has been developed in context, (ii) it is generated over time through experience and trial and error, and (iii) it can incorporate the ideas and constructs of the end users of technologies.

Researchers and facilitators have most often gathered farmer knowledge as a means of quickly identifying problems and issues related to a specific topic. This is typically done through the use of structured questionnaires and semi-structured focus groups (Escalada and Heong 1997). In some cases, insights gleaned from such activities can also lead to the rapid development of effective solutions, building on traditional pest management practices. The gathering of indigenous knowledge might also assist a researcher or facilitator to understand how farmers are likely to respond to a possible solution, and how best to structure and present information in a way that will make sense to end users.

In addition, the *process* of gathering indigenous knowledge can itself produce benefits:

- informal discussions with farmers can build trust;
- talking about what *they* know can give farmers confidence to participate in discussions;
- incorporating *their* knowledge into development can give farmers a feeling of empowerment; and
- discussing *their* knowledge helps farmers to articulate new ideas and can lead to an enthusiasm to test these in the field.

Methods and study area

An initial focus-group interview was conducted with a small group of about 15 farmers (in this case, all men) to explore their knowledge about rodents and rodent ecology. Several open-ended questions were prepared by the facilitator in order to cover topics pertinent to the problem, but a general discussion was also encouraged. Visual tools including skulls, skins or bodies and a map of the commune proved useful to focus the discussion. Hall and Hall (1996) quote Fielding (1993) who describes semi-structured interviews as an ethnographic process where "the interviewer asks certain, major questions…but is free to alter their sequence and to probe for more information". Hall and Hall add that open-ended questions allow informants to discuss the issues more freely than they could with the closed or forced-choice questions of the structured questionnaire.

The diversity of opinions expressed during the focus-group meeting suggested that knowledge about rodents is not uniformly shared among all members of the Somrong community. As in any society, individuals have different personal experiences, they have been exposed to different bodies of wisdom, either within families or other social groups, and they may have varying levels of interest in particular topics. For this reason, the interview has been supplemented with numerous discussions with individuals or small groups of farmers, probing for information about their rodent problems, their personal observations of rodents and their understanding of the dynamics of rodent populations. This is an ongoing process, and almost every new conversation with farmers brings to light new information and insights. The information presented here is thus a composite of many conversations, although, so far, conducted exclusively with men, and is very much a preliminary account of farmer indigenous knowledge in the Somrong community.

Somrong commune supports approximately 7000 people living off a total cropping area of c. 700 ha. The cropping area is divided into distinct cropping areas: the dry-season cropping area (DSCA) and the wet-season cropping area (WSCA). The DSCA supports a mosaic of low scrubby vegetation and cultivated rice fields during the period November to February, but this area is inundated from June to November every year by the rising floodwaters of the Mekong River. The DSCA is progressively replanted as the floodwaters recede. The WSCA is located above the high-water level. It lies fallow during the dry season, but is planted with rice during the wet season as water becomes available either through local rainfall or by pumping from the rising floodwaters via a system of canals. A total of 11 densely settled villages are scattered across the WSCA. Vegetables are grown in small gardens within the village complexes.

Rodent specimens collected during this study were identified through comparison with reference material in the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Australian National Wildlife Collection in Canberra.

Results

The farmers of Somrong generally enjoy discussing their knowledge of rodents and the chance to share their observations. As noted above, the level of knowledge is quite varied within the commune, most farmers saying that they learnt their knowledge partly from their older relatives and partly from observation. During the focus-group discussion, farmers voiced a range of opinions on every question, although two or three individuals generally led the group. The responses to some questions were very specific, however on other topics they admitted to having more limited knowledge. The forest patches and the villages feature in the farmers' responses as important habitats for rodents. Similar general observations apply to the many individual discussions carried out subsequent to the group meeting.

Rodent taxonomy

Most farmers recognise three types of rats: *kondol preing, kondol promeh* and *kondol bie,* with the names *kondol ot mien chmua* and *kondol propeh* mentioned as alternative names for *kondol bie*. *Kondol prieng* refers to the largest of the local rodents, members of the genus *Bandicota*. There are two species of *Bandicota* present in Somrong: *B. indica* and *B. savieli*, but these are apparently not distinguished; they differ mainly in maximum adult size. *Kondol promeh* and *kondol bie* refer to the smaller rats of the genus *Rattus*. There are at least four *Rattus* species in Somrong: *R. argentiventer, R. losea,* and two members of the *R. rattus* complex (an endemic southeast Asian form and the 'European' black rat). *Kondol bie* is said to be slightly bigger than *kondol promeh* but is mainly recognised by its reddish colour. Specimens of *R. argentiventer* were frequently identified as *kondol bie* but if a specimen lacked the reddish colouring typical of that species, then it was sometimes referred to *kondol promeh.* One *Rattus* specimen was identified by a farmer as a baby *Bandicota* because of its greyish colouring. In general, it seems that pelage colour is the most important feature in Somrong for identifying the type of rat, followed by its size.

Two species of *Mus* have been collected at Somrong, *M. caroli* and *M. cervicolor.* Some farmers in Somrong believe mice to be the babies of the larger rats and do not consider them to be important targets for control in their own right. However, other farmers know that they are fully grown and can provide details as to when and where they breed, and describe how they can climb the rice plants to cut ripening panicles. These farmers consider mice to be major pests of their rice fields. The extent of farmer knowledge of particular rodents may be proportional to the crop damage that they experience from any given species.

Jahn et al. (1999) stated that farmers in Cambodia recognise two to six kinds of rats, however this was not referenced to area. The number of different kinds recognised may reflect the importance of rodents as pests in a particular area. However, it might also reflect farmers' perception of their ability to control any of the rodent species. The fact that the farmers in Somrong ascribe only three names to what are at least seven species may also reflect their belief that all rats are pests of rice and that all should be targets of control (see below).

Rodent habits and breeding

Somrong farmers believe the habits of the three types of rodents are essentially the same. In their view, the same kinds of rodents inhabit the villages and the fields. In the villages, rats eat rice stored under the houses. They mainly come out at night but are sometimes active during the day. During the dry season, they live in burrows in the DSCA, but when the flood comes, many rats move up to the WSCA. However, some remain in the flooded forest areas for up to 3 months. Although during the wet season rats can be found through all parts of the WSCA, they prefer to live in the 'forest' or in the villages. For this reason, more damage is expected in rice fields situated adjacent to these habitats. The farmers also claim that rats prefer to stay close to the flooded zone during the wet season, rather than moving into the more distant parts of the WSCA. This belief affected their placement of TBS units for the 2002 wet-season crop, the majority of which were positioned near the flooded area. At the end of the wet season, rats are said to move back down to the DSCA where they attack the recession rice crop.

Rats are said to breed all year round but with most young appearing at the end of the dry season. The number of pups per litter is said to vary but an average of six pups was generally given for all types of rats. Some farmers believe that rats can breed three times in one month. Rats are said to have their pups under the ground.

Rodent numbers and crop damage

Somrong farmers claim that the largest numbers of rats are present during harvest time in the dry season from February to April; and in the wet season from July to September, after the flood has reached its upper limit. They mentioned that rats tend to aggregate around the last fields to be harvested. Poison baits are generally placed at this time, sometimes resulting in observations of large numbers of dead rats around these fields. This is generally regarded as a sign of effective treatment.

Rats are thought to attack all stages of rice but mainly the booting stage. However, during the 2001–2002 dry season (the first TBS season), they claim that rats were attacking mainly the flowering stage, because this was when they caught the most rats in the TBS. One farmer explained this by saying that the flowers produce a good smell that attracts the rats. This was seen as a benefit of using an attractant crop inside the TBS and also as a reason why the TBS crop needed to be ahead of the surrounding crops.

All types of rats are said to eat rice, but *kondol promeh* and *kondol bie* (*Rattus* spp.) are believed to do more damage than *kondol preing* (*Bandicota* spp.). Rats do not store rice in their nests but they sometimes take it back to their nests if they live in the forests. Farmers mentioned that damage in the fields tends to be concentrated toward the centre rather than around the edges. The degree of damage is reported to be much higher in fields located near the villages and forests. Within the WSCA, damage is highest in fields close to the flooded zone, and generally very slight in fields that are distant from this zone. In most years, the highest-level damage is said to occur to the dry-season crops.

Farmers mentioned that rat numbers fluctuate from year to year. They also claim that the number of rats present during the dry season can be predicted from the amount of rain and the extent of flooding during the previous wet season. Before planting the 2001–2002 dry-season crop, farmers predicted that there would be fewer rats than usual and little damage, and attributed this to the high flood and heavy local rainfall of the 2001 wet season. This prediction was borne out by the results of the first TBS season—few rats were caught and there was relatively little damage other than in fields located close to major forest patches.

Discussion and conclusion

There is little comparative data from Southeast Asia against which to assess the extent of indigenous knowledge of Somrong farmers in regard to rodents. Although they clearly have a good understanding of many aspects of rodent biology, there is a tendency to view all rodents as having similar habits and as posing similar threats to rice crops. The number of different rodents distinguished is much fewer than the true number of species, but this is not surprising, given the very slight differences in size and morphology that separate some of the species. At an ecological level, Somrong farmers clearly appreciate the impact on rodent numbers of the annual flooding and cropping cycles, and they also appreciate the importance of refuge habitats (forest and villages) as potential ‘source’ habitats. Trapping studies at Somrong over coming years should reveal to what extent the farmers’ concept of cyclic movements and refuges matches up with the ecological reality, however for the present, their views would appear to be reasonable in view of the general landscape ecology.

A more important observation in the context of the rodent management project is that Somrong farmers not only form a clear conceptual link between rat numbers and crop damage, but also appreciate that rodent numbers are unevenly distributed, both within the landscape and through time. These dual pillars of understanding may well have a strong influence on their ability to independently assess the effectiveness of the TBS and ultimately may help them decide whether or not the TBS will be cost-effective for any particular location, or for any particular season before the start of that season.

Our improved understanding of farmers’ perceptions about the localised distribution of rats, the pattern of migration during flooding, and the relative damage to crops in different areas allows for:

- an appreciation by scientists and facilitators of the farmers’ logic in application of the TBS;
- a more purposefully designed and facilitated future research process; and therefore
- the development of an improved rodent management strategy.

Although farmer knowledge of rodent biology and ecology is extensive, particularly in relation to rodent distribution and movement, our results suggest that knowledge about rodent life cycles is limited. Providing farmers with some additional information in this area may help them formulate a more accurate picture of rodent ecology. An understanding of the present limits to knowledge also enables the facilitator to develop a more strategic and focused learning process revolving around rodent life cycles (e.g. the breeding cycle of rats, and which species are present and important to target).

The farmers involved in the research presented here were all men. In the future, it would be useful to hold similar discussions with women, as they are concerned with different aspects of rice cultivation and may well have additional and alternative knowledge and ideas to contribute. King (2000) documented the complementary contributions of men and women’s knowledge to understanding complex systems, noting, however, that women are often conspicuously absent from research, development and extension (RD&E) activities.

Recent interest in the contribution and incorporation of farmer knowledge in scientific research has tended to focus on what can be termed ‘indigenous technical knowledge’ (ITK), i.e. the knowledge farmers possess about technical aspects of their farming system and biophysical environment. Scoones and Thompson (1994) suggested that this interpretation of local people’s knowledge and abilities is too narrow, and introduced the concept of ‘rural people’s knowledge’ in which ITK is seen as only one of many components of a knowledge system. This notion was taken a step further by King (1998) who demonstrated the significance of ‘indigenous process knowledge’ (IPK), especially in the context of participatory research and complex systems management. In the present case study, the data-gathering process was initially focused on ITK. However, many of the farmers’ ‘ecological’ observations stray outside of this sphere and qualify as elements of IPK. As mentioned earlier, indigenous knowledge is generated in context, often learnt from experience, and reflective in nature. It is these characteristics that articulate so well with the adaptive management methodology used to drive the participatory research in the Somrong rat management project. Close attention to both indigenous technical and indigenous process knowledge is a key component in the development of appropriate rodent management strategies and, more importantly, in their adoption by end users.

Gathering indigenous knowledge should be seen as an ongoing process. Knowledge is often diffuse within rural communities and it is important to try to gain as broad an understanding as possible of both the knowledge available within a complex farming community and of the social context of that knowledge. The new understanding that emerges from this process will facilitate the learning process and help build a better relationship between researchers, facilitator and farmers. A variety of semi-structured and casual methods must be used to obtain a complete understanding. Farmers may have issues, problems, information or ideas that will not surface within the confines of a structured survey. Adult learning theory also suggests that farmers may be better able to grasp or assimilate a new idea if it is related to their personal experiences or existing knowledge base. Without a prior understanding of indigenous knowledge as a baseline for planning, new knowledge or ideas presented to a farmer may be misunderstood or lost. Gathering indigenous knowledge and incorporating indigenous knowledge into the research process also increases the confidence and interest of farmers and this, in itself, is a successful outcome for any RD&E project.

Acknowledgments

The authors would like to acknowledge the participation in this research by the farmers of Somrong commune, Mr Chheng Nareth from the Office of Agricultural Extension, Kampong Cham, Mr Seth Sopheap from the Cambodian Agricultural Research and Development Institute (CARDI), Dr Ken Aplin from the Community Ecology Group in CSIRO Sustainable Ecosystems for comments and advice, and the support of the Australian Centre for International Agricultural Research (ACIAR).

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Economic factors influencing integrated rodent management in rural areas of Yunnan, China

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Abstract. Integrated rodent management (IRM) was adopted as a scientific control method in 1985 in some counties of Yunnan province in China. After 10 years, there is significant success in some counties (e.g. Tonhai and Daili), but in most other counties of Yunnan, there are still many problems with IRM. Many questions need to be addressed regarding under what conditions IRM would be successful. Why is IRM not successful in some places? Are there economic factors that affect IRM? In this study, three townships, six villages, and 100 farmers in Tonhai, and one township, one village, and 197 farmers in Qijing were selected for sampling information on benefits and costs of IRM. Farmers generally had a good understanding of the benefits and costs of IRM while the government tended to overemphasise the benefits. From our surveys, we conclude that the government needs to support the organisation of IRM by providing financial inputs and training courses for farmers. Efforts by the government should be distributed across all government levels to increase awareness and competence in IRM. Correctly estimated benefit–cost ratios provide proof of effective IRM to both government and farmers and can help in the decision-making process in IRM.

Introduction

Yunnan is a province in the south-west of China where 80% of the population engages in agriculture (Anon. 1992). About 85% of land is mountainous and only 19% is forested. Rice, wheat, corn, potato and soybean are the major food crops. Cash crops include tobacco, sugarcane and tea. Every year, greater than 10–20% of the agricultural production is damaged because of pests. Among the four major pests—disease, insects, rodents and weeds—rodents are a serious problem, causing an average 1–3% loss of crops in Yunnan province. In recent years, rodents damaged about 0.2–0.6 million t of food every year and there is also the problem of disease transmission from rodents to humans and livestock.

Integrated rodent management (IRM) is an ecological approach to rodent suppression. The goals of IRM are to reduce loss in crops and foodstuffs caused by rodents and to increase net profits to the farmer. Methods that cause minimal environmental damage and pose little or no risk to human health are selected, e.g. trapping rodents, digging out burrows, using cats to catch rats, integrating the use of rodenticides, and improving food storage technology (wood store, bamboo store etc.).

IRM was adopted in 1985 in a few counties of Yunnan province, and after 10 years, there has been significant success in some places (e.g. in Tonhai and Daili counties), but in most other places in Yunnan there are still many problems with IRM. Although IRM still needs to be improved (Zhang 1999), it is potentially a good method for controlling rodents, but it is still not widely adopted. Many questions need to be addressed as to conditions under which IRM could be successful. Why is IRM not successful in some places? Are there economic factors that affect IRM? Although it has been estimated that 30% of success and failure is determined by technical factors and 70% is determined by organisation (Wan and Den 1984), more detailed studies are needed to reveal those important factors and relationships.

The aims of this study were to:

- compare and analyse the IRM performance between successful and unsuccessful counties;
- identify important economic and organisational factors affecting the adoption of IRM; and
- determine the economic factors that affect the effectiveness of IRM once adopted by farmers.

Methods

We compared socioeconomic aspects between areas that were successful or unsuccessful in implementing IRM. All problems were approached from a socioeconomic viewpoint, i.e. the distribution of crops and cultivating practices, the benefit–cost, including the comparative net benefit, control cost and net benefit from rescuing losses, and benefit–cost of different methods in different places.

We compared successful IRM in Tonhai county to places where there are many problems with IRM, such as in Qijing county. Random sampling techniques were used when choosing the villages and farmers. Most of the indices used belong to the unified standards of the official rodent control agency for IRM inspection: (1) benefits–costs of IRM, e.g. the direct benefits (the value in avoiding losses), and the external benefits (potential value of public health); (2) perceived IRM benefits, from interviewing farmers and from official sources (government)—these perceptions were used to estimate the expected benefits of IRM; and (3) the monetary costs of IRM.

Three townships, six villages, and 100 farmers in Tonhai and one township, one village, and 197 farmers in Qijing were selected for sampling information. Tonhai is one of the counties in Yunnan that adopted IRM early. It has about 245,000 people and 26,230 ha of cultivated land. The elevation is 1793 m. Qijing is located in the northern part of Yunnan province, with 301,000 people, 38,560 ha of cultivated land and an elevation of 1860 m.

Results and discussion

IRM performance

IRM in these two counties, as in other parts of Yunnan province, depended on good organisation, financial support, and concerted actions which, when operating together, carried through to good results. There are still many problems with IRM as practised in Qijing county. These include: (i) the difficulties of IRM actions in large rural areas; (ii) the lack of financial support for practising IRM; and (iii) the different levels of organisation of IRM, i.e. the shortage of recognition of IRM at the different levels of prefecture, county, township, village and farmer. Also, in Qijing county the low quality of rodenticides, the confusion associated with marketing of rodenticides, and the farmers' attention to IRM combined to create problems for putting IRM into action. In a survey of people from different levels (province to farmer) in both counties, it seemed that the adoption of IRM was most likely to be inhibited at the local level (farmer and village) (Table 1).

Socioeconomic factors influencing IRM

In the two counties sampled, the total financial input was highest at the village and farmer levels (Figure 1). The inputs at village and farmer level were mainly the grain for rodenticides and the labour required support IRM. These two components amounted to more than two-thirds of the total input in Tonhai and in Qijing.

Farmers have different perceptions of benefit–cost than the government (Table 2). There was a significant difference between the farmers' opinion and the government's opinion of the benefit–cost ratio of IRM ($t = 6.13$, $P < 0.01$). The estimation of farmers' benefit–cost ratio may not be exact, but this will determine the IRM adoption rate by farmers. In Huanlong, Wanjiai and Qiling townships, we began to investigate a more objective benefit–cost ratio:

$$B/C = (B_n + B_p)/C \quad (1)$$

Table 1. Perceived source of problems for integrated rodent management as seen by respondents from Tonhai county (T) and Qijing county (Q).

Respondents see source of problem in:	Respondents represent					
	Province	Prefecture	County	Township	Village	Farmer
Province			TQ			
Prefecture	TQ	Q	T			
County	TQ	Q	TQ	TQ	TQ	TQ
Township	TQ	TQ	TQ			
Village	TQ	Q	TQ	TQ	TQ	TQ
Farmer	TQ	TQ	T	TQ	TQ	TQ

Table 2. Benefit–cost ratio perceived by government authorities and farmers (farmers in brackets) in Huanlong and Wanjiai townships in Tonhai county and in Qijing and Qiling townships in Qijing county.

County	Township	Year						
		1994	1995	1996	1997	1998	1999	Mean ± se[a]
Tonhai	Huanlong	4 (3)	7 (2)	10 (1)	15 (13)	13 (3)	10 (2)	9.8 ± 3.9 (2.2 ± 0.8)
	Wanjiai	5 (2)	7 (1)	15 (3)	9 (1)	8 (1)	10 (1)	9.0 ± 3.4 (1.5 ± 0.8)
Qijing	Qijing	7 (1)	6 (1)	6 (2)	3 (2)	2 (1)	5 (2)	4.8 ± 1.9 (1.5 ± 0.5)
	Qiling	6 (3)	10 (2)	15 (1)	10 (1)	7 (1)	6 (5)	9.0 ± 3.5 (1.6 ± 0.8)

[a] Average perceived benefit–cost ratio for Tonhai is 9.5 by government authorities and 1.9 by farmers, and for Qijing is 6.9 by government authorities and 1.55 by farmers.

where: B_n is the benefit of IRM; B_p is the potential control of IRM, e.g. effects of disease control (B_p is >0 but undetermined); and C is the total costs (material, labour).

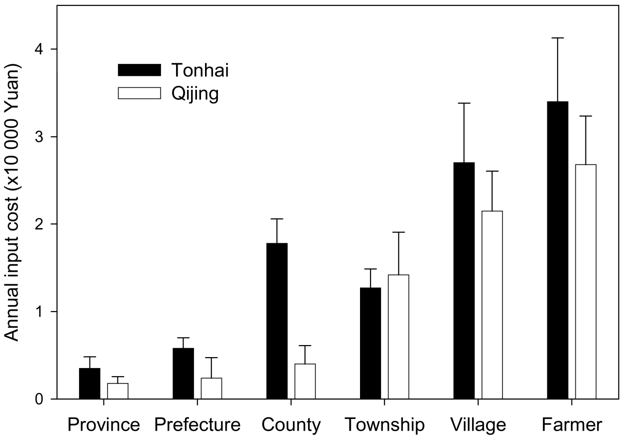

Figure 1. Mean annual input (yuan) for integrated rodent management (1993–1998) for Tonhai and Qijing counties.

We assumed that a rodent, on average, destroys 9 kg of crops per year and that the average value of a 1 kg crop is about 2.2 yuan (¥) (US$1 = ¥8.2). The social and health benefits of IRM are unknown, but thought to be substantial.

A questionnaire survey of 200 farmers in Huanlong, Wanjiai and Qiling townships revealed B_n values of ¥1300–2800, and C values of ¥860–1560. Although B_p remains undetermined, we can calculate B_n/C for farmers and government authorities. There was a significant difference between the government's perception of benefit–cost ratios and the benefit–cost ratios calculated by us (t = 5.44, $P < 0.01$). There was no significant difference between the farmers' perception of benefit–cost ratios and the benefit–cost ratios calculated by us (t = 2.18, $P > 0.1$). It seems that the farmers' perception of benefit–cost ratios is a reliable estimate of real IRM benefit–cost ratios.

Other socioeconomic factors

Monitoring benefits and costs is an important factor in evaluating the results of IRM and in encouraging the adoption of IRM practice by farmers. However, monitoring is rarely conducted, especially at the local levels of township and farms, where only 30% of the surveyed units did monitoring. Public places (e.g. toilets, storage rooms, fallow fields, ditches, canals) were always ignored regarding management actions by both the government and the farmers. This will certainly interfere with the effects of IRM control action because in these habitats pest rodents are sheltered and offspring generated there may invade crops.

Conclusions

Howard (1984) has pointed out 39 factors that could interfere with IRM. In this study, we found that four economic factors have a key influence on the practice of IRM in Yunnan province.

4. The government needs to support the organisation of IRM by providing financial inputs and training courses for farmers.
5. The efforts by the government should be distributed over all government levels (province to farmer) to increase awareness and competence in IRM.
6. Correctly estimated benefit–cost ratios provide proof of effective IRM to both government and farmers and can help in the decision-making process in IRM.
7. Increased yield is only one positive outcome of rodent control in agro-ecosystems. Farmers will also have a benefit if the time spent controlling rats decreases, even if the yield does not increase. The farmers can use the time gained for other cash-generating activities or for leisure. If IRM can be conducted without or with little use of chemicals, the environmental benefits may be considerable.

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Developing a rodent management strategy for South Africa's Limpopo province

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Abstract. A crop post-harvest needs assessment was conducted in the Limpopo province, South Africa. Six villages from three districts were surveyed using participatory methods to assess the livelihood constraints of subsistence farmers. Farmers indicated that rodents were a serious agricultural constraint, and were often ranked as the most important post-harvest constraint for a range of stored crops. In addition to damage to stored staple crops, rodents were noted also to feed on the crop in the field, cause damage to buildings, and bite people in their homes. Farmers knew little about the source of these rodents or how to control them, and they had little faith in any of the available rodenticides. A follow-up pilot trial with kill-traps in homesteads showed a catch rate ranging from 2% to 48%, trapping *Rattus rattus*, *Rattus norvegicus* and *Mastomys* spp. Newly initiated research in Limpopo province is focused on developing more sustainable and ecologically based rodent management strategies for both pre- and post-harvest rodent problems. The aims of these farmer participatory trials are to determine the: (1) population dynamics and breeding ecology of the main pest species; (2) impacts of rodents on crop losses and other livelihood issues; (3) effectiveness of trapping on rodent populations and the damage they cause; and (4) incidence of rodent-borne diseases and the risks they pose to humans.

Introduction

The Limpopo province (formerly the Northern province) is historically comprised of three 'homeland' areas with 91% of the population settled in rural areas. Per capita income is the lowest in South Africa, with an average disposable income of 2112 rand. A study by Rwelamira (1997) estimated that three quarters of the rural households subsist below the poverty line of 900 rand per month, while one in four households managed on less than 800 rand per month. Agriculture is the second largest sector of the province's economy (after mining) and is characterised by subsistence production of staple crops and vegetables.

A project funded by the Crop Post-Harvest Programme of the United Kingdom Department for International Development was initiated to determine the potential for integrating post-harvest technologies available in other African countries into the small-scale food production systems in Limpopo province. The aims of this study were to improve household food security by analysing the post-harvest constraints and opportunities and how these influence the livelihood strategies of rural households. It was expected that the outputs of this study would lead to new projects aimed at addressing the constraints identified.

Materials and methods

A participatory rural appraisal (PRA) survey was implemented in six villages during the out-of-season period after harvesting was completed and before the rainy season when planting commences (July to September 2000). The six villages were randomly selected from the three districts (two villages per district) of the province with the highest populations of small-scale or resource-poor farmers (Lowveld, Northern and Southern districts). The survey used PRA tools with groups of the community to determine agricultural activities and constraints, survival strategies, information pathways and the role of different stakeholders. A questionnaire with individual households focused on activities related to the production and storage of the main crops. Information from each village surveyed was compiled in a report that was presented at workshops attended by representatives of the farming communities and other role players.

Results and discussion

Results of the survey showed that agriculture and income from government pension grants were perceived by the communities as their most important survival strategies. Few farmers produced enough surplus food for sale.

Table 1. Agricultural constraints as listed and ranked by the six villages surveyed in Limpopo province. Shaded areas were not listed as constraints. Men (W) and women (W) in each village ranked the constraints separately by apportioning 100 stones among the constraints identified by the entire community (‘0’ indicates it was scored as 0, while ‘–’ indicates it was not scored because it was not listed). (Source: von Maltitz et al. 2001.)

Constraint	Lowveld district				Northern district				Southern district			
	Basani		Nkomo-B		Mapate		Vhurivhuri		BBkloof		Ga-Phaahla	
	M	W	M	W	M	W	M	W	M	W	M	W
Physical												
Lack of tractor/implements	34	21	13	20	18	17	16	31	11	8	10	9
Lack of fences	15	21	10	10			11	6	19	5	8	5
Lack of thresher											14	7
Lack of mills									–	10		
Lack of co-op									–	8		
Transport: field to home	6	8			6	5			7	6	8	4
Transport: home to market					4	6			8			
Distance to mill	5	11										
Distance to market							9	0				
Lack of market			4	0					7	7	0	7
Lack of grazing							6	0				
Lack of dip tank			4	6								
Lack of irrigation			11	0								
Lack of storage											0	7
Susceptible hybrid seed	3	2										
Natural												
Insect pests and diseases			7	8	10	12	4	4	4	13	11	5
Insect pests in storage	3	7					6	19	2	5	3	6
Termites							7	11			11	7
Diseases									5	–		
Damage by birds									5	–	11	9
Rodents	6	5	6	11							2	5
Witch weed							4	10	5	–	13	8
Drought							7	7				
Wild animal damage									–	6		
Soil erosion							5	6				
Infertile soil											3	9
Lack of water/irrigation			30	38	7	3			–	11		
Waterlogging											4	4
Human												
Lack of information			14	7					9	7		
Lack of info processing									–	3		
Labour to fence	2	4										
Labour shortage	3	2			7	7						
Labour to clear fields	17	9										
Weeding laborious					8	8						
Theft	1	4									4	5
Harvesting laborious					7	5			8	–		
Shelling laborious					5	8						
Poor agricultural practices											2	5
Financial												
Transport cost	5	6										
Lack of pesticides					8	–			–	4		
Lack of seed			7	10	9	14	9	8	7	3		
Lack of fertiliser			4	0	11	15	9	10	–	4		

Table 2. Methods used by farmers in Limpopo province to protect their stored crops from rodent damage. (Source: von Maltitz et al. 2001.)

Method of rodent management cited	Village name						Total
	Basani	Nkomo-B	Mapate	Vhurivhuri	BBkloof	Ga-Phaahla	
Rattex (difethialone)	7	12	3	5	5	12	44
Cats	5	2	1	2	1	5	16
Traps	1	2	1		1	1	6
Sticky glue	1	1					2
Carbaryl/gamma-benzene hexachloride	1						1
Pour hot water in rat holes	1						1
Mud/cattle dung for sealing entry holes in granary				1			1

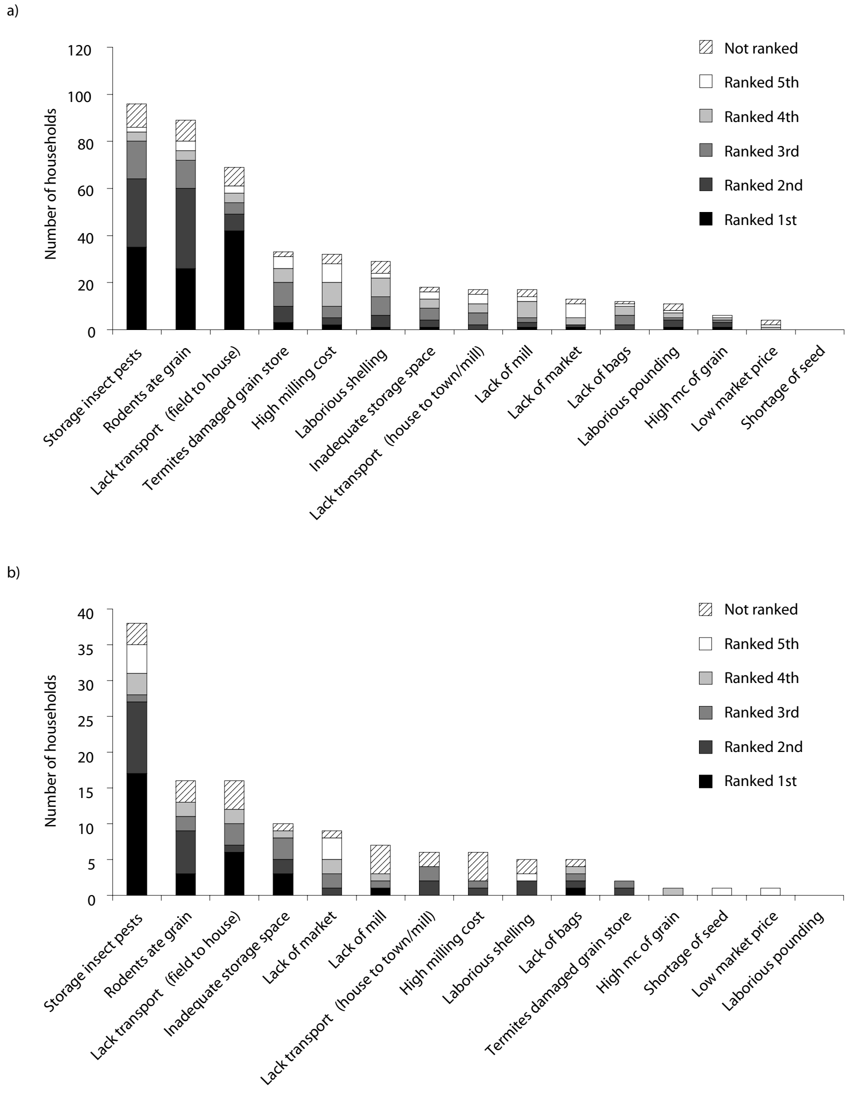

Figure 1. Post-harvest constraints identified and ranked by farmers in six villages in Limpopo province showing a) the problems experienced by 128 farmers growing maize as their staple crop and b) the problems experienced by 40 farmers growing sorghum as their staple crop (mc = moisture content).

Open-pollinated maize varieties were the major staple crop, while sorghum and millet were the staple crops in the more arid southern area. Groundnuts and legumes were major crops in the northern and eastern areas. Nearly all crop yield was stored on-farm, with maize cobs stored in granaries and all the other crops threshed for bag storage in the home.

Each community was asked to list their agricultural constraints, which were then ranked separately by the men and women in the community (Table 1). Natural constraints, particularly insect and rodent damage in storage, were considered the most important in all communities, as shown by farmers growing maize and sorghum as their main crops (Figure 1). Rodent damage to stored millet, groundnuts and legumes was ranked as the first and/or second most important problem. Surveys that specifically dealt with rodent problems indicated that 40% of respondents used a preventative method against rodent damage—the most common method was the occasional single-dose use of a chronic rodenticide in and around the house and food store (Table 2). Rodents were noted also to feed on the crop in the field, cause damage to buildings, granaries, furniture and household belongings, and bite people at night in their homes. Farmers knew little about the source of these rodents, how many types there were, or how to control them. Post-harvest hygiene and waste management was a problem in the villages surveyed, and agricultural waste was often left in the yard, providing shelter for rodents. Open-structure granaries used for maize storage were raised less than 1 m from the ground, allowing rodents free access.

A pilot trial with kill-traps placed inside people's homes and stores showed that capture rates per trap night varied between 2% to 48% over 3 days of trapping. The rodent species trapped were *Rattus rattus*, *Rattus norvegicus* and *Mastomys* spp., with *R. rattus* being the dominant species at the time of the survey (November 2001). A new project to develop rodent management strategies for pre- and post-harvest rodent problems has recently commenced with a view to understanding the rodent ecology and control options that can lead to reductions in rodent impacts on people's livelihoods.

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Socio-cultural and economic assessment of community trap–barrier system adoption in southern Vietnam

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Abstract. The community trap–barrier system (CTBS), an ecologically based rodent management strategy, was introduced to rice farmers in the Mekong Delta in 1997 to facilitate farmer adaptation and eventually adoption on a large scale. This paper explores factors for, and constraints to, CTBS adoption. Southern Vietnamese farmers are likely to adopt the CTBS considering their perceptions of the technical effectiveness, profitability, assuming the cost is shared among the members within the protected area, reductions in chemical usage to control rats, and their social and cultural practices. Major constraints to its adoption are the high initial costs for establishing one TBS and the uncertainty of farmers within the protected area to equally share these costs. To ensure large-scale adoption of CTBSs in southern Vietnam, it is suggested that the government should subsidise farmers by providing them with TBS materials. The farmers would provide labour equity. Improvements to the CTBS technology suggested by farmers are presented.

Introduction

A farmer's choice of action—adoption of a new technology—is mainly influenced by his/her evaluation of the new technology. That evaluation is largely based on his/her perceptions on the effectiveness of the technology and the feasibility of the technology for farmer use. Technological feasibility may include economic profitability, technological simplicity, and social and cultural acceptability. A technology is likely to be adopted if the economic advantage is superior to the existing and alternative technologies. Likewise, to ensure that the technology is likely to be accepted by the target users—the rice farmers—it should be simple to implement and compatible with their culture, such as their norms, beliefs, and practices.

The use of a trap–barrier system (TBS), with an early-planted crop within the barrier, has shown promise for controlling rodent pest populations in lowland irrigated rice crops (Singleton et al. 1999). The adoption of this simple technology requires community participation and so has been described as the community trap–barrier system (CTBS). This paper aims to explore factors influencing CTBS adoption, and the constraints to its adoption, for controlling rodent pests in the Mekong Delta region of Vietnam.

Materials and methods

This study had two treatments: with CTBS and without CTBS, with a total of 24 TBSs established. One TBS was established in each of six hamlets in Cai Be and Cai Lay districts, Tien Giang province, and My Tu and Long Phu districts in Soc Trang province. Another two hamlets from each of the two provinces were chosen to serve as the control group. Key informant interviews, focus group discussions, and a partial input–output survey on rice production using semi-structured questionnaires with personal interviews, were conducted to elicit information on farmers' rodent pest management practices, farmers' perceptions of rodents as a constraint to rice production, profitability of the CTBS, and to assess the potential factors and constraints to farmer adoption of the CTBS. In all, 233 farmers were interviewed: 114 from the 12 treatment hamlets (six from each province), and 119 from the control hamlets.

The establishment of TBSs in the treatment sites was financed by the project, and included materials, including fences, rat traps, seeds for the planting of the trap crop, labour for pumping water because the trap crop was planted early, and establishment labour. Farmers' equity was in the form of labour, such as checking the rat traps daily and keeping records of the total numbers of rats caught. Those farmers who had crops within the area protected by a CTBS were responsible for the maintenance and management of their CTBS. Different dynamics and institutional arrangements in the management of the CTBS were noted. A marginal benefit–cost ratio (MBCR) was estimated to assess the economic viability of the CTBS.

Results and discussion

Farmers' perceptions on the technical effectiveness of the CTBS

Adoption of the CTBS among southern Vietnamese farmers can be assessed from the following angles: technical, economic, social and cultural. In terms of technical acceptability, it should be perceived as an effective rodent control method. Table 1 shows farmer ranking of the effectiveness of different rodent control methods, as well as ranking of other attributes, such as labour and cost requirements. Farmers perceived CTBS as the most effective control method, and recognised that it requires low labour, and its use can be sustained in all three cropping seasons. However, the establishment of a TBS is perceived as the most costly because it requires high initial investment in terms of the plastic fence, rat traps, labour, and land preparation.

Farmers further perceived the CTBS as an effective rodent control method in terms of percentage rodent damage (Table 2). Farmers observed a marked damage reduction after CTBS implementation: from 12% before to 4% after CTBS implementation in My Tu, and from 21.4% before to 16.5% after CTBS implementation in Cai Be. In contrast, farmers in the control group perceived that rat damage had increased or remained the same. CTBS farmers from the other two districts, however, perceived that damage due to rats remained the same. It is surmised that the technical effectiveness would be more apparent if CTBSs were established in areas of known high rodent damage.

Economic viability

One measure for assessing the economic viability of a CTBS is through the marginal benefit–cost ratio (MBCR), which is the ratio of additional benefits and additional costs due to adopting CTBS. Additional benefits due to CTBS adoption equal the sum of the value of yield difference between CTBS and non-CTBS users, reduction in rodenticide costs, including the cost of baiting and labour, and the value of rats caught from the traps in CTBS (Table 3). Most of the CTBS farmers did not use rodenticides (70–97%), while most of control farmers were still using them (70–80%). This is an important finding because often the chemicals used in this region are not those recommended by the Plant Protection Department and are therefore likely to have a high negative environmental impact, including poisoning of non-target species. Also of concern is that people consume rats caught in this region.

The additional costs of adopting CTBS technology is estimated to be Vietnamese dong (VND)135,000 (US$1 = VND14,500), which largely included material costs and labour.

From the four villages, three had positive MBCRs, ranging from 2–6. This indicates that a farmer participating in a TBS would incur a minimum additional return of VND2 and a maximum return of VND6 for every VND1 invested. There was one village, Long Phu, which had a negative MBCR, implying a negative return (Table 3). One of the reasons for this negative MBCR was that at Long Phu there was a late start to the summer–autumn season because of drought. This led to significant crop losses due to disease affecting the late-planted crop. However, the control site was minimally affected.

Table 1. Ranking by farmers from Tien Giang, southern Vietnam, of the effectiveness of their different rodent management practices (1 = most effective, 7 = least effective). Also shown are some key factors that influence the decisions of farmers to adopt management practices (H = high, M = medium, L = low; Y = method adopted, N = method not adopted; I = individual, C = community). In this region there are three rice-growing seasons each year.

Control method	Effectiveness ranking	Consume rats caught?	Costs	Labour	Season			Community or individual action
					1	2	3	
Trapping	5	Yes	M	H	Y	Y	Y	I
Using rodenticides	6	NO	M	H	Y	N	N	I
Catching by hand	6	Yes	L	H	Y	Y	Y	C
Hunting by dog	3	Yes	L	H	Y	Y	Y	C
Smoking the holes	8	Yes	L	H	Y	Y	N	C
Sound of machinery, then digging	4	Yes	M	H	Y	Y	N	C
Wood trap	2	Yes	M	M	N	N	Y	C
Circling with grass	4	Yes	L	H	N	N	Y	C
Sling shot	7	Yes	M	M	N	Y	Y	C
Long pole at night	3	Yes	M	M	N	Y	Y	C
Community trap–barrier system	1	Yes	H	L	Y	Y	Y	C

Table 2. Mean values of farmers' perception of rodent damage (%) before and after community trap–barrier system (CTBS) implementation, summer–autumn season 2001.

Village	With CTBS		Without CTBS (control)	
	Before	After	Before	After
Tien Giang				
CaiBe	21.44a	16.55b*	12.87a	15.57a
CaiLay	14.95a	17.06a	12.87a	15.57a
Soc Trang				
MyTu	11.86a	3.59b**	11.79a	7.56a
LongPhu	18.74a	19.82a	9.28a	11.03a

Note: means of the same letter in a row are not significantly different at the 0.05 level; * = significant at the 0.10 level; ** = significant at the 0.01 level.

Table 3. Marginal benefit–cost ratio (MBCR) associated with using community trap–barrier system (CTBS) technology in four districts in southern Vietnam. Values (in Vietnamese dong, VND) are estimated through comparing costs of actions on treated and control sites.

Village	Yield (kg/ha)		Value of yield difference (VND)	Value of rats caught (VND)	Reduction in cost of rodenticide, bait and labour (VND)	Additional benefit (VND)	Additional costs (VND)	MBCR
	With CTBS	Without CTBS						
Tien Giang province, winter–spring 2000								
Cai Be	6969	6882	120,060	154,500	18,416	292,976	135,000	2
Cai Lay	5589	5124	641,700	147,000	73,532	862,232	135,000	6
Soc Trang province, summer–autumn 2001								
My Tu	6120	5763	399,840	222,000	–6050	615,790	135,000	5
Long Phu	5432	5986	–620,480	186,000	44,870	–389,610	135,000	–3

Social and cultural practices

Community action for rodent control is not new to Vietnamese farmers. Eighty per cent of the existing rodent control methods are done as a group (Table 1)—only rodenticides and small traps are used by individuals without consideration of the actions of their neighbours. Thus, the CTBS, which calls for community participation, is likely to be feasible for widespread implementation for controlling rodents. In Cai Be, the integrated pest management (IPM) 'club' is strong. Checking the rat traps was done according to schedules prepared by the members of the club and those within the area protected by a CTBS. Also, farmers prefer CTBSs to rodenticides because the latter are hazardous to both animals and human health.

In southern Vietnam, rat meat is part of the food culture. Millions of rats are caught each year, especially during the months of February, March and April (Khiem et al., this volume). Rat meat is a particular delicacy, which is an added incentive to farmers to use live-traps (i.e. CTBS) instead of poisons. One can buy live rats at VND6000/kg.

Constraints to CTBS adoption

Constraints to farmer adoption of the CTBS are high initial investment and the sustainability of CTBS management. At VND135,000, the CTBS is expensive for one farmer to bear all the costs. Farmers acknowledge the difficulty in getting others to share the costs. It is therefore suggested that the government should subsidise farmers by providing CTBS materials. In this case, farmers' equity would be the labour for establishing the CTBS and the daily monitoring of the rat traps. In terms of managing the CTBS, it requires daily checking of the rat traps. One way to improve sustained checking of traps is to place the trap crop near the houses of the trap-crop owners and members of the CTBS group (Morin et al., this volume). Another way is to place the CTBS where those who have crops within the protected area are related.

Farmers' suggestions for improving the CTBS

Currently, the TBS materials are replaced every season. The farmers suggested that the plastic should be thicker so that it can be used for more than one season. One way to reduce TBS investment is to reduce the height of the plastic fence and to use smaller traps. Furthermore, farmers suggest that traps should be placed inside the trap crop, so that if some rats get inside the TBS fence, they will be trapped, minimising the damage done to the trap crop.

Conclusion

The CTBS is likely to be adopted by southern Vietnamese farmers considering farmers' perceptions of the technical effectiveness of the CTBS as a rodent control method, the profitability of the CTBS—assuming the cost is shared among the members within the protected area, the reduction in chemical usage, and their social and cultural practices. The major constraints to farmer adoption of the CTBS is the high initial investment or expenditure and the difficulty in getting farmers to share the costs. It is therefore suggested that the government should subsidise farmers by providing them CTBS materials to ensure large-scale adoption of CTBSs in southern Vietnam.

Acknowledgments

This study was part of a collaborative project of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Sustainable Ecosystems, the International Rice Research Institute, the Institute of Agricultural Sciences of South Vietnam, Southern Regional Plant Protection Department, the Plant Protection Department of South Vietnam, and the Cuo Long Rice Research Institute. The study was funded by the Australian Agency for International Development (AusAID) under their Capacity-building for Agriculture and Rural Development (CARD) program. We thank Grant Singleton for his comments on this paper.

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Farmers’ beliefs and practices in rat management in the Mekong Delta, Vietnam

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Abstract. A survey of 400 farmers in four villages in the Mekong Delta showed that they considered rats as the most important yield constraint to rice production. A variety of control methods were being used, most common among them rat poisons such as zinc phosphide and warfarin, and crudely constructed electric fences. Generally, farmers spent 5–8 days per season on rat control, spending about US$17. They believed that if they did not control rats, crop losses amounting to about 700 kg (or US$63) per ha would be incurred. Most farmers believed in a group-based approach to rat management, but few practised it. These observations provide important information for facilitating the introduction of a non-chemical community-based trap–barrier system.

Introduction

Rats are important yield constraints to rice production in Vietnam. Crop losses have been estimated at 300,000–400,000 t of rough rice each year (Brown et al. 1999). In the Mekong Delta, there are two main rat species attacking rice, namely, the rice-field rat (*Rattus argentiventer*) and the lesser rice-field rat (*Rattus losea*). Farmers generally resort to the use of poison baits to kill rats. The efficiency of baiting is unreliable and rat poisons are also highly hazardous to human health. The trap–barrier system (TBS) introduced in Malaysia has been found to be an effective, non-chemical system (Singleton et al. 1999). To facilitate adoption of this system, a baseline survey on farmers’ knowledge, attitude and practice was conducted to provide information on farmers’ beliefs and practices in rat management in Tien Giang and Soc Trang provinces.

Materials and methods

Treatment, study sites and sampling procedure

The survey was conducted in two provinces, namely, Tien Giang and Soc Trang. These provinces have a history of significant rat problems in rice crops. In each province, two villages about 10 km apart were selected and a sample of 100 farmers was selected randomly for interviews. One of the villages was designated as treatment (cTBS) where the TBS was introduced to a community of 30 farmers. Here, farmers were trained to construct and maintain the TBS and monitor rats caught. The other village was designated as the control where a TBS was not introduced. The survey was conducted in March and April 2001 when the TBS training was provided but before the farmers had used the technology. Two focus-group discussions were conducted in the survey areas to obtain information for drafting of the questionnaire. The draft questionnaire was then translated into Vietnamese and pre-tested among 10 farmers individually and revised accordingly. Trained agricultural technicians administered the questionnaire.

Measuring beliefs

Twelve attributes developed from focus group meetings were used in the questionnaire to assess farmers’ beliefs in rat management. Beliefs were scored using a response cue card with descriptor phrases in Vietnamese expressing their degree of agreement. Each point was assigned a numerical value from 1 to 5 following a Likert scale. The descriptors were: 1 = definitely not true; 2 = in most cases not true; 3 = may be true; 4 = in most cases true; and 5 = always true.

The responses of the farmers from within each village were combined to form a control group of 100 and experimental group of 100 for each province.

Results and discussion

Respondents’ profile

The profile of the sample farmers is shown in Table 1. Most of the farmers in Tien Giang and Soc Trang were about 40 years old and had about 5–7 years of education, which was similar to previous surveys by Mai et al. (1997). Farmers in Tien Giang cultivated about 0.9 ha (range 0.2–7.0 ha) of rice while in Soc Trang they tilled about 1.2 ha (range 0.2–6.0 ha). Respondents' characteristics between the experimental and control villages, except rice area cultivated, were not significantly different. In Tien Giang, farmers in the experimental village had rice areas of 1.1 ha, while farmers in the control village had 0.7 ha. In contrast, in Soc Trang, farmers in the experimental village had 1.2 ha, while those in the control village had 1.7 ha.

Rat management practices

Farmers in Tien Giang reported 12 rodent control measures (Table 2a) while those in Soc Trang mentioned nine (Table 2b). The popularity of the methods used varied among farmers between provinces. In Tien Giang, cleaning the field was found to be the most common (64% on average), followed by digging (59%) and use of chemicals (54%). In Soc Trang, 75% of farmers used chemicals, followed by cleaning the field (51%) and digging (47%). Electrocution was used commonly by farmers in Soc Trang (41%) but had never been applied by farmers in Tien Giang. Electrocution is a rat control method that presents a dangerous hazard to human health. Its use in Soc Trang may be due to lack of information because extension and Plant Protection Department (PPD) technicians and the mass media seem to have had little influence on farmers' rat management methods in this province.

Table 1. Profile of respondents in treatment (cTBS) and control villages. The *t*-test was used to compare mean values between villages. The *t* values were used to determine significance. Probability (*p*) indicates the level of significance, with * = significant and ** = highly significant.

Category	Control (*N* = 100) (mean)	cTBS (*N* = 100) (mean)	*t*	*p*
Tien Giang				
Age (years)	41.4	42.1	0.436	0.66
Years of schooling	6.0	6.7	1.860	0.06
Rice farming experience (years)	19.1	17.9	0.910	0.36
Rice area cultivated in dry season 2001 (ha)	0.7	1.1	2.570	0.01*
Rice area cultivated in wet season 2000 (ha)	0.7	1.1	2.360	0.02*
Soc Trang				
Age (years)	43.3	43.5	0.160	0.87
Years of schooling	4.9	4.6	0.910	0.36
Rice farming experience (years)	19.4	20.4	0.380	0.70
Rice area cultivated in dry season 2001 (ha)	1.7	1.2	3.540	0.00**
Rice area cultivated in wet season 2000 (ha)	1.7	1.2	3.580	0.00**

Table 2a. Rat control methods used by farmers (% farmers using) in Tien Giang province, comparing treatment (cTBS) and control villages.

Control method	Wet season 2000		Dry season 2001	
	Control (*n* = 100)	cTBS (*n* = 100	Control (*n* = 100)	cTBS (*n* = 100
Use chemical	60	43	64	47
Trapping	6	26	5	20
Hunting	39	66	39	63
Flooding the field	50	25	48	30
Cleaning the field	69	64	65	59
Digging	39	78	45	75
Rat round-up	7	3	8	1
Trap–barrier system	0	4	0	3
Biological	4	14	4	14
Plastic strip barrier	1	6	1	7
Wood trap	0	1	0	1
Fumigation	0	0	0	1

Table 2b. Rat control methods used by farmers (% farmers using) in Soc Trang province, comparing treatment (cTBS) and control villages.

Control method	Wet season 2000		Dry season 2001	
	Control (*n* = 100)	cTBS (*n* = 100	Control (*n* = 100)	cTBS (*n* = 100
Use chemical	73	70	78	78
Trapping	11	5	10	8
Hunting	36	33	35	35
Flooding the field	14	11	14	12
Cleaning the field	47	54	47	54
Digging	53	39	54	42
Rat round-up	2	1	3	2
Biological	2	1	1	1
Electrocution	39	42	42	40

Farmers in Tien Giang and Soc Trang used two groups of chemicals to control rats. The first group included the rodenticides warfarin (anticoagulant), zinc phosphide (acute poison), and one from China whose active ingredient was not known. The second group consisted of insecticides, such as cartap and methamidophos although the Ministry of Agriculture and Rural Development has banned the latter for use in agriculture.

There was a slight difference in rodenticide use between the two provinces. In Tien Giang, the most common rodenticide used was warfarin (trade name: Rat–K), which accounted for 63% of usage followed by zinc phosphide (trade name: Fokeba) (37%). The Chinese rodenticide was not so widely used in this province (Table 3a). In Soc Trang, however, the most commonly used rodenticide was zinc phosphide (43%), followed by warfarin (33%) and the Chinese rodenticide (30%) (Table 3b). No clear difference in rodenticide use was found between control and experimental villages in the two provinces.

Table 3a. Rodenticides used by farmers (% farmers using) in Tien Giang province, comparing treatment (cTBS) and control villages.

Chemical name	Wet season 2000		Dry season 2001	
	Control	cTBS	Control	cTBS
Rat-K (warfarin)	60.7	67.4	57.8	64.4
Fokeba (zinc phosphide)	31.7	39.5	32.8	44.4
Chinese rodenticide	10.0	2.3	10.9	2.2
Padan (cartap)	0.0	0.0	1.6	0.0

Table 3b. Rodenticides used by farmers (% farmers using) in Soc Trang province, comparing treatment (cTBS) and control villages

Chemical name	Wet season 2000		Dry season 2001	
	Control	cTBS	Control	cTBS
Rat-K (warfarin)	31.5	35.7	32.1	32.1
Fokeba (zinc phosphide)	49.3	35.7	47.4	38.5
Chinese rodenticide	21.9	35.7	25.6	37.2
Monitor (methamidophos)	0.0	2.9	0.0	3.8

Farmers' choice of particular rat control methods did not differ between wet and dry season. Farmers in both provinces used more than one method to control rats; they believed that no single method would be effective. However, more than 50% of the farmers mainly relied on chemicals in both wet and dry seasons. Among farmers' reasons for using chemicals to control rats, 73.6% specified their high efficiency, followed by labour saving (28.7%), low cost (15.4%), and ease of use (14%).

Different rat management actions should be conducted at the right time during a growing season based on the ecology of the rodent pest species in the area (Brown et al. 1999). Although our survey did not record the timing of application for each method, we collected data on control measures used for particular growth stages of the crops (two or three crops are grown in this region each year). Farmers in Tien Giang and Soc Trang took rat control action at various rice growth stages, from seedling to maturing. However, most control actions were targeted at booting stage in both provinces (Table 4). This was consistent also with farmers' perception of the critical stage for rat control as shown in Table 5. Perhaps farmers focused their control efforts at this stage due to the visible symptoms of rat damage.

To assess the economic benefits of rat control, we computed farmers' actual expenses on rat control and their estimation of loss. Farmers spent between 5–8 days/ha/season controlling rats (Table 6). Cost of chemicals and other materials for rat control was highly variable, with a mean of US$5.90/ha/season in Tien Giang and US$6.29/ha/season in Soc Trang. On average, the total cost of rat control/ha/season was about US$19.20 in Tien Giang and US$14.00 in Soc Trang. Farmers' perceived benefits from controlling rats were about 792 kg and 617 kg of paddy/ha/season in Tien Giang and Soc Trang, respectively. With the farm-gate price of US$0.09 per kg, the perceived benefits were computed to average US$73.45 and US$56.70/ha/season in Tien Giang and Soc Trang, respectively. Thus, the perceived cost–benefit ratio would be 1:3.8 in Tien Giang and 1:4.0 in Soc Trang. No difference in the number of days spent and labour cost for rat control was found between control and experimental villages in both provinces. However, the cost of chemicals and other materials for rat control was significantly higher in the experimental village in Tien Giang (Table 6).

With regards to the mode of implementing their rat control efforts, 82% of control village farmers in Tien Giang did it alone, while only 40% in the experimental village controlled rats individually. The remaining 60% in the experimental village said that they worked together with other farmers. In Soc Trang, more than 90% of farmers interviewed said they controlled rats alone and very few controlled rats as a group.

Farmers' beliefs in rat management

Most farmers in Tien Giang and Soc Trang believed that rats are important yield constraints and that controlling rats would maintain rice yields. The belief that rats can only be controlled if they worked together with other farmers was stronger in Tien Giang than in Soc Trang. However, most farmers in both provinces strongly believed that the cost of control could be reduced if farmers worked together with other farmers.

The belief that rats can be controlled effectively only by the use of chemicals was low in both provinces. However, there was a difference in the degree of belief about the environmental concern when using chemicals between farmers in Tien Giang and Soc Trang. More farmers in Soc Trang (65.5%) than in Tien Giang (20%)

believed in the statement that it does not matter whether use of chemicals to control rats will harm the environment, as long as rats are killed. In both provinces, most farmers evaluated the efficiency of rat control as more important than its cost.

Conclusion

Farmers in both provinces strongly believed in the need to control rats as well as in the advantages of a group-based control approach in terms of efficiency and cost reduction.

Table 4. Timing of rat control efforts of farmers (% farmers) in Tien Giang and Soc Trang, comparing treatment (cTBS) and control villages (DAS = days after sowing).

Crop stage	Wet season 2000		Dry season 2001	
	Control	cTBS	Control	cTBS
Tien Giang province				
Seedling (0–15 DAS)	51.0	60.6	46.0	45.5
Tillering (16–40 DAS)	49.0	69.7	51.0	61.6
Booting (41–60 DAS)	96.9	81.8	97.0	80.8
Heading (61–70 DAS)	61.2	41.4	58.0	44.4
Maturing (>70 DAS)	15.3	11.1	13.0	12.1
Soc Trang province				
Seedling (0–15 DAS)	73.0	66.0	76.0	81.0
Tillering (16–40 DAS)	21.0	17.0	16.0	28.0
Booting (41–60 DAS)	80.0	81.0	87.0	81.0
Heading (6–70 DAS)	57.0	47.0	64.0	59.0
Maturing (>70 DAS)	21.0	7.0	22.0	7.0

Table 5. Rice growth stage perceived by farmers (% farmers) to be most effective for controlling rats, comparing treatment (cTBS) and control villages.

Crop stage	Tien Giang		Soc Trang	
	Control (*n* = 100)	cTBS (*n* = 100)	Control (*n* = 98)	cTBS (*n* = 98)
Seedling (0–15 DAS)	16.0	20.0	24.5	15.3
Tillering (16–40 DAS)	5.0	18.0	0.0	6.1
Booting (41–60 DAS)	73.0	57.0	56.1	68.4
Heading (61–70 DAS)	2.0	2.0	18.4	10.2
Maturing (>70 DAS)	4.0	3.0	1.0	0.0
Total	100.0	100.0	100.0	100.0

Table 6. Farmers' rat management expenses (in US$) and their estimation of loss (on a per ha basis, based on the arithmetic mean).

Crop stage	Wet season 2000		Dry season 2001	
	Control (*n* = 100)	cTBS (*n* = 100)	Control (*n* = 98)	cTBS (*n* = 98)
Tien Giang				
Number of days spent on rat control	5.1	8.7	5.6	8.0
Labour cost for rat control	10.91	15.91	12.04	14.88
Cost of chemicals and other materials for rat control	2.44	8.74	2.70	9.23
Total cost of rat control	13.34	24.65	14.73	24.11
Perceived loss if no rat control (kg of paddy)	704.79	782.83	965.20	715.58
Cost of perceived loss (VND) if rice was sold at VND1300/kg	65.44	72.69	89.63	66.45
Soc Trang				
Number of days spent on rat control	4.3	3.2	4.9	4.6
Labour cost for rat control (VND)	8.04	5.55	9.14	8.04
Cost of chemicals and other materials for rat control (VND)	4.82	6.20	5.68	8.28
Total cost of rat control (VND)	12.87	11.85	14.82	16.40
Perceived loss if no rat control (kg of paddy)	655.20	373.90	810.5	629.30
Cost of perceived loss (VND) if rice was sold at VND1300/kg	58.27	34.72	75.26	58.44

This presents an opportunity that could facilitate the introduction of community control actions, such as required for the use of TBS technology. Farmers' reliance on chemical measures and their lack of concern for their environmental impact suggest a need to educate the masses of farmers on non-chemical rat management methods in the region.

Acknowledgments

This research was supported in part by the Australian Agency for International Aid (AusAID) under its Capacity-building for Agriculture and Rural Development (CARD) program. The authors are grateful for the efforts of technical staff in Tien Giang and Soc Trang plant protection sub-department for their field work. Thanks are also given to Mr Ho Van Chien and his staff in Southern Plant Protection Department for valuable assistance in organising the interviewer training.

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SYMPOSIUM 7: MANAGEMENT—URBAN RODENTS AND RODENTICIDE RESISTANCE

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Ecological perspectives on the management of commensal rodents

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Abstract. The need to control Norway rats in the United Kingdom has led to heavy reliance on rodenticides, particularly because alternative methods do not reduce rat numbers as quickly or as efficiently. However, such reliance has led to concerns that repeated use of rodenticides poses unacceptable risks to other animals as well as encouraging resistance in the target species. In agricultural areas, frequent use of poison baits is unavoidable when control is concentrated on individual, resource-rich patches, such as farm buildings, because even if total elimination is achieved, reinvasion is inevitable. Population density is highest around buildings during winter when food supplies are most abundant and locations for baits most restricted. Control can be improved by, for example, changing the location of food sources within buildings, so that the environment is less predictable to rats. Rats with the smallest home ranges are most likely to succumb to rodenticide treatment, but those with the largest ranges who nevertheless consume poison bait may pose the greatest risk to predators. Populations reduced to very few animals may take two years or more to recover to their previous levels if there are no nearby reservoir colonies. Not surprisingly, recovery can be severely impeded by limiting the food supply, but in practice the resources of food and harbourage can rarely be controlled to a significant degree on a working farm. Consequently, reducing cover to expose rats to increased predation risks is practicable, but the most successful control strategy necessitates breaking links between populations in resource-rich patches. This may be achieved by treating several patches simultaneously, as well as removing rats in transit between them. Although the initial control may be carried out with rodenticides, the need for subsequent treatments using poison baits should be greatly reduced.

Introduction

The need to control commensal rodents is rarely controversial, as the public has always associated rats, in particular, with lethal, disease-causing organisms, such as bubonic plague. While plague has long been absent from some countries, including the United Kingdom (UK), the potential health threat from commensal rodents is now focused on other zoonotic diseases, such as leptospirosis (Weil's disease) and salmonellosis. While pressure to control problem populations continues, the means of doing so are coming under closer scrutiny, particularly regarding issues of humaneness and environmental impact, in addition to cost-effectiveness. Nevertheless, control tactics need to reduce rapidly the number of potentially disease-carrying rodents and non-lethal management methods are generally unable to achieve this. For example, repellents at best keep rodents at a distance and at worst push the problem elsewhere, while fertility control might only reduce problems over too long a period. Moreover, for many, the only acceptable level of control that mitigates disease risks is total elimination of the rodent population, an objective that, while ideal, is difficult to prove, let alone achieve. Hence, populations invariably recover, largely because the underlying reasons for the problem population developing in the first place are seldom addressed. As the recovery progresses, at some point re-treatment becomes inevitable, but experience has shown that the same level of control is not guaranteed on subsequent occasions. The dynamics of each new population, including the behaviour and physiology of individuals, are subject to change, not only because of the selection pressure imposed by intensively applied control measures, but also because resources vary in distribution and abundance. In this paper, we use the Norway rat (*Rattus norvegicus*) in rural habitats in the UK as a model to illustrate how these ecological processes influence the effectiveness and safety of commensal rodent management strategies.

The Norway rat first arrived in the British Isles nearly 300 years ago, then spread rapidly and largely displaced the ship rat (*Rattus rattus*) that had been present since Roman times. Today, the Norway rat in rural areas is seen predominantly as a storage pest that exploits supplies of harvested cereals, root crops and livestock feeds to be found in farm buildings. It also lives along field margins but rarely digs burrows in the fields. Changes in the agricultural landscape that came with increasing mechanisation resulted in loss of harbourage for rats as field boundaries were ploughed up to make larger fields. Consequently, the significant damage that the rats reportedly caused to standing crops is now negligible. Despite being a relatively recent arrival and its association with human activities, the species can survive independently in the UK, but large (damaging) populations seem to occur only on working farmsteads with abundant resources. While much of their food may be found indoors, rats prefer to nest in burrows dug in undisturbed ground between buildings or along adjacent hedgerows and ditches. Control measures seem to be particularly successful if they intercept rats before the animals reach their food source and the most extreme form of interception is to dispense poison bait directly into the burrow (Quy et al. 1996). However, active burrows are not always easy to find and rats are also highly mobile (Taylor and Quy 1978), such that some burrows may be 1 km or more away from food sources.

Controlling Norway rats presents similar challenges to achieving successful control of other commensal rodents. The most practicable technique on farmsteads is to use rodenticide bait, but the animals live in a complex, three-dimensional habitat where attractive food is, for weeks at a time, virtually unlimited and where places to put the bait may be restricted. Under such circumstances, bait may be totally ignored while damage and contamination continue unabated. However, the food supplies can also ‘disappear’ suddenly and there may be little time to intensify baiting before the rats disperse. Harbourage is always available, although it often varies in quantity, quality and distance from food sources. Control measures are usually instigated on farms when the population reaches some arbitrary nuisance or damage threshold, but it is only when such measures fail that the number of rats which can be supported by farmstead habitats is shown to greatly exceed the numbers previously considered to be too high. As rat population density increases, it sometimes becomes impossible to lay the required amounts of bait and efficacy is reduced or treatments prolonged. In this paper, we will consider the ecological factors that affect the efficacy of rodenticide use, in particular those that determine population size, ranging behaviour and the rate of recovery. Placing the operation of control measures in an ecological context should, at the very least, prevent much wasted effort and at best achieve maximal control with minimal risk to other species.

Materials and methods

Data sets

Data on the size of rat populations living in and around farm buildings were collected during all seasons from a total of 102 farms in three counties of the UK: Sussex (*n* = 24), Hampshire (*n* = 24) and North Yorkshire (*n* = 54) between 1990 and 2000. The predominant activity on the Hampshire farms was cereal growing (67%), livestock rearing on those in North Yorkshire (61%), and 42% livestock/42% arable on the Sussex farms. Farming activity on one site in Hampshire, four in Sussex and eight in North Yorkshire was classified as mixed. The location and type of stored food accessible to rats on each farm was recorded. Rats in Hampshire were typically warfarin-resistant with some resistant to difenacoum and bromadiolone also, while rats in Sussex were mostly anticoagulant-susceptible (Cowan et al. 1995); resistance to anticoagulants has also been found in North Yorkshire rats. Population size was estimated immediately before a rodenticide treatment using a calibrated tracking plate technique (Quy et al. 1993). Briefly, tracking plates were evenly spread across each site at a nominal density of 400/ha. The area of each plate covered with rat footprints was given a score and summing the scores gave an index of total rat activity. A mean of 3–4 consecutive daily total scores was then converted via a calibration curve to give an estimate of rat population size.

The ranging behaviour of rats was recorded between 1994 and 1996 on two farms in the county of Warwickshire as part of a study investigating the role these rodents play as vectors of cryptosporidiosis (Quy et al. 1999). Adult rats of >300 g living in and around cattle sheds and those living along field margins on an arable farm 5 km away were fitted with radio-transmitters that also contained mortality sensors. Each tagged rat was tracked intensively for a week approximately every 4 weeks until the animal died, was lost, or the tag came off. Fixes were obtained every 6 hours and a home range was calculated by the minimum convex polygon method for each rat with >10 fixes. Every effort was made to recover animals that had apparently died in order to determine the cause of death. Anticoagulant treatments were carried out periodically on the livestock farm by the farm staff, but no control was carried out along the field margins on the other farm.

The rate of recovery of 20 rat populations in the county of Surrey in south-eastern England was monitored at 2-monthly intervals for approximately one year between 1976 and 1979. Each population was reduced by an acute rodenticide and, where necessary, an anticoagulant to eliminate as far as possible every rat. Hence, reinfestation should have arisen largely by reinvasion rather than by surviving residents reproducing. All treatments were conducted against rats living in and around farm buildings and the degree of control was assessed independently by tracking plates laid before and after treatment. The plates were set out as described above, but rat footprints were recorded as present or absent only and thus gave an index of numbers. Recovery rates were calculated as a percentage of the pre-treatment track score. The same tracking plate positions were used each time a recovering rat population was monitored. The distribution of stored food on each farm was recorded during each monitoring period, along with any major structural alterations that might have affected the ability of rats to recolonise the farm.

Methods of management

The application of rodenticide baits, especially anticoagulant formulations, has become the first, last and only means of controlling rats for many in the UK. Products containing the second-generation anticoagulants difenacoum and bromadiolone now dominate the market, with use of the less potent, first-generation compounds declining. Despite their advantage in controlling warfarin-resistant rats, the more potent anticoagulant baits did not markedly reduce treatment length, leading to speculation about social factors delaying approaches to bait stations. Although resistance has developed to second-generation compounds, it has not, with some notable exceptions, fully explained the poor efficacy that sometimes occurs. Population size differences and the presence of alternative food have been more convincing explanations (Quy et al. 1992a,b). To control rats highly resistant to anticoagulants, zinc phosphide and calciferol formulations are available. Other control methods, such as trapping, fumigation of burrows and contact formulations are suitable only in specific circumstances or to eradicate small numbers of rats. Proofing of buildings to prevent rodent entry is rarely considered cost-effective and physical barriers often seem incompatible with modern methods of bulk-handling grain and other commodities.

Results and discussion

Ecological determinates of population size

Rat population changes are closely tied to the agricultural cycle; in a northern-hemisphere temperate climate this consists of harvesting cereals, such as wheat and barley, in July–August. Fields are ploughed in September–November and then re-sown with winter cereal varieties; spring cereals are sown in February. Harvested grain is transferred from the fields to purpose-built or makeshift silos/clamps/grain bins to be dried and where it may remain throughout September to March, until it is sold. Usually, all of the previous year's harvest is removed by early spring (April/May) and the grain storage areas are cleaned out ready for the next harvest. Rat activity in standing crops increases noticeably during late May–June as the cereals begin to ripen. The average size of rat populations around farm buildings did not vary across the seasons, although the density did (Table 1). Density increased sharply after harvest in late summer and early autumn, perhaps as animals followed the food from the fields to the buildings. In summer, field populations of rats were likely to be at their highest. It was also likely that reproductive rates of rats around buildings increased to take advantage of the concentrated resources. The greatest density of rats coincided with the smallest infested area and probably reflected the reduced cover to be found outside buildings, as vegetation was either killed by frosts or stopped growing. The lowest density occurred in late winter/early spring, as deaths presumably exceeded births at this time. Huson and Rennison (1981) also recorded a similar pattern of activity after examining changes in infestation rates on agricultural premises.

In contrast to arable farms, stored food is often permanently available where livestock are kept, particularly dairy cattle and pigs reared indoors. Beef and dairy cattle are often kept indoors over winter, but are released into the fields in spring. The pens where these animals have been kept are then cleaned out, displacing any rats in the process. Mixed farms, which perhaps offered the greatest range and abundance of food throughout the year, had a higher average rat population density than the other two farm types (Table 2).

Regional differences were also apparent between southern (Hampshire/Sussex) and northern (North Yorkshire) England, with smaller populations in the northern county (Table 3). However, the average infested area was significantly smaller in the Yorkshire sample, resulting in higher densities than in the southern counties. The reason for the difference is uncertain, but might have been related to the larger proportion of pig rearing farms in the Yorkshire sample. Such farms offered greater scope for rat numbers to grow, as the buildings were often constructed with hollow walls and false ceilings, in contrast to the relatively open-plan nature of those holding cattle. Population density is of particular importance for the dynamics of zoonotic diseases where maintenance of infection is dependent on contact rates between animals.

Table 1. Comparison between rat populations in and around farm buildings with respect to season in terms of area infested, population size and population density. Data are means ± sd. The infested area was calculated by the number of tracking plates laid at the predetermined density of 400/ha (ANOVA = analysis of variance, NS = not significant).

Season	*n*	Area infested (ha)	Population size	Population density (*n*/ha)
February–April	32	0.223 ± 0.103	82.5 ± 63.1	373.8 ± 211.0
May–July	19	0.141 ± 0.060	57.3 ± 41.3	400.7 ± 203.2
August–October	38	0.204 ± 0.122	109.3 ± 99.6	513.0 ± 256.6
November–January	13	0.114 ± 0.041	76.2 ± 48.8	635.4 ± 237.4
One way ANOVA	df 3,101	F 5.4, *P* = 0.002	F 2.24, NS	F 5.05, *P* = 0.003

Table 2. Comparison between rat populations in and around farm buildings according to farm type in terms of area infested, population size and population density. Data are means ± sd (ANOVA = analysis of variance, NS = not significant).

	Arable	Livestock	Mixed	One way ANOVA
n	39	50	13	
Area infested (ha)	0.215 ± 0.125	0.164 ± 0.082	0.187 ± 0.11	F 2.67 df 2,101 NS
Population size	92.5 ± 68.8	74.1 ± 63.1	119.8 ± 125.4	F 2.06 df 2,101 NS
Population density (*n*/ha)	445.1 ± 214.0	438.4 ± 230.6	619.3 ± 334.0	F 3.14 df 2,101 $P = 0.048$

Table 3. Comparison between rat populations living in and around farm buildings in Yorkshire and those living similarly in Hampshire/Surrey in terms of area infested, population size and population density. Data were collected during all seasons between 1990 and 2000. Data are means ± standard deviation (ANOVA = analysis of variance).

n	Yorkshire	Hampshire/Sussex	One way ANOVA
	54	48	
Area infested (ha)	0.119 ± 0.050	0.263 ± 0.100	F 87.12 df 1,101 $P < 0.001$
Population size	66.2 ± 53.7	110.4 ± 90.5	F 9.219 df 1,101 $P = 0.003$
Population density (*n*/ha)	523.0 ± 249.0	397.7 ± 224.1	F 70.69 df 1,101 $P = 0.009$

Ecological determinants of management effectiveness

It seems obvious that total removal of the food supply would control rats without recourse to rodenticide use, but in reality supplies can rarely, if ever, be so restricted on a working farm that rats are denied any access. Thus, rodenticide baits will invariably be competing with other foods for the rats' attention and in one study of anticoagulant effectiveness, 12 populations were reduced within 7 weeks by a mean of only 24% when stored cereals were present, but by 75% ($n = 19$) when such cereals were absent (Quy et al. 1992a). However, a change in the distribution of stored cereals, not involving their complete removal, led to greater control (mean 62%, $n = 8$). Such change often meant little more than relocation of grain within a building, thus suggesting that predictability of supply was more important than its abundance or continuity and that creating controlled habitat disturbances would encourage rats to approach baits. In this respect, rats are more likely to consume bait on livestock farms, because the movement of farm animals and high turnover of feed gives a degree of inherent habitat instability (Quy et al. 1994).

Poison baits intended to control commensal rodents are applied as spot treatments and are never broadcast. When setting up rodenticide treatments, it is therefore simplest to distribute baits according to the density of rat signs rather than the movements of individuals, which cannot easily be determined. Animals that have home ranges larger than the size of the treated area may not encounter bait often enough to maximise treatment efficiency. Equally, as the density of signs decreases, the spacing between baits is likely to increase, reducing the likelihood that such baits will intercept rats with large ranges. From the perspective of the efficacy and safety of rodenticide use, the ranging behaviour can reflect the likely fate of rats. The observed ranges of four rats living in and around farm buildings were remarkably small (<0.1 ha), some moving no more than 20 m from a nest, presumably to and from their food supply; these animals succumbed to an anticoagulant rodenticide, as confirmed by signs of haemorrhage on recovery of their bodies (Table 4). Away from farm buildings, resources are often more widely dispersed and rat signs are therefore less concentrated: 11 rats that survived for up to 3 months between collar attachment and the battery failing had a mean observed range of 0.2 ha. However, rats sometimes move long distances, greater than perhaps necessary to find sufficient resources (Taylor and Quy 1978), involving journeys into probably less-familiar parts of their range. Predators (mostly foxes and dogs) killed six rats with the largest home ranges (mean 1 ha). Despite small sample sizes, the differences between the ranges for the three groups shown in Table 4 were significant (Kruskal–Wallis non-parametric analysis of variance,

$\chi^2 = 8.71$ 2 df, $p = 0.03$). These data suggest that rodenticide efficacy is enhanced if rats have ranges smaller than the treated area and, provided predators seldom venture near farm buildings, the risk of secondary poisoning might be relatively small. In contrast, poisoned rats whose ranges extend outside the treated area may have sufficient time to move into a predator's territory, given the delay between ingesting a lethal dose of anticoagulant and death. An inference that may also be drawn from these data is that manipulating habitat features to modify range size might enhance the effectiveness of particular management techniques.

Table 4. Fate of radio-collared rats in relation to home range size on two farms in the county of Warwickshire, United Kingdom. Individuals were tracked for up to 3 months (the life of the transmitter battery) between 1994 and 1996. Data are means ± sd.

Fate	*n*	Home range size (m^2)
Survived till recapture or transmitter battery failure	11	1954.5 ± 2470.4
Predated	5	9580.0 ± 7761.0
Rodenticide	4	450.3 ± 420.0

Ecological effects on population recovery

While ranging behaviour provides an ecological context for efficacy and risk assessment, it also can explain the recovery of rat populations during and after treatments. The influence of adjacent hedgerow populations on the efficacy of treatments around farm buildings was to extend the period of bait exposure in order to achieve the equivalent level of success on those farms without hedgerow populations (Quy et al. 1992b). It was impractical to treat the adjacent infestations simultaneously with those in the buildings and the prolonged treatments probably reflected continual reinvasion that replaced animals succumbing to the poison. Hedgerow populations of rats are particularly common in the eastern half of the UK, where cereal growing predominates.

Conceptually, the rate of recovery is a function of productivity of any residual population and reinvasion into the target habitat, which should diminish as the distance from reservoir populations increases. These processes were explored when 20 rat populations were reduced/eliminated from farms in south-eastern England in a mixed-farming area of cereal growing and pasture and with relatively insignificant numbers of rats along field margins. On one farm, putative immigrants were trapped and removed every 2 months and on two others data were incomplete. The rate of recovery of 17 farm rat populations showed an approximately linear increase over 12–14 months (Figure 1). (Data were insufficient to examine seasonal effects.) Assuming the trend remained linear, the projected mean time to full recovery (i.e. to the size of the initial population) was 27 months. Given the high intrinsic rate of increase of Norway rat populations, recovery seemed to be surprisingly slow and suggested that in this area, by accident or design, ecological factors constrained growth. To illustrate this, two populations with very different recovery rates were selected from the sample (Figure 2). Both were first treated at approximately the same time of year (summer), but there was very little stored food to support the rats on the arable farm during this pre-harvest period. However, seemingly unlimited supplies of food for dairy cattle supported a much larger population on the livestock farm. Post-treatment, both residual populations were of similar size, but that on the arable farm recovered to its pre-treatment level within 2 months as harvested grain was stored in open-topped bins. In contrast, over an extended monitoring period, rat numbers failed to recover (but did not disappear entirely) on the livestock farm, probably because structural alterations to the buildings made any stored food less accessible. In this case, restricting resources did not stop rats invading the farm, but it did reduce the carrying capacity and hence probably prevented significant recolonisation. Given the unlimited food on the arable farm, it was not surprising that a subsequent poison treatment carried out by the farmer had a minimal effect. While these examples present a simple and perhaps self-evident ecological concept, its significance seems to have been lost for many who now rely exclusively on rodenticide use for Norway rat management.

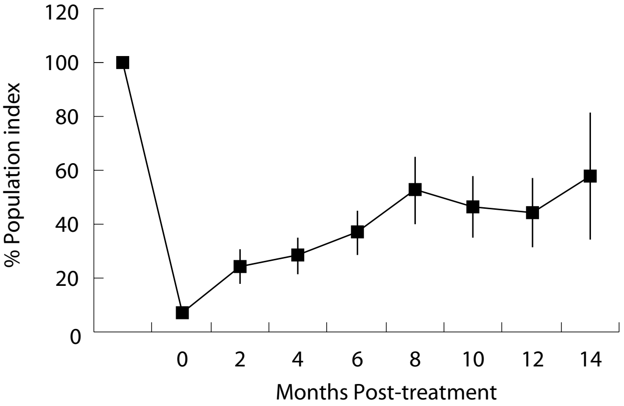

Figure 1. Recovery of rat populations following rodenticide treatment on 17 farms. An index of the post-treatment population size for each farm was derived from tracking plate scores expressed as a percentage of the pre-treatment size (mean ± se).

Ecologically based management strategies

Currently, the economics of rodent control in the UK favour rodenticide use, and to reduce large numbers of rats quickly, its utility is unquestionable. However, repeated use of rodenticides can be avoided if the underlying reasons for population recovery and movements are understood. One approach is to consider rats having a metapopulation structure, whereby they occupy the whole agricultural landscape with population subunits concentrated in resource-rich patches. Transfer between patches takes place along linking corridors, such as hedgerows and ditches. Breaking these links effectively isolates the patches, although in lowland agricultural areas patches (e.g. farmsteads) can be so close as to fall within the normal home range of many rats. To counteract this problem, the best tactic might be to treat several neighbouring farmsteads simultaneously, thereby removing obvious sources of immigrants. This is contrary to present rodent control practice, which typically focuses on an individual group of farm buildings as this represents (commercially) an easily definable habitat to treat. Such control will inevitably fail long-term because of reinvasion and compensation (density-dependent birth/death rates). To keep rat numbers low in the individual patches post-treatment, it is unlikely, except on rare occasions, that the food supply or harbourage can be controlled. More practicable perhaps is to reduce the cover between the harbourage and food source, thus increasing the risk of predator attack. A recent study by the Central Science Laboratory (unpublished) followed the fate of 13 radio-tagged rats living around farm buildings where the ground cover (e.g. vegetation) was kept permanently short and 18 tagged rats where the cover was untouched. Over a 30-day period, 10 rats in the cleared areas moved away or died with three confirmed predator kills. In the uncleared areas, 10 animals remained *in situ* with only one confirmed predator kill.

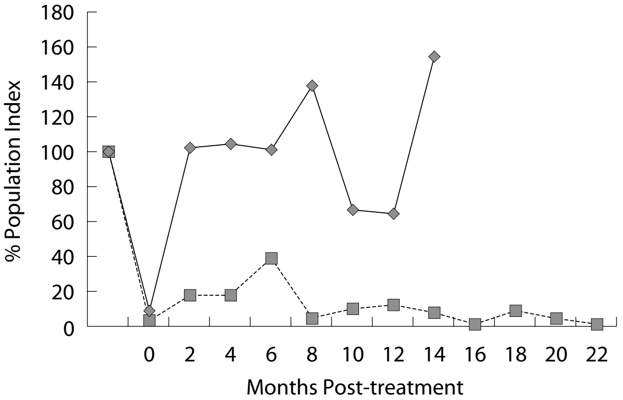

Figure 2. Recovery of rat populations depends on access to food. Numbers recovered rapidly on the arable farm (solid line) after control in June because bulk stores of harvested grain were accessible to rats shortly after the initial treatment and remained so for 12 months. After 8 months, the farmer, concerned about increasing levels of contamination, carried out a treatment, which had a short-lived effect on numbers. In contrast, on the livestock farm (dashed line) after control in August, food was constantly present between 4 and 22 months, but rats were denied easy access to it.

Habitats, such as field margins, which link the patches together support less dense, perhaps ephemeral populations that cannot be controlled cost-effectively and hence are usually ignored. Removing hedgerows and filling ditches might isolate patches, but would conflict with current initiatives to enhance biodiversity by restoring lost hedgerows. The alternative is to intercept animals in transit by creating an artificial resource-rich patch that will attract them, rather than wait for a chance encounter with a trap or bait point. Once there, they can be removed by any humane method. This strategy is similar to the trap–barrier system developed to control rats in the tropics (Singleton et al. 1999). If successful, this strategy would both attract dispersing rats before they settle in farm buildings and also reduce connectance between local populations, perhaps making eradication over large areas feasible. Such an approach would be especially useful in combating anticoagulant resistance and thus needs to be evaluated as a practical management strategy for whole rural rat populations.

Conclusions

New rodenticides are unlikely to be developed in the foreseeable future that will alleviate all public concerns about humaneness and non-target effects. In the meantime, current formulations will continue to be used until either resistance in the target species or restrictions on their use lead to product withdrawal. A more strategic application of rodenticides, along with other measures, has been suggested above that takes account of the potential mobility of rats and the ability of populations to recover when resources are seemingly unlimited. If effective, the strategy should minimise re-application of rodenticides once established populations are brought under control, given that lowland agricultural environments in the UK will always be habitable by Norway rats. This should retain the effectiveness of rodenticides whilst also minimising potential adverse environmental consequences of their use.

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Managing rodent pests in households and food stores through intensive trapping

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Abstract. Field trials involving 1200 rural households from three villages (Pinda, Mutange and Mugaveia) in Mozambique were established to test whether intensive daily trapping inside household-level food stores could effectively reduce rodent pest populations. The species caught inside dwellings where food was stored were *Rattus rattus* [*alexandrinus*] and *Mastomys natalensis*. The proportion of each species caught varied among the three villages and over the 16-month duration of the trial. *R. rattus* was more abundant inside households in Pinda and Mutange; whereas *M. natalensis* was more abundant inside homes in Mugaveia. Pregnant females of both species were caught throughout the year, showing no clear breeding seasonality. Householders that trapped rodents inside their house on a daily basis were able to significantly reduce the level of infestation when compared with householders who did no rodent management. The level of population reduction among households in the same village was similar, but the degree of reduction significantly varied among the three villages. The average weight of *R. rattus* trapped inside households through intensive trapping declined by 40% when compared with those caught in households that did not intensively trap; however, no significant weight difference was noted in populations of *M. natalensis*. The population reduction caused by intensive trapping was maintained over the duration of the trial, and assessments of food stocks indicated that food remained in store up to 3 months longer, with loss assessments indicating savings of 30–40% when compared with households in which rodents were not controlled. The implications of these results are discussed in the context of implementing ecologically based rodent management strategies for poor rural communities in Africa.

Introduction

Ecological studies and the control of rodent pests in rural agricultural settings have largely involved the use of rodenticides (Makundi et al. 1999). However, especially in rural parts of Africa, there are several constraints to their use. Primarily, rodenticides are not affordable for the rural poor who are most affected by rodent pests. Even when rodenticides are widely available, they are often used inappropriately, leading to low efficacy and to health and environmental risks. Recently, there has been an increased effort to apply our understanding of rodent population dynamics to develop more ecologically based methods of rodent management (Singleton et al. 1999).

Most households in Mozambique traditionally store their food inside their dwelling for security and spiritual reasons. However, this storage practice makes it difficult to exclude rodents from the food store, exacerbating food losses and contamination caused by rodents. Rural extension programs have tried to introduce separate food storage structures to the area, but adoption and uptake have been limited. Farmers in Zambezia province have indicated that stored food losses by rodents can be severe and have prioritised rodent pests as one of their most important constraints to improving their livelihoods (Taylor and Phillips 1995). In addition to food losses, recurrent outbreaks of plague (*Yersinia pestis*) occur in parts of Mozambique, and preliminary studies have shown that leptospirosis (*Leptospira icterohaemorrhagiae*) prevalence (IgG) can be as high as 17% (Thompson et al. 2002).

The development of ecologically based rodent management strategies that are affordable and easily implemented by the rural poor of Africa could substantially improve public health and local economies. The objectives of our research have been to test management strategies that attempt to reduce rodent pest problems in rural areas. Although some researchers have argued that trapping is an ineffective means of population management (Buckle and Smith 1994), previous research has shown that trapping can, under some circumstances, be an effective method of rodent management in field crops (Gebauer et al. 1992; Tobin et al. 1993) and grain markets (Ahmad et al. 1995). In this paper, we test whether trapping can significantly reduce local populations under the high density of rodents found in household-level food stores in Mozambique.

Materials and methods

Three villages in different districts of Zambezia province, Mozambique, were selected for involvement in the trials based on reports from farmers indicating that rodents were a significant pest problem, particularly after harvest when crops are stored within the dwelling. The village of Mutange in Namacurra district lies within a flat lowland rice-growing area, the village of Pinda in Morrumbala district is in a highland plateau maize-growing area and the village of Mugaveia in Gurué district is in a mountainous mixed forest–cropland area. Each village has approximately 400 domestic dwellings which typically consist of a mudded timber-frame rectangle (approx. 4 × 5 m) with a grass or palm-leaf thatched roof. The open-plan interior contains a raised platform where food is stored, a cooking fire and a sleeping area for approximately eight people.

Each village was divided into two portions, one half acting as the treated area and the other as the untreated area (experimental control). The 200 households in the treated area were each given 10 break-back traps (big snap-e-trap™, Kness Manufacturing Ltd, USA), with all 10 traps placed in the dwellings along interior walls and walkways, especially in places where food is usually stored. Farmers were given individual training on the operation of the traps and instructions to set them each evening. Dwellings in the treated area of the three villages were visited each morning, and the number of rodents trapped the night before were recorded daily for the duration of the trial (November 2000 to March 2002). Householders in the untreated area did nothing to manage their rodent problems over this time, and every month a subset of 30 households was randomly selected from this area and the occupiers set traps in the same manner as in the treated dwellings but over three nights only. The number of rodents caught during these three nights from households in treated and untreated areas was recorded, including their sex, weight, species, and whether any females caught were observed to be pregnant. Representative samples of each species were collected for later taxonomic identification. The number of rodents caught among farmers and villages was analysed by analysis of variance (ANOVA) with a post-hoc least significant difference (LSD) test to separate the mean values. Comparisons between treated and untreated areas in the same village were analysed using an independent sample *T*-test evaluating the number of rodents caught and their average weights. The potential interactions between populations of *R. rattus* and *M. natalensis* within each village were evaluated by linear and non-linear regression models using the data obtained on the total number of each species caught in each household during the trial.

A subsample of 10 randomly chosen farmers in each treated and untreated area in Pinda was selected to store 5 kg of their maize cobs in an open-topped basket. The basket of commodity was placed in the same area of food storage as the main household stocks over the usual storage period (May to December 2001), and householders were instructed not to remove any cobs from the basket. The baskets were weighed every 4 weeks from May to December 2001. Maize cobs were assessed for rodent damage by counting the number of missing maize grains on 10 randomly chosen maize cobs from each basket every 4 weeks and calculating the percentage of missing grains per cob. Data from treated and untreated areas were evaluated using the non-parametric Mann–Whitney *U*-test.

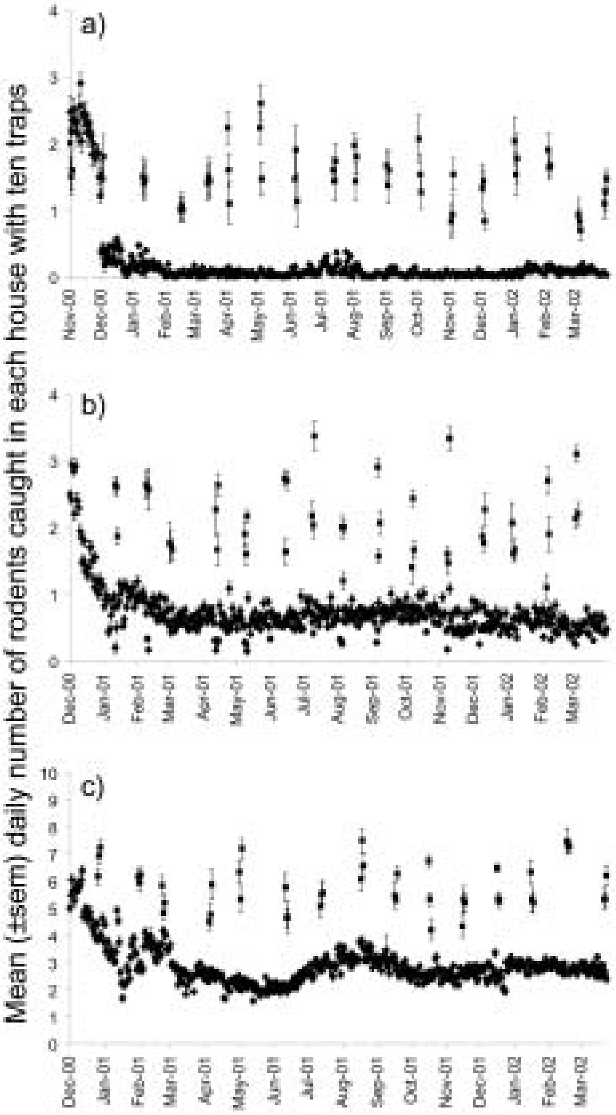

Figure 1. Comparison between the mean number of rodents caught by householders setting ten break-back traps each night (treated = ◆, $n = 200$) and householders that did no rodent management, but where a sample of rodents were trapped over three nights each month from a different sub-set of houses (untreated = ■, $n = 30$) in the villages of a) Pinda, b) Mutange and c) Mugaveia.

Results and discussion

The mean daily catch rate by each householder continuously trapping significantly varied among farmers in the same village (ANOVA with LSD, $P < 0.01$) and among the three villages (ANOVA with LSD, $P < 0.01$).

However, the daily number of rodents caught in households in the same village was relatively similar compared with the numbers caught among the three villages (Figure 1). Higher numbers of rodents were caught during the first month of intensive trapping in all three villages (2.47 ± 0.05, 1.24 ± 0.04, 3.98 ± 0.07 rodents/day/dwelling (mean ± sem) in first 30 days of trapping in Pinda, Mutange and Mugaveia, respectively) when compared with the number of rodents caught in subsequent months (ANOVA with LSD, $P < 0.01$). The decline in the number of rodents caught was most pronounced in Pinda, where relatively few rodents were caught after the first month (0.08 ± 0.002 rodents/day/dwelling over the next 15 months of the trial), followed by Mutange and Mugaveia (0.66 ± 0.006 and 2.78 ± 0.01 rodents/day/dwelling, respectively). The two species, *Rattus rattus* and *Mastomys natalensis*, were present in all three villages and were trapped inside all households (Figure 2). Approximately equal numbers of *R. rattus* and *M. natalensis* were caught in households in Pinda and Mutange, however approximately three times more *M. natalensis* were caught than *R. rattus* in Mugaveia. Linear and non-linear regression analyses showed that the relationship between the number of each species caught within a dwelling was best represented by power regression models for data from Pinda ($F = 215.7$, $r^2 = 0.52$, $P < 0.01$) and Mutange ($F = 176.5$, $r^2 = 0.47$, $P < 0.01$). In these two villages, higher numbers of *R. rattus* were associated with higher numbers of *M. natalensis* (Figure 3). Regression analysis on the data from Mugaveia showed that the relationship between the two species was best represented by a cubic polynomial regression model ($F = 5.15$, $r^2 = 0.42$, $P < 0.01$). The number of each rodent species caught in households in Mugaveia indicated that high numbers of *R. rattus* may regulate the numbers of *M. natalensis* present inside dwellings in this village (Figure 3).

Households within each area of the three villages where continuous trapping did not occur (untreated control) were shown to have greater numbers of rodents inside their houses at each of the 3-day monthly assessments when compared with those where trapping was carried out daily (*T*-test with equal variance not assumed, $P < 0.01$, Figure 1). These households caught approximately twice as many rodents throughout the trial (Figure 1). On average, householders in the untreated area of Pinda caught 1.49 ± 0.26 rodents/day throughout the 16-month trial duration, with 2.11 ± 0.17 and 5.80 ± 0.35 rodents/day caught in Mutange and Mugaveia, respectively. On average, the weight of *R. rattus* caught in untreated dwellings was significantly higher than that of the same species caught in treated dwellings (75.3 ± 1.6 g and 45.9 ± 2.0 g, respectively, *T*-test with equal variance not assumed, $t = 7.46$, df = 30.5, $P < 0.01$). However, there was no significant weight difference between the corresponding samples of *M. natalensis* (untreated = 52.3 ± 3.2 g, treated = 46.5 ± 3.3 g, *T*-test with equal variance not assumed, $t = 1.15$, df = 31.1, $P > 0.05$). No significant differences were noted with respect to changes in the sex ratio of rodents caught between treated and untreated dwellings (Mann–Whitney *U*, $P > 0.05$).

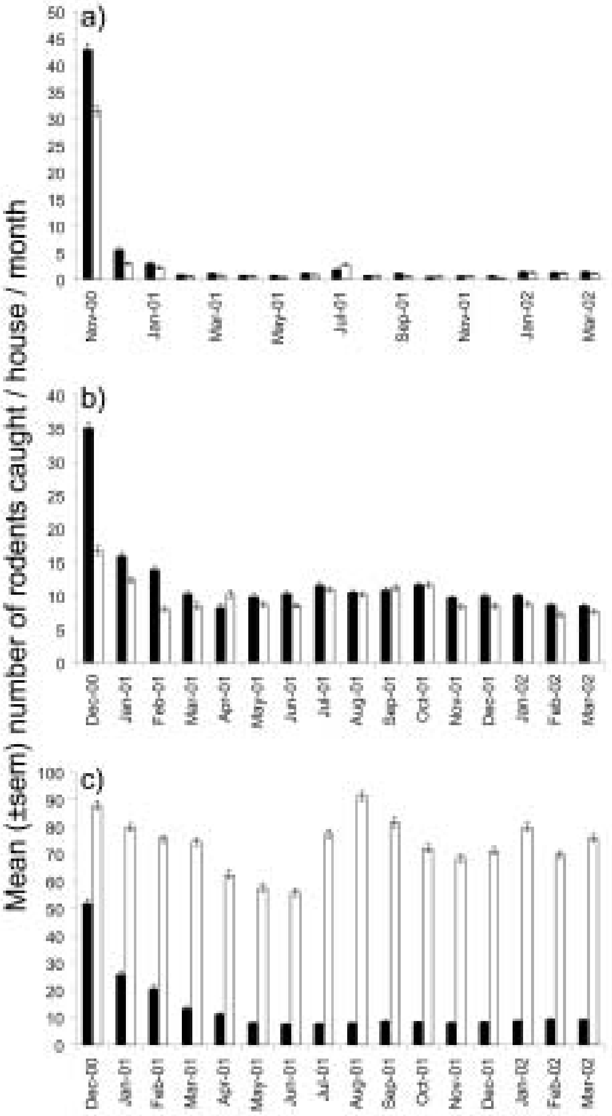

Figure 2. Comparison between the mean number of *Rattus rattus* (■) and *Mastomys natalensis* (❏) caught inside 200 dwellings in traps set by householders each night in the villages of a) Pinda, b) Mutange and c) Mugaveia.

Weight loss of the standard 5 kg baskets of maize was attributed to both rodent and insect damage (Table 1). The main insect pest found in stored maize cobs was the maize weevil, *Sitophilus zeamais*. Damage characteristics to maize caused by insects and rodents are very distinctive, with rodents completely or partially removing grains from the cob, whilst weevils infest grains internally. All missing grains on cobs were attributed to rodent pests. Rodent damage was observed to occur from the outset of the assessment period, whereas weevil damage only became apparent after three or more months of storage. Damage due to rodents was lower in dwellings that intensively trapped compared with dwellings in the untreated areas, while insect damage levels were similar between treated and untreated dwellings. Questionnaires with farmers in the treated and untreated areas of the village indicated that householders that had been intensively trapping maintained stocks of food for approximately 3 months longer than householders in the untreated area. Farmers that trapped also noted that their food stocks lasted longer when compared with previous years when harvested yields were similar.

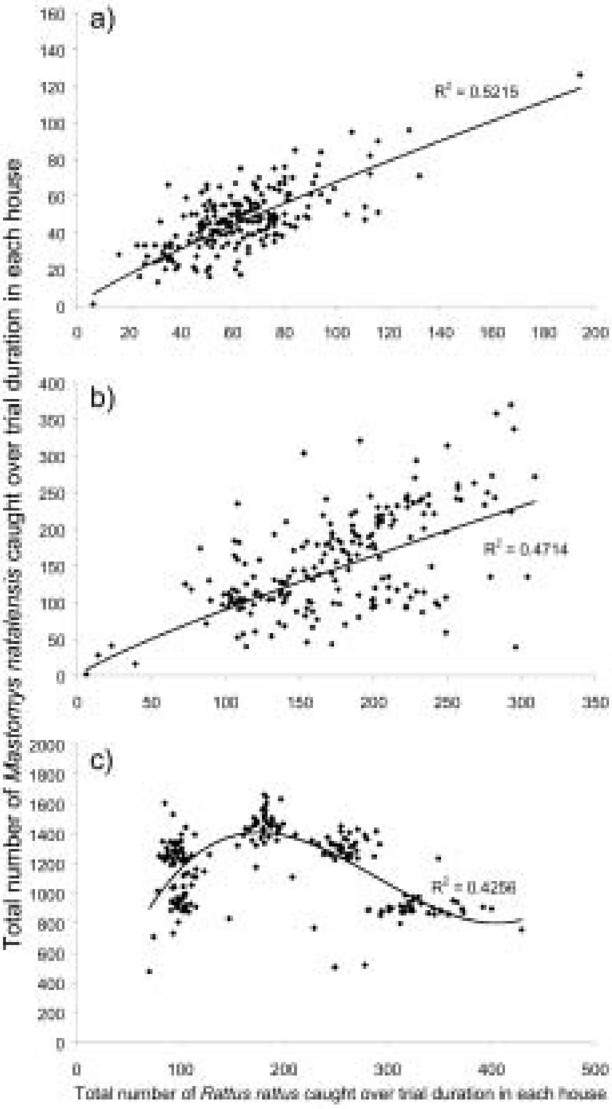

Figure 3. Relationship between the total number of *Rattus rattus* and *Mastomys natalensis* caught inside each dwelling, trapped on a daily basis in a) Pinda, b) Mutange and c) Mugaveia. Regression analysis indicated that data obtained from Pinda and Mutange were best represented by non-linear power models, whereas a cubic polynomial model best represented the data obtained from Mugaveia.

Conclusion

Our study showed that intensive trapping of rodents can effectively reduce their localised population densities within rural African dwellings. Although trapping is labour-intensive, the relatively low cost of inputs and the benefits accrued to the family unit could favour the technique. Household benefits not only included reduced food storage losses as demonstrated in this study, but as rodents are widely eaten by people in Zambezia province, household trapping was seen to provide families with a reliable source of much-needed protein.

At the commencement of the intensive trapping trial, it was not known whether rodent population densities would vary among dwellings or areas. However, it was considered likely that rodent density would be generally dependent upon food availability in the dwelling (Boutin 1990; Krebs 1999). Food stores provide an ideal environment for rodents, offering harbourage and a relatively unlimited food supply. Although building structures and food storage practice were similar in all three villages, there were marked differences in the number of rodents caught among the three villages, the relative abundance of species and in the efficacy of the trapping regime. These differences among the three villages must be related to factors outside the household and to the differing habitats and ecology found in the localities (Ferreira and Aarde 1999). There are two observations that are likely to contribute to these differences. In all three villages, *R. rattus* made nests in the roof thatching of the dwelling, while *M. natalensis* lived in burrows in the fields. Our research on the field trapping of rodents in the area (to be reported elsewhere) indicates that *R. rattus* is very rarely trapped in the bush or in farmers' fields, and the species appears to be predominantly confined to areas of human settlement. Our research would support this difference in nesting behaviour between the two species because *R. rattus* populations appeared to be more susceptible to the trapping program inside dwellings. A second factor likely to be important in explaining the observed differences among the villages is the relative distance between dwellings in the village. Buildings in the village of Pinda were relatively close to each other (50–200 m), whereas buildings in Mugaveia were farther apart (500–1500 m). Our results would suggest that *R. rattus* populations are higher when villages are relatively densely populated, and *M. natalensis* are more prevalent in villages where houses are isolated from each other. In a village such as Pinda, intensive trapping on a community level could have a greater impact because rodent immigration/emigration is reduced and *R. rattus* immigration from the bush will be slow. In a village such as Mugaveia, immigration of *M. natalensis* from the surrounding bush is unaffected by community trapping, and trapping may be relatively less effective in modulating household rodent density. This needs to be tested.

Despite the observed differential efficacy achieved among the three villages, intensive trapping with 10 traps did constrain populations when compared with untreated dwellings in the same area. This was reflected in reduced capture rates and the reduced average rodent weight of *R. rattus* in treated dwellings. A reduced average weight could indicate changes in age structure arising from reduced survival. However, it could be argued that both of these factors are explained by the development of trap-shy animals.

As commonly suggested, long-term development of neophobia could result from an intensive trapping regime

Table 1. Comparison between the cumulative percentage weight loss and percentage damage to 5 kg of maize cobs stored in baskets over 8 months inside dwellings in the village of Pinda where rodents had (treated) or had not (untreated control) been intensively trapped daily ($n = 10$).

Assessment period (2001)	Weight loss (%) (mean ± sem)		Rodent damage (%) (mean ± sem)		Insect damage (%) (mean ± sem)	
	Treated	Untreated	Treated	Untreated	Treated	Untreated
May	0	0	0	0	0	0
June	2.5 ± 0.04	3.1 ± 0.17	0	1.5 ± 0.03	0	0
July	3.6 ± 0.09	5.1 ± 1.23	0.5 ± 0.01	2.8 ± 0.02	0	0
August	4.1 ± 0.15[a]	12.8 ± 3.07	0.5 ± 0.08[a]	3.4 ± 0.95	0	0.5 ± 0.07
September	8.2 ± 0.96[a]	16.5 ± 3.40	1.4 ± 0.13[a]	6.7 ± 1.26	2.0 ± 0.56	2.8 ± 0.77
October	11.0 ± 1.11[a]	28.3 ± 5.67	3.3 ± 0.77[a]	10.9 ± 3.55	3.1 ± 0.79	3.5 ± 0.92
November	17.0 ± 3.55[a]	46.1 ± 5.45	5.5 ± 0.65[a]	25.0 ± 4.58	9.2 ± 2.32	10.1 ± 2.01
December	18.9 ± 4.15[a]	54.7 ± 5.08	5.8 ± 1.95[a]	28.3 ± 3.83	11.7 ± 2.38	12.3 ± 2.18

[a] Treated value is significantly different from the untreated value (Mann–Whitney *U*, $P < 0.01$).

(Mathur 1997). As well, smaller size could indicate better survival of young animals with the removal of older animals, or better breeding performance—i.e. the population is compensating.

The two species trapped, *R. rattus* and *M. natalensis*, are known to occur in other parts of eastern and southern Africa (Fiedler 1988). *M. natalensis* is a known carrier of plague (Gratz et al. 1997), and its foraging inside dwellings could increase the risk of human infection. Although much higher numbers of *M. natalensis* were caught in Mugaveia, plague outbreaks are relatively uncommon there, whereas plague cases are recorded nearly every year in Pinda. The degree of interaction between *R. rattus* and *M. natalensis* in these environments is unknown, and the pathways of plague transmission could be complex with infected fleas moving between populations of *M. natalensis* and *R. rattus* in and around human settlements (Mills and Childs 1998). Villagers in all three areas consumed rats as a significant part of their diet. Plague bacilli are known to survive for several days on dead rodents (Liu 1991), and thus the handling and preparation of rodents for food could result in plague transmission. As the trapping program increases the number of dying rodents within dwellings and the handling of dead rodents, it is possible that such a strategy could increase plague incidence within the locality. Using multi-catch live-traps instead of break-back traps may offer a way to reduce plague-infected fleas from remaining inside the dwelling. Further research is planned to determine anthropogenic and interspecific factors that impact upon plague outbreaks. Other rodent-borne zoonoses have been recorded in the area, particularly leptospirosis (Thompson et al. 2002), and research is planned to determine how zoonosis transmission could be affected by intensive trapping inside rural dwellings.

Losses of stored food to rodents were reduced significantly by the intensive trapping. As the baskets of known quantity were placed on top of the household food store, the observed losses in the basket could be an overestimate of the total rodent loss to the overall food store in the dwelling. Some of the observed weight loss is due to a reduced moisture content of the maize as the dry season progresses, particularly in the first 3 months of storage. However, relative comparisons between households in the treated and untreated areas of the village indicate that rodent pressure on the food store was considerably reduced by intensive trapping because relative weight loss and rodent damage was reduced. Questionnaires with farmers indicated that the effects of trapping were noticeable, as the stored food lasted longer than usual, particularly so in the most food-insecure households which normally do not produce enough to meet their household requirements. Other benefits were also noted by farmers, notably a regular supply of rat meat and fewer rat bites to family members.

In conclusion, intensive trapping is likely to be part of any integrated and ecologically based rodent control strategy for rural dwellings in these areas of Mozambique. Further research is required to determine the optimal number of traps needed to effectively modulate rodent populations given particular habitat and population parameters. Studies on the population responses of the two species at a landscape level also are required to understand possible compensatory responses and routes of reinvasion. The cost–benefits of trapping need to be more adequately understood in order to inform and encourage rural communities and agricultural extension programs to adopt trapping as part of an ecologically based rodent management program.

Acknowledgments

The authors are grateful for the taxonomic expertise of Margaret Hills from the Natural History Museum, United Kingdom (UK), who identified all rodent species from field-collected specimens. This research was funded by the UK Department for International Development (DFID) through their Crop Post-Harvest Programme and

Zambezia Agricultural Development Programme. The views expressed are not necessarily those of DFID.

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Urban commensal rodent control: fact or fiction?

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Abstract. United Nations' predictions on urban development over the coming 30 years indicate that some 2.1 billion extra people will be living in urban areas by 2030. The increase will be most significant in less developed regions.

Any explosion in urban development will favour commensal rodents. The increase will be most significant in those areas least able to cope with the consequences of urban explosion, where refuse, sewage and low housing quality will particularly favour their development. Such increases in rodent populations will bring with them increases in the risks of disease transmission, rat bites and structural damage and contamination of the human environment.

The efficacy of effectively applied proactive rodent control programs has been clearly demonstrated. Yet, resources for such proactive work are being withdrawn in favour of less effective and poorly targeted reactive strategies. This trend must be reversed. The collection of sound data on the costs (financial and social) of rodent infestation, rather than the efficacy of proactive rodent control (which has been clearly demonstrated) must assume a priority. The cost–benefits of proactive rodent control must be clearly demonstrated.

Introduction

Commensal rodents live in particularly close association with people, by all accepted definitions—they 'live off man's table'. In fact, the name suggests a happy and almost symbiotic relationship, an image that is very far from the truth. Their relationship with humans would perhaps better be termed 'cleptoparasitic'. In their wild state, rodents effectively 'steal' from humans and the adverse effects of their presence are significantly detrimental, with people rarely benefiting. The commensal rodents that we find in urban areas make a very good case for being parasitic on people!

With some 2000 rodent species found worldwide, there are in fact very few true commensals. Lund (1994) restricted his list to: the Norway rat (*Rattus norvegicus*), the ship rat (*Rattus rattus*) and the house mouse (*Mus* spp.), all distributed worldwide; the multimammate rat (*Mastomys natalensis*), in Africa; the lesser bandicoot rat (*Bandicota bengalensis*), in central Asia; and the Polynesian rat or the Burmese house rat (*Rattus exulans*), in the Pacific and Asia. There may be a case for including other locally abundant species in this list, but the numbers of species remains relatively small.

None of these species, of course, evolved within urban environments—the development of urban environments suits their ecological requirements and they are very good at exploiting the urban opportunity! They have thrived as urbanisation has thrived and there is no reason for us to suppose that anything will change in the future. Thus any consideration of the future of commensal rodent control must start with a review of the future of urban areas. Are we likely to be creating more of the habitats within which these species will thrive?

The answer is well documented within the *World Urbanization Prospects: The 2001 Revision*, prepared by the United Nations Population Division (UNDP 2001). The conclusions for urbanisation include:

- The world's urban population reached 2.9 billion in 2000 and is expected to rise to 5 billion by 2030. Whereas 30% of the world population lived in urban areas in 1950, the proportion of urban dwellers rose to 47% by 2000 and is projected to attain 60% by 2030. At current rates of change the number of urban dwellers will equal the number of rural dwellers by 2007!
- Virtually all the population growth expected at the world level during 2000–2030 will be concentrated in urban areas. During that period the urban population is expected to increase by 2.1 billion people.
- Almost all the population growth expected at the world level during 2000–2030 will be absorbed within the urban areas of the less developed regions whose populations will likely rise from approximately 2 billion in 2000 to just under 4 billion in 2030.
- The process of urbanisation is already very advanced in the more developed regions, where 75% of the population lived in urban areas in 2000. Nevertheless, the concentration of population in cities is expected to increase further so that, by 2030, 83% of the inhabitants of the more developed countries will be urban dwellers.

- The level of urbanisation is considerably lower in the less developed regions, where 40% of the population lived in urban areas in 2000. This proportion is considerably higher than it was in 1950 (18%) and is expected to rise substantially to reach 56% by 2030.

If you are a commensal rodent, your future is assured. More importantly, for those involved in rodent control, are we able to control them?

What can we learn from history?

The levels of infestation that will be reached will depend upon the conditions in the specific conurbations—the poorer the conditions, the higher the levels of infestation.

Ideal conditions for the development of commensal rodent populations are provided by the increasing availability of food and water sources and, of course, harbourage within which the rodents can live. Thus, exploding human populations can provide increasing availability of these resources because the city and town amenities and the town planning authorities are unable to cope. Rubbish and waste is not efficiently removed, water and sewage facilities are not developed and maintained, and housing quality is poor and develops without the benefits of planning.

All these characteristics are likely to lead to ideal conditions for the rodents and significant rodent populations. There is clear evidence that levels of commensal rodent infestation are determined by the quality of the environment (Meyer 1978). Surveys undertaken in Amman in Jordan, showed that 79% of the variation in Norway rat infestation levels between the different housing types could be accounted for by differences in the levels of hygiene.

Perhaps Europe is the best guide to what may happen elsewhere in the world over coming decades. Table 1 shows how European urban populations have stabilised ahead of most other areas of the world. Indeed, over 50% of Europeans were living in urban areas by 1950.

The history of Europe demonstrates that during the periods of rapid urban growth, particularly when this was associated with poor urban areas with little or no urban facility management, rodent populations thrived. They did this to the extent that some 50% of the European human population died from rodent-borne diseases in the Middle Ages, specifically the plague and rat typhus. The human populations were living in very close contact with the rats that inhabited their dwellings, much as many developing urban populations do today and are likely to increasingly do so in the future.

In these early days, most rodent control would have been by rat catchers working for individual customers. However, there is evidence that city-wide or town-wide attempts were made to control rats. The fable of the *Pied Piper of Hamlyn* in Germany being an example of centralised rodent control! It was probably not until the 19th century, and even more so in the 20th century, that rodent control operations began to be handled on a national basis. In the United Kingdom, for instance, it was not until the Rats and Mice Destruction Order in 1919 that rodent control was to any extent centralised. Even then, the progress was probably very limited, largely due to the absence of any sound scientific information on the ecology of the target commensal rodent species. In addition, the techniques (largely trapping and the use of the acute rodenticides) available at the time were not very efficient and difficult to apply in urban areas.

Urban rodent control is more difficult than in other, less-densely populated rural areas. The higher and denser the human population, the more difficult it is to gain the cooperation of that population and the more difficult it is to gain access to the habitats within which the rodents are living, because the habitat is compartmentalised.

It was not until the middle of the 20th century that science was first effectively applied to commensal rodent control. At this point, the Bureau of Animal Population at the University of Oxford in England was given the specific remit to research effective techniques for control-

Table 1. Percentage (%) of world populations living in urban areas, 1950–2030. (Source: UNDP 2001.)

Region	Year				
	1950	1970	1990	2000	2030
World	29.8	36.8	43.5	47.2	60.2
More developed	54.9	67.7	73.7	75.4	82.6
Less developed	17.8	25.1	35.0	40.4	56.4
Africa	14.7	23.1	31.8	37.2	52.9
Asia	17.4	23.4	26.9	37.5	54.1
Europe	52.4	64.6	72.1	73.4	80.5
Latin America & Caribbean	41.9	57.6	71.1	75.4	84.0
Central America	39.8	53.8	65.7	68.2	77.1
South America	43.6	60.2	74.4	79.6	87.9
North America	63.9	73.8	75.4	77.4	84.5

ling commensal rodents. The Bureau undertook much basic research on rodent control, developing many improved strategies for using the available control techniques. Perhaps their most lasting legacy, however, was to start to identify, for the first time, the key elements relating to the population dynamics of the three main commensal species.

The research indicated that breeding success was a key element in the survival strategies of the rodents. This research was complemented by parallel research in the United States of America (USA) by Davis and colleagues. Knowledge relating to this and to their behaviour patterns helps us set very basic objectives for our control operations today (see Krebs 1999 for review). These studies in the United Kingdom (UK) and the USA highlighted that strategies need to be developed that achieve levels of mortality in excess of 80%. In addition, the target must be to reduce the carrying capacity of the urban areas by developing effective environmental management techniques.

The 50 years following this research not only led to much further research carried out worldwide on the techniques for urban rodent control, but also to the development of strategies designed to use the results of the research as effectively as possible.

Strategy development

There are, practically, three ways of approaching urban rodent control—‘**reactive**’ control; ‘**proactive**’ control; or a combination of the two. Both strategies have been applied in many parts of Europe and North America over the last 50 years and a brief review of both and their apparent efficacy is appropriate.

Reactive rodent control

Reactive pest control is particularly popular amongst politicians and other policy-makers. This is particularly true when considering those rodent control programs that are funded by local or central government. This is because reactive control essentially means that those with a rodent problem can request that something is done about it. If the work is being undertaken by a governmental organisation, the complainant reports an infestation, the work is done, and the complainant is satisfied that his/her concerns have been met.

A free rodent control service is most likely to reach those with an infestation and the more that payment is involved the lower the level of penetration (control) of the rodent population because people are less likely to respond to infestation. Clearly, the higher the level of the penetration of the problem, the more likely that overall levels of infestation can be reduced. Conversely, the lower the levels of penetration, the less impact that will be achieved.

Accepting that it would be ideal if everyone with a rodent problem did something about it, it would be useful to know what the level of active response is to a rodent infestation. There are few data available worldwide on this issue, although there are data from within the UK.

A survey was undertaken in 1993 (Meyer et al. 1995) involving the inspection of some 11,000 randomly-selected premises in England and Wales for rodent infestation. In domestic premises, about 20% of house mouse and about 30% of Norway rat infestations remained untreated. At this time, a free service for both house mouse and Norway rat infestation was provided by almost all local governments, and about 50% of house mouse infestations were reported to and were treated by local authorities. About 65% of Norway rat infestations were reported to the same local authorities. Owners and occupiers of premises claimed to be treating about 30% of house mouse infestations and about 10% of rat infestations. Contracted servicing companies were rarely used by domestic occupiers.

Thus, even with a free service, only about 50% of mouse infestations and 65% of rat infestations were being treated by professional technicians. There is evidence that as charges are introduced for these services the percentage of infestations that are reported decreases.

Even these figure provide an overly optimistic view of the effective levels of control, because the spatial limits of an ‘infestation’ will not necessarily coincide with the boundaries of the premises from which the report was received. Work in the London Borough of Lambeth (Meyer and Drummond 1980) on house mice showed that house mouse infestations were not randomly distributed; they were clumped (Table 2). Only 33% of those infested were single premise infestations—the remainder varied between two and six contiguously infested premises. If no proactive control were undertaken and only complaining premises were treated, it is unlikely than more than about 30% of infestations (with a 50% reporting level) would be eliminated by a reactive complaints based strategy. Treated premises within clumps would probably be re-infested from adjoining unreported and therefore untreated infestations, further reducing levels of efficacy.

As a part of the subsequent proactive control program, attempts were made to access all premises. About 39% of the occupied premises could not be surveyed during the normal working week and were surveyed at weekends. The infestation levels of those that were surveyed at weekends (house mouse 52% and Norway rats 7% infested) were higher than for those where weekday access was possible (house mice 29% and Norway rats 2% infested). Thus, in any proactive strategy, both work patterns and occupier activity profiles have to be kept in mind, or disproportionate numbers of infestations may be missed.

The overall conclusions of this work were that numbers of infested premises could be maintained at a level of over 90% lower through the application of proactive control, with only a marginal increase in costs.

It is also likely that reactive strategies may miss the proportion of the population that are most at risk from rodent infestation. If we accept that poor housing and poor environmental conditions encourage rodent infestation, then it is likely that highest rodent infestation levels will occur in those areas with the poorest housing (Meyer 1978). Those living in these areas will therefore also be at the greatest risk from rodent-borne diseases and rodent damage.

Table 2. Distribution of house mouse infestations within a block of terraced housing (428 premises) in the London Borough of Lambeth, United Kingdom.

Number of contiguously infested premises	Number of clumps	Total infestations (%)
1	45	33
2	23	34
3	4	9
4	4	12
5	1	4
6	2	8

A reactive strategy requires those who are experiencing a rodent problem to complain, in order to initiate a reaction! Those who are most likely to be aware that they can complain and those who are most able to complain—because they have access to a telephone or to transport or indeed to the time to complain—will be those in the higher rather than the lower housing categories. Those in the lower housing categories, who are effectively more at risk, are less likely to complain!

Thus, a complaints-based or reactive strategy is least likely to serve those at greatest risk, and is also unlikely to access sufficient of the infestations to have a significant impact on overall levels of infestation.

Proactive rodent control

The alternative strategy, proactive rodent control, enables resources to be targeted where risk is greatest and in a way that is most likely to achieve effective control. The question is, do proactive strategies work?

Large-scale programs to control rodents in urban areas have been undertaken in many parts of the world, particularly since the discovery of the association between rats and plague. Initially, they usually made use of traps, cyanide and zinc phosphide and usually employed too few resources to make much impact with these relatively inefficient control techniques.

The commercial development of the anticoagulant rodenticides in the early 1950s and their ready availability over the last 50 years provided an ideal catalyst for the application of proactive strategies.

The first attempt seems to have taken place in Lahti in Southern Finland in 1950 and over a period of 3 months some 5000 properties were systematically inspected and the 40–50% found to be infested were made rat-free. The rat problem then remained at an acceptable level by handing out free warfarin bait to householders (Myllymaki 1969). Similar programs were initiated in many towns in Lower Saxony in the 1960s, following pioneer work in Cuxhaven (Steiniger 1956). Unfortunately, although initial levels of infestation are recorded, there were no attempts to monitor progress through random surveys nor resurveys of treated properties.

One of the first attempts to develop an urban rodent control program on any scale—and at the same time to record the progress of the operations in some detail—was probably initiated in the town of Folkestone, on the south coast of England in the early 1960s (Drummond et al. 1977).

In New York State, proactive programs were carried out between 1969 and 1973 in some of the more rat-infested areas (an average of 24% of premises infested) (Brooks 1974). Brooks recorded not only the reduction in infestation levels but also a range of environmental factors and their management, which contributed significantly to the strategy. The work in New York was extended in Boston, USA in the 1990s. Here a comprehensive rat control program was introduced, designed to incorporate all the elements of an effective strategy identified in earlier work (Colvin 1990). The elements of much of this work as well as the concepts of urban rodent control are thoroughly summarised in a later paper (Colvin and Jackson 1999).

Perhaps the most comprehensive and long-term urban rodent control program has been undertaken in Budapest, Hungary. Here, a strategy applied and monitored over some 30 years has incorporated not only effective control strategies but also an analysis of the behaviour and habitat use of urban environments by rats (Bajomi 1983, 1993).

All these programs demonstrate the advantages of proactive rodent control. The later work in particular demonstrates that, when combined with effective environmental management, the strategies can be particularly effective.

If there is a criticism of many of them, it is that whilst they address the efficacy of the control operations, they do not address in the same detail the cost–benefits of such operations when compared with the reactive strategies discussed earlier. This is not only because the costs of the monitored programs are not well documented, but because there is an absence of good data throughout the rodent control literature on the real costs of rodent infestation. There is an abundance of data on the potential problems that rodent infestation can cause, in all its diversity—disease transmission, structural damage, contamination of food… the list is almost endless! But data on the collective costs of rodent infestation are almost totally absent! The question remains: What are the collective costs of heavy rodent infestations in urban areas?

The current situation

In the UK, in spite of all the evidence that proactive control is more effective at reducing rodent infestation than reactive control, the move to reactive control continues. It is cheaper and more politically productive. In the absence of good data on the real economic cost–

benefits of proactive control, to the community as a whole, the trend will continue.

Some years ago, the World Health Organization (WHO) ran a very effective unit advising on the control of rodents in urban areas. That unit no longer operates and there is little input from WHO to commensal rodent control.

In the UK, there is currently no central government department with responsibility for rodent control in urban areas, the Ministry of Agriculture having withdrawn support in the early 1980s. Local authority responses, whereas once very much proactive, are now almost entirely reactive, with resources being withdrawn and indeed increasingly minimal efforts are being made to address the urban rodent problem in any effective strategic sense.

In the USA, “technical support for urban rodent control is very limited. Active research programmes do not exist on the federal, state or university levels. Most States and municipalities have limited knowledge and skill in urban rodent control, resulting in limited effectiveness when programmes are implemented. Most efforts by local authorities are reactive.” (Colvin and Jackson 1999)

Conclusion

The almost universal withdrawal of resources for proactive urban rodent control is a product of pressures on financial expenditure. The cost–benefits of applying proactive control are not apparent.

Risk assessments require data on the real costs of rodent infestation in all their infinite diversity. The priority for the future must be to clarify these risks and their associated costs.

The predicted increases in human urban populations provide an opportunity for the commensal rodents such as they have never had before. The technology for the control of these urban rodent populations is available. It is essential that over the coming few years priority be given to identifying the cost–benefits of proactive rodent control. Failure to do so may allow the rodents to demonstrate all too clearly the costs of failure.

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Adapting baiting tactics to match the foraging behaviour of Norway rats: a balance between efficacy and safety

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Abstract. The need to protect rodenticide baits from non-target animals is self-evident, but too much protection can impede control if it stops rodent pests from expressing their natural foraging behaviour, which has evolved to maximise food gain and minimise the risk of attack. One element of foraging is how long individuals are prepared to remain at food sources, which during control operations include rodenticide baits. The duration of visits by wild Norway rats to plain baits placed in burrows and boxes was measured under semi-natural and field conditions. Median visit length in the field to burrows was 12 s (n = 1304 visits) and to a box 17 s (n = 1272), a difference unlikely to be biologically significant. Such short visits are likely to result in bait transfer in which bait particles are removed from secure locations by individual rats and taken anywhere to be eaten or abandoned. However, 80% of visits to the box were ≤145 s and to burrows ≤42 s and under semi-natural conditions rats feeding in groups on whole wheat stayed longer in boxes than those that fed alone. Longer feeding bouts probably minimise the likelihood of bait transfer. To maximise efficacy, containers should therefore be open enough to allow several rats to feed together, a feature not present in some commercial products on grounds of safety. Bait transfer can, however, be used to familiarise rats with a formulation type, such as a wax block, that they have difficulty recognising as edible, especially when it is held securely inside a box to prevent it being removed and eaten by other animals. In the field, the bait that rats are allowed to transfer should not, of course, contain a rodenticide.

Introduction

Despite widespread concern about the impact on wildlife populations of rodenticide use, no cost-effective alternative means of quickly controlling Norway rats (*Rattus norvegicus*) is currently available in the United Kingdom, and thus rodenticides are likely to remain the means of first choice when an infestation needs to be controlled. However, recognising the potential risk that may arise, the pest control industry has designed bait containers that make it difficult for animals larger than rats to gain access to the bait—described at 'tamper-resistant'—and has developed formulations that are supposedly less likely to be eaten by non-target animals. One such formulation type is the wax block, which is apparently relatively unattractive to birds (Johnson 1988). While such baits are generally thought to be relatively unattractive to rodents also, a degree of unpalatability might be countered with a highly potent rodenticide (Buckle 1994).

In an intensive study of the efficacy of anticoagulant treatments, loose-grain baits were applied for up to 7 weeks in wooden bait boxes. The results showed that the main reason rats survived treatment was that they ate little or no bait (Quy et al. 1992). The number that survived in each case varied from a few individuals to almost the entire population. The presence of alternative food, particularly stored cereals, notably 'prevented' rats consuming lethal quantities of bait. However, applying the same baits directly into rat burrows overcame any apparent reluctance to feed on bait presented in boxes (Quy et al. 1996). Unfortunately, baiting burrows is not always possible as active burrows are sometimes difficult to find and uneaten bait is not easily recoverable. On grounds of safety, therefore, a protected bait container seems desirable but it has long been recognised, and shown experimentally, that any kind of bait container appearing as a novel object to rats is likely to be avoided at first (Inglis et al. 1996). To allow rats time to overcome their initial wariness of new objects, empty containers have been put out several days in advance and then rat activity has been monitored during the treatment to distinguish baits that remain uneaten because they are misplaced from those uneaten because rats are still reluctant to approach the container (Quy et al. 1994). It became apparent during such monitoring that a third category existed, namely, boxes that were entered by rats which then ate little or no bait, regardless of how palatable the bait had seemed to be during laboratory tests. During some treatments, the majority of baits fell into this third category. To rats, baits are potential food sources and the strategies they use to find, approach and finally eat their usual foods should apply to these also. A more detailed knowledge of these strategies might enable the tactics deployed during rodenticide treatments to be modified to achieve control more quickly without compromising the safety of other animals.

There have been few accounts of the foraging behaviour of free-living rats when new food sources are introduced into their environment. Rats seem prone to transport food and, according to optimal foraging theory, they do so to minimise the risk of predation while maximising food gain. Indeed, the likelihood of bait transfer has provoked manufacturers to mould wax block baits, which weigh about 20–30 g, with a central hole so that they can be secured on a rod inside a bait box and hence cannot be carried away. Rats that transfer bait may subsequently eat it, cache it or abandon it, but do not appear to deliberately give it to another rat. It has been suggested that rather than minimise predation risk, transfer occurs in order to avoid conspecific aggression (Whishaw and Whishaw 1996). Thus, small rats are particularly prone to make frequent brief visits to food sources to collect particles, which may or may not subsequently be stolen by other rats that find the cache.

In this study, we have attempted to answer three questions: (1) because all rats are likely to transport food, how long will individuals be prepared to stay at a food source (i.e. bait point) if they cannot take particles away; (2) is the apparent success of burrow baiting over container baiting due to rats feeling safer when feeding close to where they presumably nest, so making risky foraging trips unnecessary; and (3) under what circumstances would rats be prepared to stay long enough at a distant bait point, so that if rodenticide baits are introduced, relatively little is carried away and the rate of bait uptake is sufficiently high to minimise poison bait exposure periods while ensuring effective control?

Materials and methods

Field trial

Rat activity at baited burrows and a bait box was recorded on a farm in North Yorkshire, United Kingdom (UK), between April and May 1997. The farm buildings were used mainly for storage and the site was therefore relatively undisturbed. Rats were present in and around the buildings and along a ditch that ran parallel about 10 m away. The ditch, which was about 1.5 m deep and 2.4 m wide at the top, had shallow pools of water intermittently along its length. Eight active rat burrows, identified by well-padded soil and lack of debris in the entrances, were found along a 74 m long section. The distance between one burrow and the next one varied from 2–18.7 m. (There were other active burrows along the same section that had too small an entrance or were too close to the ditch bottom and thus liable to be flooded.) A tube, 60 mm long with internal and external diameters 80 mm and 107 mm, respectively, was pushed into each of the 8 burrows until it was flush with the entrance. Care was taken not to damage the walls of the burrow as the inhabitant might then abandon it. The tube was made of a hard resin, which encased a detector designed to energise and receive signals from a passive integrated transponder (PIT tag). A PIT tag lying along the central axis was detectable not more than 50 mm beyond the end of the tube. An armoured cable carried the signal from the detector to a reader unit and then to a four-channel data logger (Francis Scientific Instruments, Cambourne, UK) up to 20 m away. Two loggers were needed to monitor activity at the eight burrows. The bait box was 360 mm (l) × 260 mm (w) × 140 mm (h) and made of marine plywood, but had a metal lid. Entrances at both ends were 70 mm × 70 mm and an internal baffle 25 mm high prevented bait spilling out. Two square-section tunnels (plastic drainpipe), 320 mm × 76 mm × 76 mm, were attached to each side of the box. Each tunnel was fitted with two PIT tag detectors 300 mm apart and was protected by a wooden case designed to be compatible with the bait box. The signals from the four detectors were relayed to a four-channel data logger via cables of 20 m in length. Each data logger channel was time synchronised so that the direction of movement could be determined from the time stamp recorded with the PIT tag identification. Twelve-volt car batteries powered the loggers and detectors.

Nineteen rats (9 males, 10 females) were live-trapped and each animal was lightly anaesthetised with isoflurane before a Sokymat® PIT tag, encased in a biocompatible glass tube 12 mm (l) × 2 mm (d), was injected subcutaneously between the shoulder blades along the line of the spine. Each animal was sexed and weighed and was released at its point of capture when it had fully recovered. Of the 19 rats, 6 were juvenile (<100 g) and the adults weighed 280–620 g. On the first day of the trial, 100–200 g of bait was placed into each of the eight burrows just beyond the end of the detector tube so that it could be easily seen. The bait consisted of pinhead oatmeal (92.5% w/w), caster sugar (5% w/w) and corn oil (2.5% w/w). A chemical bait marker (decachlorobiphenyl) was dissolved in the corn oil to give a final concentration in the bait of 0.01% (w/w). The baits were inspected daily for 10 days, the take at each burrow being recorded as partial or completely eaten and the bait replenished to maintain a surplus until the next inspection—although the amount that could be laid was limited by the capacity of the burrow. The data loggers recorded visits by tagged rats to the burrows every day. On day 10, the bait box was placed on a rat run along the bottom of the ditch. The box was sited at one end of the 74 m section where it was dry: the furthest logged burrow was 58.9 m away and the closest 4.3 m away. The box was baited with initially 500 g of the pinhead oatmeal bait; any uneaten bait remaining in the burrows was removed and replaced with a 1:1 maize meal:barley meal mix (97.5% w/w) and corn oil (2.5% w/w). This bait contained the chemical marker hexachlorobiphenyl (0.01% w/w) dissolved in the oil. (The markers were present as part of another study which is not reported here.) The bait in the box was inspected daily for the next 12 days, the amount remaining each day recorded and replenished to maintain a surplus until the following day. After 12 days, all uneaten marked bait was removed from the box and burrows and dry whole wheat was placed in the box for a further 2 days. The data logger recorded visits by tagged rats to the box every day for 14 days.

Enclosure trials

Untagged rats may have influenced the responses of the tagged rats at the box in the field. To examine the effect of social interactions more closely, family groups of rats were established in enclosures. For ethical reasons, it was not possible to study relationships between unrelated individuals under such circumstances, but interactions based on size differences could be investigated. The enclosures, which were erected inside a large building, were 12 m long and 2.5 m wide, bounded by sheet-metal walls bolted to a concrete floor. They were naturally lit through windows in the roof and there was no artificial heating, although a cooling fan could be switched on during hot weather. A tunnel connected two adjacent enclosures so that the nest area could be separated from the bait box by up to 15 m. Hay was provided as cover and wooden boxes were supplied for the animals to build nests in. Water was available in both enclosures ad libitum from founts, and a tray containing surplus amounts of a ground laboratory animal diet was placed near the nest area and was present during all experiments. A bait box identical to the one used in the field trial, but with a perspex lid, was placed in the adjacent enclosure. Pittag detector tunnels of similar design and construction to those described above were attached to each side of the box and the signals were relayed to a data logger located outside the enclosure. Additional detectors were placed by the connecting tunnel. Since all rats had to pass through the tunnel that separated the box from the nest area, these detectors served as back-ups, because tagged animals, particularly if they were moving fast, could be missed as they entered or left the bait box.

Three family groups were derived, each from a wild-caught adult male and two wild-caught adult females. The females were allowed to produce 1–2 litters; sufficient to give a colony of 10–20 individuals. Subsequent litters were removed as soon as they were found to prevent overcrowding. After the young were at least 6 weeks old, each family group was trapped and each animal was sexed, weighed, lightly anaesthetised with isoflurane and injected subcutaneously with a PIT tag.

Two series of experiments were conducted once most individuals in each group were regularly visiting the bait box. This was done to avoid any neophobic responses confounding interpretation of the results. Firstly, using whole dry wheat as the bait, the number and length of visits to the box were compared between the adults and members of the litter when the litter was at different stages of development. A further factor was whether each animal was alone or with at least one other rat. The respective mean weights of adults and litter in each of group were: 412 g ($n = 3$), 107 g ($n = 12$) immature; 447 g ($n = 3$), 210 g ($n = 17$) maturing; and 503 g ($n = 2$), 470 g ($n = 12$) fully mature. The responses of each group when presented with surplus amounts of whole wheat in the box were recorded over one night.

In the second experiment, each of two groups was presented with 10 wax blocks (a commercial blank formulation, each block weighing 20 g) threaded onto two wires fixed inside the box. One group was familiar with the formulation after previously being presented with loose blocks until they consistently carried them away and ate them. The other group was naïve. The responses of the ‘trained’ group on their third presentation of the secured blocks were compared with those of the naïve group on their sixth presentation. (By the third and sixth presentations, respectively, it was clear that the responses were not being influenced by other factors such as temperature.)

Data analysis

The data loggers were designed with a time base that incremented every 62.5 ms. If the four detectors attached to the box were numbered as channels 1 to 4 in sequence, then the output would show, in time order, that a rat passing through the box was detected by channels 1, 2, 3, 4 or 4, 3, 2, 1, where 2 and 3 were the internal detectors closest to the box and 1 and 4 at the entrances/exits to the tunnel. The entrance detectors were set into the tunnel so that they did not detect a rat passing by. For a rat entering and leaving by the same tunnel, the sequence would be 1, 2, 2, 1 or 4, 3, 3, 4. The length of a visit was taken to be the time difference between the first and last channel number in a string of 2s and 3s before an entrance/exit channel (1 or 4) was recorded. A string would occur if a rat moved relatively slowly through the detection field. Thus, rats that entered the tunnel and then backed out could be distinguished from those that went into the box. By recording the time that the loggers were started each day, all visits were related to real time. The detectors fixed into burrow entrances were single channel and could not give direction of movement. However, as the detectors could nominally record many events every second, a rat feeding on the bait in the burrow entrance would remain in the detection field and its tag identification (ID) would be logged repeatedly for as long as it stayed there. The number and length of visits recorded for each rat to each burrow therefore depended on the time difference between two consecutive detections that signified the end of one visit and the beginning of another. By convention in this study, two events at a burrow separated by more than the average visit length ≤22 s, derived from a log-transformed distribution of visit lengths) to the box in the field study were taken to indicate separate visits. (In practice, halving or doubling the interval made little difference to the average visit length to burrows.)

The distribution of visit lengths was highly skewed and therefore the median is given as the most appropriate summary statistic. Differences between visit lengths related to the various factors under study were examined by t-test after first log transforming the data (Inglis et al. 1996). In most cases, the test formula for unequal variances was used. All tests were two-tailed and the level of significance (α) was $p < 0.05$.

Results and discussion

Field trial

Over 10 days, 1623 visits were recorded at the 8 burrows by 12 of the 19 tagged rats. No juveniles were detected. Tagged rats visited seven of eight baited burrows on the first night. Only two rats (males) visited all the baited burrows during the trial. From the total number of visits, 1304 involved multiple detection events within the time reference for a valid visit and were therefore classified as putative feeding visits. The median visit length was 12 s and 80% of visits were ≤42 s (Figure 1). Mean visit length for males (median 16 s, $n = 432$) differed from that of females (median 11 s, $n = 872$) ($t = 2.82$, $p < 0.005$). The average number of feeding visits to each burrow by 5 males over the 10 days was 10.8, and 15.6 by 7 females, although one female made a total of 413 visits to 4 burrows over the period.

No visits were made to the box by tagged rats and no bait was eaten by any rat for the first 2 days. Thereafter, over the next 12 days, 11 tagged rats made 1272 putative feeding visits, the first visit by each tagged rat occurring at different times over the period. The median visit length was 17 s and 80% of visits were ≤145 s (Figure 1). Mean visit length for males (median 21 s, $n = 373$) differed from that of females (median 17 s, $n = 899$) ($t = 2.28$, $p = 0.02$).

The median length of a visit to a baited burrow and that to the box differed by 5 s and is probably of little biological significance. (Equally, the differences between visit lengths for males and females may have little biological meaning.) More significance should perhaps be attached to the differences that can be seen at higher percentiles (Figure 1). At the highest percentiles, not shown in the figure, extremely long visits confound any comparison, as such visits are probably the result of tag IDs being missed, which can happen if rats move too quickly through the detection field. The time synchronisation of events recorded by the logger meant that it was possible to determine how many tagged rats were in the box at the same time and whether the number feeding together had any effect on the time individuals were prepared to remain there. There may be a selective advantage in feeding together, in that ‘safety in numbers’ can be a defence against predator attack. Such social facilitation might be advantageous when rodenticide baits are laid, as rats may be encouraged to eat more bait at each visit. In contrast, the confines of a burrow necessarily restrict the number of rats that can feed at any one time and while the burrow occupant may feel safe emerging from its nest, passing individuals that feed opportunistically risk attack from behind as they reach for the food. However, the number of rats feeding together in the box or by each burrow remained unknown, because untagged animals might also have been present. This problem was overcome by marking every rat in an enclosed colony.

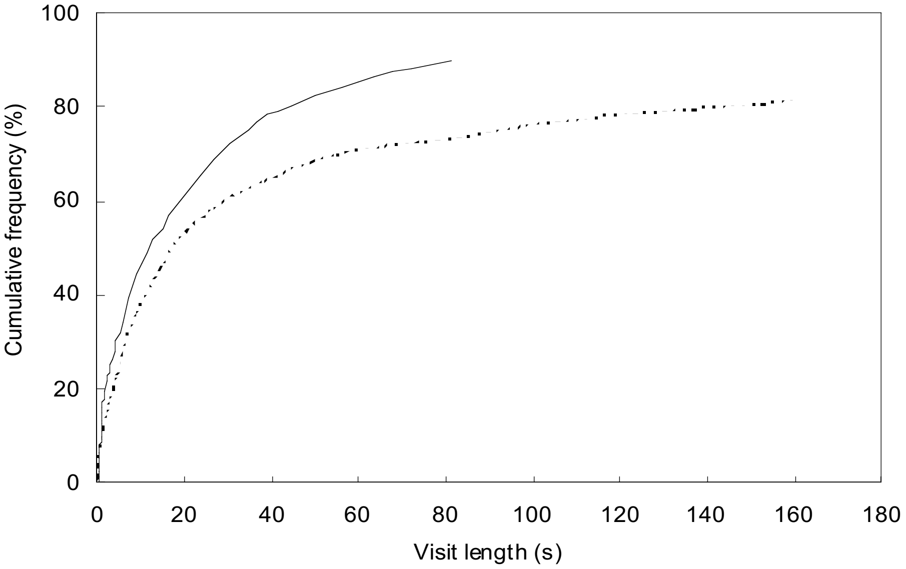

Figure 1. The length of time rats spent over a 10-day period at the entrances of burrows (solid line) located along the sides of a ditch near farm buildings and then inside a box (dashed line) placed on the ditch bottom for a further 14 days. The same loose-grain plain bait that was placed in the burrows was dispensed into the box for the first 12 days. The median and its 95% confidence limits for each curve are: 12 s (10–14 s) for visits to burrows, and 17 s (15–21 s) for visits to the box.

Enclosure trials

Regardless of the age or size of the rat or the type of bait in the box, visits by single rats were short, with a range of median values from 2–15 s (Table 1). With whole wheat laid in the box, visits by an adult, when at least one other rat was present, were longer than those by an immature rat (juvenile) that was also not alone ($t = 2.27$, $p = 0.03$) — a difference that was not found when members of a fully grown litter were the same size as their parents ($t = 0.29$, $p = 0.8$). Despite a difference of 76 s between the median visit lengths for a group with at least one adult and a group with at least one young adult (maturing) rat, the difference was not statistically significant ($t = 1.26$, $p = 0.2$). Nevertheless, these results support the interpretation that the foraging behaviour of rats is dictated more by fear of conspecific aggression than by fear of predation (Whishaw and Whishaw 1996), even when, as in this case, the animals were related. It could not be determined if every visit to the box was to obtain food, but incidental observations revealed that any rat, entering the box alone, often emerged after a few seconds carrying grains of wheat in its mouth and would then move elsewhere in the enclosure to eat them.

In a study in which the apparatus used to monitor rat feeding patterns apparently permitted only one individual at a time to obtain food (Berdoy and Macdonald 1991), the minimum duration of a feeding visit (presumably to take food rather than eat it on the spot) was found to be 0.4 s, while the majority of visits lasted 1–8 s. The implication of such behaviour during a rodenticide treatment is that bait transfer becomes more likely when only one individual at a time can access the bait. The rats in our family groups appeared to prefer eating in the presence of one or more other individuals, provided they were not obviously larger than themselves. By staying longer, bait transfer probably occurs less often. It is noticeable that the design of many commercial bait boxes seems to restrict access to bait with high internal baffles intended to deter non-target animals.

Rats unfamiliar with wax blocks had made no attempt to gnaw the blocks secured on the wires after six consecutive presentations. The median length of 91 visits on the sixth night by 13 out of 14 colony members was 8 s; solitary animals made 65 (71%) visits (Table 1). For rats familiar with the block bait, on the third presentation all the blocks were eaten. The median length of 494 visits by 18 rats was 14 s; solitary animals made 196 (40%) visits. The ratio of solitary:group visits for the naïve colony was different to that for the trained group ($\chi^2 = 30.1$, 1 df, $p < 0.001$), largely because of group visits by the offspring in the trained group. The commercial block used was rather brittle and it was probably easy for rats to break off relatively large pieces with their incisors. Such pieces were then most likely to have been carried outside the box instead of being eaten inside it and may explain why the visit length for the trained group was similar to that of the naïve group. Wild rats seem to have difficulty recognising wax blocks as food items, a characteristic that has long been recognised (Bentley 1960). Moreover, the presentation of blocks on a wire suspended above the floor of a box prevents a rat feeding in its preferred manner—which is to pick up a food particle in its mouth, then sit on its haunches, rotating the particle with the paws as it is eaten (Whishaw and Tomie 1987). Nevertheless, training rats by allowing them to take loose (plain) blocks away and eat them at least allows the animals to become familiar with similar objects and to discover that they are, after all, edible. For practical control purposes, such 'training' may be deemed unworkable, as there would be no means of knowing where blocks were taken and how many rats would be 'informed' in the process. The alternative is that secured poison blocks are left in containers until such time as rats feel able to eat them. In the meantime, other animals, less inhibited than rats, might eat them instead.

Table 1. Median duration (s) of visits (*n* in brackets) by individual rats in different colonies (family groups) to a bait box containing plain whole wheat or plain wax blocks. Visits are divided into those by an individual on its own or with at least one other rat (adult or offspring) present in the box. For the latter category, statistical differences between adult and offspring visit lengths within each family group are shown as * ($p \le 0.05$) or † (not significant). Each colony had an alternative food source available. The 'training' given to the colony presented with wax blocks threaded onto wires consisted of offering the rats loose blocks until all were regularly removed and eaten. The 1:>1 ratio of total number of visits for the naïve group (65:26) differed from that for the trained group (196:298, $p < 0.001$).

Bait	Number of rats in box	Status of litter					
		Immature		Young adults		Fully mature	
		Adults	Offspring	Adults	Offspring	Adults	Offspring
Whole wheat	1	2 (9)	6 (95)	2 (15)	6 (79)	–	15 (17)
	>1	200 (44)	28*(250)	96 (39)	20†(170)	100 (38)	105†(206)
		Status of colony					
		Naïve		Trained			
		Adults	Offspring	Adults	Offspring		
Wax blocks on wires	1	3 (12)	7 (53)	5 (28)	9 (168)		
	>1	11 (14)	23 (12)	13 (23)	24 (275)		

Conclusion

Because current rodenticides are not species-specific, it is imperative that every effort is made to prevent other animals eating the bait during treatments. Whatever measures are taken should not also discourage rats from eating bait and in practice many operators find it hard to balance efficacy with safety. Some designs of bait boxes and formulations seem to be out of tune with rat foraging behaviour, through which the animals seek easy access and an easy escape from food sources. Such boxes and baits should perhaps not be used if a population needs to be controlled urgently. Baits laid in burrows may be found quickly by rats during nightly excursions across their home range, especially if they follow established runs that will naturally pass close to such burrows. But the restricted access to such baits leads to a series of brief visits that can be interrupted by the presence of other rats. Clearly, to capitalise on such short visits during control operations, a highly potent rodenticide is desirable.

In contrast, baits available in a more open container that allows the possibility of group feeding, need not be quite so toxic, as the rate of bait uptake should be higher. However, the bait chosen to present to rats in such circumstances should not be one that is easily carried away in bulk and also not one that cannot be carried away. This apparent contradiction can be resolved with a loose-grain cereal bait, which rats living on farms clearly have no difficulty in recognising as food. The disadvantage of loose-grain baits is that they are attractive to a wide range of other animals and are easily lost if the container is disturbed. Faced with a damaging infestation, the choice seems to be either a short intensive treatment with high rates of bait uptake and relatively rapid elimination of rats, but with a greater short-term risk to other animals, or a longer treatment with lower rates of bait consumption, slower elimination of rats, but less risk of primary poisoning to animals bigger than rats. While both strategies should be equally effective in reducing damage, albeit at different rates, the latter would seem to offer more chance of selecting resistant individuals, especially when second-generation anticoagulants are used.

A solution to the problem of having safety with efficacy is to test whether rats can be ‘trained’ with unsecured, plain block baits to eat poison blocks ‘on the spot’ inside protected containers. By careful adjustment of the number of plain blocks available for transfer and the location and density of stations with poison blocks, a practicable method for use in the field may be possible.

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Coumatetralyl residues in rats and hazard to barn owls

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Abstract. The secondary poisoning hazard of coumatetralyl was evaluated through analysis of residues in rats (*Rattus norvegicus*, *R. tiomanicus* and *R. sordidus*) that had eaten coumatetralyl baits in laboratory and field trials, and in a feeding trial with captive barn owls. In *R. norvegicus* fed Racumin® over three nights, approximately 4% of the coumatetralyl eaten was detected as residue in the whole body. In a similar study with *R. tiomanicus*, approximately 3.7% of the coumatetralyl eaten was detected in the whole body. The range of total body coumatetralyl residues per body weight found in three rodent species had similar maximum values, despite interspecies differences in body sizes and bait intake. Three-day laboratory feeding studies with Racumin® produced similar maximum residue concentrations in tissues to those measured in field-poisoned rodents. Captive barn owls fed for 6 days on coumatetralyl-poisoned *R. tiomanicus* did not exhibit any secondary poisoning symptoms during the subsequent 30-day period, consistent with other findings that suggest coumatetralyl presents a relatively low hazard of acute secondary poisoning to predatory birds.

Introduction

Reports of anticoagulant residues in predatory birds (e.g. Newton et al. 2000) and other wildlife (e.g. Eason et al. 2002) appear to have increased over the last decade, heightening worldwide concern regarding non-target effects of rodenticide use. While this increase may be due in part to more sensitive monitoring and analytical techniques, the presence of residues indicates that primary or secondary exposure of non-target wildlife occurs. Non-target risk is a function of both exposure and hazard, and estimates of secondary poisoning hazard to rodent predators may be derived from evaluating residue concentration and distribution in rodent carcasses following lethal, or sublethal, bait intake. Studies have addressed aspects of secondary poisoning risk to owls from first- and second-generation anticoagulants (e.g. Lee 1994), but most have not included the first-generation anticoagulant coumatetralyl (Racumin®). An oral LD_{50} of 5 × 0.3 mg/kg coumatetralyl has been determined for rats (Hermann and Hombrecher 1962). Racumin® products (375 ppm coumatetralyl) are increasingly used on farms and crops, thus there is potential for predators to be exposed to poisoned rodents. To assess hazard, residues of coumatetralyl were determined after poisoning three rat species in laboratory trials, and in rodents collected after Racumin® application in the field. A feeding study investigated the effect of repeated consumption of coumatetralyl-poisoned rats on barn owls.

Materials and methods

Residues in *Rattus norvegicus* following coumatetralyl bait ingestion

Rats (*R. norvegicus* Wistar) were maintained at the Landcare Research Animal Facility, in a controlled-temperature environment (18°C ± 2°C) with water available *ad libitum*. Seventy-eight young adult rats were offered Racumin® wax block bait (375 ppm coumatetralyl: Bayer AG) without alternative food over three consecutive nights. On the fourth day, rats were anaesthetised using CO_2 gas, then killed by cervical dislocation. Six of these rats, chosen at random, were analysed for coumatetralyl concentrations in liver, gut (stomach, intestines and contents), and remainder of carcass (including skin, feet, and tail). The analytical limit of detection was 0.01 µg/g and uncertainty (95% confidence interval; c.i.) was ±11%.

Secondary hazard to barn owls from coumatetralyl-poisoned *Rattus tiomanicus*

Thirty adult wood rats (*R. tiomanicus*) were trapped and maintained at the Malaysian Cocoa Board Research and Development Centre, Hilir Perak. Rats were fed with Racumin® over 3 days *ad libitum* and without alternative feed. Six rats were euthanased by cervical dislocation on the fourth day. Samples of liver, gut (stomach, intestines and contents) and the remainder of carcass were frozen at –20°C for later analysis. The analytical limit of detection was 0.02 µg/g ± 9% (95% c.i.). The remaining dead, whole rats were utilised in a feeding trial with barn owls (*Tyto alba*). Four owls were wild-caught and allowed one month acclimatisation to individual housing of timber and chicken wire construction, approximately 12 m^2, with a nesting box in one top corner. Owls were offered one unpoisoned rat per day as their normal diet, and during the trial offered one poisoned rat per day for six successive days. Food intake by owls was monitored, and the owls observed for 30 days after being returned to a normal diet.

Residues in *Rattus sordidus* following coumatetralyl bait ingestion

Cane-field rats (*R. sordidus*) were captured from cane fields near Ingham, Queensland, Australia. After 7 days on a sunflower seed diet, the individually caged rodents were offered a fresh Racumin® wax block each day in addition to sunflower seeds. Water was available *ad libitum* and food consumption recorded daily. One group of six rats was euthanased, using CO_2 gas, after 2 days and a second group after 4 days. Analysis for coumatetralyl concentration in the liver, gut (stomach, intestines and contents) and carcass (including skin, feet, tail and remaining internal organs) was carried out by Conmac Laboratories, Bethania, Queensland, according to the method described by Mundy and Machin (1982). The limit of quantification was 0.1 µg/g with average recoveries of 87% (Bureau of Sugar Experiment Stations, unpublished data, 1998).

Field residues in Australian rodents following application of Racumin®

In October 2000, the Australian National Registration Authority approved an emergency use permit for use of Racumin® wax blocks to control *R. sordidus* and the climbing rat (*Melomys burtoni*) in sugarcane crops. Baits were applied once in November 2001 to two field locations in Tully, northern Queensland, at a rate of 3 × 25 g blocks on a 15 × 15 m grid pattern (Bureau of Sugar Experiment Stations, unpublished data, 2002). After baiting, target species were collected from within and just outside the sites by breakback-trapping or carcass searches, and were sampled for liver, gut (including stomach, intestines and contents) and remainder of carcass, and frozen for later analysis. The analytical limit of detection was 0.02 mg/g ± 9% (95% c.i.).

Analysis of tissue samples for coumatetralyl

Except for the analysis of residues of coumatetralyl in *R. sordidus* in the cage trial described above, tissue samples were analysed at the International Accreditation New Zealand (IANZ) accredited Landcare Research Toxicology Laboratory, Lincoln, New Zealand, using methods based on Hunter (1983). The coumatetralyl analysis was shown to be robust with high recoveries (92.5%) and low method uncertainty. Analyses were validated in an interlaboratory comparison, where the mean coumatetralyl residues from the same (*n* = 6) rat livers were 0.75 ± 0.08 µg/g and 0.78 ± 0.08 µg/g.

Results and discussion

Residues in *R. norvegicus* following coumatetralyl bait ingestion

The six rats sampled for tissue analysis weighed (mean ± sd) 298.10 ± 84.66 g, and ate a mean of 31.1 ± 3.5 g Racumin® per night for 3 nights, resulting in each rat consuming a total coumatetralyl dose of between 81.94 and 147.80 mg/kg. This was equivalent to approximately seven times the LD_{50} value for this species (WHO 1995). Coumatetralyl concentrations by weight of tissues were: liver (13.35 ± 10.45 mg/g), carcass (5.03 ± 2.59 mg/g) and gut (2.74 ± 5.81 mg/g). These concentrations, and the weight of the respective tissues sampled, were used to calculate total mean amounts of coumatetralyl (mg) in rat tissues (Table 1). The considerable variability in concentrations detected in gut was probably attributable to the presence of visible bait fragments in some samples. Total residues in a rat were 5.21 ± 2.55 mg/kg, so that approximately 4% of the coumatetralyl eaten as bait over 3 nights was found as residues in the whole body on the fourth day.

Table 1. Coumatetralyl residues in *Rattus norvegicus* (Rn) and *R. tiomanicus* (Rt) after 3 days' feeding with Racumin® (375 ppm coumatetralyl). Amounts of coumatetralyl shown are based on concentrations of coumatetralyl measured in samples (µg/g) and the weight of tissue sampled, with the mean calculated from values for individual rats (BW = body weight, *n* = number in sample, sd = standard deviation).

Species (*n*)	Mean BW (± 1 sd) (g)	Mean total coumatetralyl eaten (± 1 sd) (mg/kg BW)	Mean (± 1 sd) total amount of coumatetralyl in tissues (µg)		
			Gut	Liver	Carcass
Rn (6)	298.10 (84.66)	123.34 (27.65)	49.56 (104.91)	135.85 (140.05)	1235.08 (602.73)
Rt (6)	103.67 (20.68)	109.15 (22.57)	119.54 (83.25)	22.91 (20.66)	264.02 (118.00)

Secondary hazard to barn owls from coumatetralyl-poisoned *R. tiomanicus*

The six rats sampled for tissue analysis weighed (mean ± sd) 103.67 ± 20.68 g and consumed a total of 30.33 ± 8.91 g Racumin® over 3 nights, resulting in a total coumatetralyl dose of 109.15 ± 22.57 mg/kg. Coumatetralyl concentrations by weight of tissue were: liver 13.37 ± 14.94 mg/g, gut 11.22 ± 6.95 mg/g and carcass 2.88 ± 0.93 mg/g. Total mean amounts of coumatetralyl in rat tissues were calculated as above (Table 1). The total residues in *R. tiomanicus* were 3.86 ± 1.36 mg/kg, so approximately 3.7% of the coumatetralyl eaten as bait over 3 nights was found as residues in the whole body on the fourth day.

Each owl consumed one entire rat on each of 6 days, eating a mean total of 661.50 ± 7.12 g of rat. Based on the total mean residue concentration estimated in *R. tiomanicus* feeding on Racumin® (described above) and the body weight of individual owls (467.50 ± 25.86 g), it was estimated that owls had each secondarily consumed a 6-day total of up to 5.89 ± 2.07 mg/kg coumatetralyl, or approximately 1 mg/kg per day. This is a substantially lower dose than an 8-day LD_{50} for coumatetralyl in hens, given as >50 mg/kg daily consumption (Worthing and Hance 1991, p. 188). No visible effects on owls were observed and all four were alive and appeared healthy 30 days after feeding on the rats. This result is consistent with survival in a steppe buzzard (*Buteo buteo*) and a spotted eagle owl (*Bubo africanus*) fed coumatetralyl-killed sparrows (Heÿl 1986). In addition, a lack of obvious ill effects on weka (*Gallirallus australis*), a scavenging New Zealand bird that ate coumatetralyl-poisoned rats over 3 days, has been reported (O'Connor et al. 2002).

Residues in *R. sordidus* following coumatetralyl bait ingestion

The six *R. sordidus* sampled for tissue analysis after 2 days feeding on Racumin® weighed (mean ± sd) 148.0 ± 34.1 g and consumed a 2-day total of 11.48 ± 9.72 g, resulting in a coumatetralyl dose of 27.23 ± 18.91 mg/kg. The six *R. sordidus* sampled for tissue analysis after 4 days feeding weighed 131.7 ± 36.7 g and consumed a 4-day total of 10.05 ± 5.84 g Racumin®, resulting in a total coumatetralyl dose of 27.77 ± 11.27 mg/kg. In comparison to the *R. norvegicus* and *R. tiomanicus* trials, where no alternative food was offered, the availability of alternative food may have partly explained the relatively smaller coumatetralyl intake in this trial by *R. sordidus*. Generally reduced feeding could also be expected 2–3 days after the first ingestion of bait due to the onset of symptoms. The group sampled on the fourth day generally had lower daily intakes of bait than the group sampled on the second day, which may explain why residues were higher in *R. sordidus* feeding for 2 days than those feeding for 4 days (Table 2). Considerable variability of coumatetralyl concentrations in gut samples after 2 days' feeding suggested the presence of undigested bait.

Field residues in Australian rodents following application of Racumin®

Coumatetralyl was detected in six *R. sordidus* recovered between 1 and 6 days after bait application. Residue

Table 2. Coumatetralyl residues in tissues of *Rattus sordidus* after laboratory feeding or field application of Racumin® (*n* = number in sample, sd = standard deviation).

Trial (*n*)	Days after baiting	Mean total bait (g/rat)	Mean (± 1 sd) coumatetralyl residues (mg/g)		
			Gut	Liver	Carcass
Laboratory (6)	2 days	11.48	20.61 (34.33)	8.02 (5.05)	2.40 (1.48)
Laboratory (6)	4 days	10.05	1.01 (2.24)	2.11 (2.32)	0.46 (0.64)
Field (6)	1–6 days	not known	8.90 (9.65)	6.16 (7.11)	1.68 (2.15)

Table 3. Coumatetralyl residues (total all tissues) found in *Rattus sordidus* (Rs) and *Melomys burtoni* (Mb) according to days after Racumin® bait treatment in sugarcane fields, and residues in *Rattus norvegicus* (Rn) and *Rattus tiomanicus* (Rt) fed Racumin® in the laboratory (BW = body weight, *n* = number in sample, sd = standard deviation).

Treatment (days)	Species	*n*	Coumatetralyl residues (mg/kg BW)		
			Mean	sd	Range
1 (field)	Rs	4	1.57	3.19	0.02–6.44
5 (field)	Rs	1	6.51	–	–
6 (field)	Rs	1	3.02	–	–
11 (field)	Mb	1	0.15	–	–
3 (lab)	Rn	6	5.21	2.55	0.51–7.98
3 (lab)	Rt	6	4.36	1.84	2.26–6.89

profiles in these rats were similar to those in the same species offered Racumin® in the laboratory for 4 days, and much less than those feeding for 2 days (Table 2). Consistent with observations in the laboratory trials with other rat species, the variable residue concentrations detected in some field-collected *R. sordidus* gut samples (mean 8.90 ± 9.65 µg/g of tissue) suggests that undigested bait may have been present in some instances. Table 3 summarises the total coumatetralyl residues detected in rodents from three laboratory and one field trial with Racumin®. The data are limited by small sample sizes and not statistically comparable, but show that the range of total coumatetralyl residues found in three rat species had similar maximum values on a body weight basis (mg/kg), despite interspecies differences in body sizes and bait intake. On this basis, laboratory studies over 3 days seemed to provide a reasonable simulation of maximum field residues of coumatetralyl found in a limited sample of rodents.

Conclusions

There were similar concentrations of coumatetralyl (approximately 4% coumatetralyl eaten as Racumin® over 3 nights) detected in tissues of *R. norvegicus* and *R. tiomanicus*. The major route of elimination after oral administration of anticoagulants in rats is through the faeces (WHO 1995), however residues are probably highest if there is undigested bait in the gut within a few days of bait application. In field scenarios, such target animals would present the greatest hazard of secondary poisoning. Rodents in the laboratory trials were expected to have consumed in excess of a lethal dose of coumatetralyl, with the corresponding residue concentrations in the whole body close to a worst-case scenario in terms of secondary hazard to predators or scavengers. Comparison of the total body residues of coumatetralyl in different species of rodents after Racumin® intakes showed that laboratory feeding trials produced similar residue concentrations in tissues to those measured in target rodents after a field application of Racumin®. These results, alongside limited data regarding the toxicity of coumatetralyl to birds, suggest that there is a low acute hazard to barn owls feeding on rats containing relatively high concentrations of coumatetralyl residues.

Acknowledgments

We thank the Director-General of the Malaysian Cocoa Board for collaboration in the barn owl study. Thanks also to Brendan Dyer and the Bureau of Sugar Experiment Stations, Queensland, Australia, for access to residue data and experimental details (Bureau of Sugar Experiment Stations Consultancy Report CO02006 March 2002; BSES Publication PR98007 June 1998) and to Warwick Madden, Bayer Crop-Science Australia. Housing of animals and the various experimental procedures described were carried out in accordance with relevant regulations, protocols and standards, Good Laboratory Practice and World Health Organisation guidelines (Malaysia), approval from an independent Animal Ethics Committee (New Zealand) and protocols established by the James Cook University Ethics Approval for Animal Based Research and Training (Australia).

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Bromadiolone resistance does not respond to absence of anticoagulants in experimental population of Norway rats

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Abstract. Resistance to anticoagulant rodenticides in Norway rats (*Rattus norvegicus*) is documented to be associated with pleiotropic effects, notably with an increased dietary vitamin K requirement. The aim of this study was to quantify these effects in small populations of Norway rat in Denmark and to see how bromadiolone-resistant phenotypes are manifested when bromadiolone selection is absent. Experimental populations were established under semi-natural conditions with wild rats trapped at two Danish farms. The individuals caught on each of the two farms were divided into two experimental groups. One group was regularly exposed to bromadiolone whereas the other group was untreated. The level of bromadiolone resistance in the experimental populations was followed for two years. The results presented here are those results obtained in the absence of bromadiolone selection.

The pleiotropic selection against resistance in the two non-treatment populations was found to be insignificant. Thus, absence of anticoagulant, under the environmental conditions provided, did not lead to a selection favouring anticoagulant-sensitive rats. However, we found some evidence of selection against presumed homozygous resistant rats under non-anticoagulant conditions. Haemorrhagic symptoms are not only observed in sensitive rats exposed to anticoagulants, but are also a symptom for severe vitamin K deficiency in resistant rats. This suggests that bromadiolone resistance leads to loss of fitness, albeit that the cost is not strong enough to reduce the phenotypic resistance level or minimise the effect of random genetic drift.

Introduction

The documented pleiotropic effect of anticoagulant rodenticide resistance in rats is an increase in the dietary requirement for vitamin K in order to maintain reasonable production of blood clotting factors (Hermodson et al. 1969). Resistant rats that become vitamin K deficient will eventually suffer from haemorrhage, leading to death of the animal (Partridge 1980).

It is generally assumed that resistance to anticoagulants is selected against when anticoagulants are absent from the environment (Partridge 1979; Smith et al. 1991). The apparent selective disadvantage of anticoagulant resistance caused by the increased vitamin K requirement may be beneficial in rodent control. It could be hypothesised that by limiting the access to vitamin K, a common additive to animal feedstuffs, selection against resistant rats may be enforced.

However, the outcome of such initiatives will depend on a number of factors such as environmental conditions, the type of resistance (defined by the vitamin K requirement) and genotype frequencies. It is obvious that fitness, and thus selection against phenotypically resistant rats, must vary in correspondence with the requirement for vitamin K, with the strongest selection being against rats with a high vitamin K requirement (e.g. Welsh type), and selection against rats with a moderate increase in vitamin K requirement (e.g. Scottish type) being markedly reduced (MacNicoll et al. 2001).

Thus, the benefit of exploiting a removal of anticoagulants from the environment as an alternative resistance management strategy will depend on the extent of pleiotropy of those resistant rat populations that are to be controlled.

This study is part of a larger study investigating and evaluating the pleiotropic effects of bromadiolone resistance in Danish rat populations. For this purpose, four enclosed populations (excluding reinvasion from resistant/sensitive rats) of free-ranging wild bromadiolone-resistant rats were established. Two populations were left untreated and the other two populations were treated with bromadiolone (0.005%) twice a year. The level of bromadiolone resistance was monitored by means of a blood clotting response (BCR) test for a period of 2 years. Here we present results obtained from the two non-treatment (not treated with bromadiolone) populations.

Materials and methods

Materials

Wild rats, *Rattus norvegicus*, were collected from two farm populations (A and B), where bromadiolone resistance was known to occur.

Before establishment of the experimental units, all animals were trapped and caged individually for 4 weeks in order to test for bromadiolone resistance. All rats from population A (n = 79) and 95% of those from population B (n = 77) were identified as resistant by blood clotting response (BCR) tests (A.-C. Heiberg and H. Leirs, unpublished data). Resistant rats from each locality were divided into two experimental groups, a non-treatment (untreated) and a treatment population, resulting in two non-treatment and two treatment populations. In each group, we introduced wild rats that were tested as sensitive to warfarin in order to ensure the presence of non-resistant alleles within the populations. Before introduction into the indoor breeding pens (13 m^2), all rats were weighed, sexed and marked with a subcutaneous passive integrated transponder (PIT) tag for later individual recognition. The wild, warfarin-sensitive rats, like the resistant farm rats, had been singly caged for a period of 4 weeks (during the resistance testing). All the introduced farm rats were assumed to be just as much strangers to each other as they would be to the warfarin-sensitive rats. We did not find any significant evidence for resistant farm rats being more successful than the sensitive rats in becoming established in the experimental populations (data not shown). Rats were at all times, when not treated with bromadiolone, fed on lab-pellets (Altromin No.1324, 3 mg vitamin K_3/kg). Items like carrots, maize and sprouting wheat were added regularly. The illumination cycle was 12/12 hours dark/light.

Experimental treatment

Every 6 months, all animals were captured and removed from the four pens. All individuals were checked for PIT tags and their weight and sex were registered. From the two non-treatment populations, animals were randomly selected for resistance testing. The proportion of animals removed in each trapping session varied between 30% and 50% depending on the number of individuals in the total sample. In the first trapping, animals were selected randomly among all individuals, whereas in later trappings, animals that were documented older than 1.5 years were removed together with individuals chosen randomly among new individuals. Though rats of 1.5 years of age still may be reproductively active, rats of that age will seldom occur in natural populations.

Those animals that were re-introduced into the pens were all, under anaesthesia, PIT tagged and blood samples from the ventral tail vein collected (blood samples were used for later DNA analysis to infer parentage in the populations; A.-C. Heiberg et al., unpublished data). All individuals were introduced into the re-established pens simultaneously.

Rats that were found dead between trappings (in all four pens) were removed and autopsied to find the possible cause of death.

Resistance testing

The rats that had not been re-introduced into the pens were kept individually in standard metal cages with mesh bottoms (31.5 × 26 × 19 cm). Rats were fed plain rye bread and water *ad libitum*. Female rats were kept in quarantine for 3 weeks to ensure that they were not pregnant during the resistance test. Bromadiolone-resistant individuals were identified by BCR test (Gill et al. 1994). Bromadiolone was supplied by Lipha Lyonaise (France).

To determine the population level of resistance in each trapping, we only considered individuals that had been born after the previous trapping event. However, the new individuals were not necessarily BCR tested when they were trapped for the first time. If an animal was released after the trapping, the BCR result of that animal was first obtained when the animal was removed from the population. This procedure was chosen as the results obtained in BCR have proven to be stable with respect to aging of the animal (A.-C. Heiberg et al., unpublished observations).

Autopsy

Animals that died during resistance testing or anticoagulant treatments and those animals found dead in between trapping sessions were autopsied in order to verify the cause of death, if possible. The cause of death was classified into four categories: (1) haemorrhage due to an anticoagulant treatment/BCR; (2) haemorrhagic symptoms with no anticoagulant treatment; (3) no anticoagulant poisoning symptoms, but other obvious sign, e.g. pneumonia or other inflammatory conditions, starvation (due to teeth damage); and (4) no cause of death found.

Results

The population level of phenotypic resistance in non-treatment A for males and females did not change over time (P_{males} = 0.65 and P_{females} = 0.99, Pearsons χ^2, STATISTICA). Likewise, the level of resistance remained unchanged in the population when not differentiating between sexes (Pearson χ^2 = 0.89, df = 4, P_{total} = 0.93, STATISTICA) (Figure 1).

In non-treatment B, the population level of resistance for females remained unchanged (P_{females} = 0.28) (Figure 1). All sensitive males that had been introduced initially died within the first month, thus presumably only phenotypically resistant males contributed to the next generation. The level of resistance remained constant (100%) over the study period. When testing for heterogeneity in the population irrespective of sex, we only included the data from the four trappings. No significant changes were observed (Pearson χ^2 = 3.81, df = 3, P_{total} = 0.28).

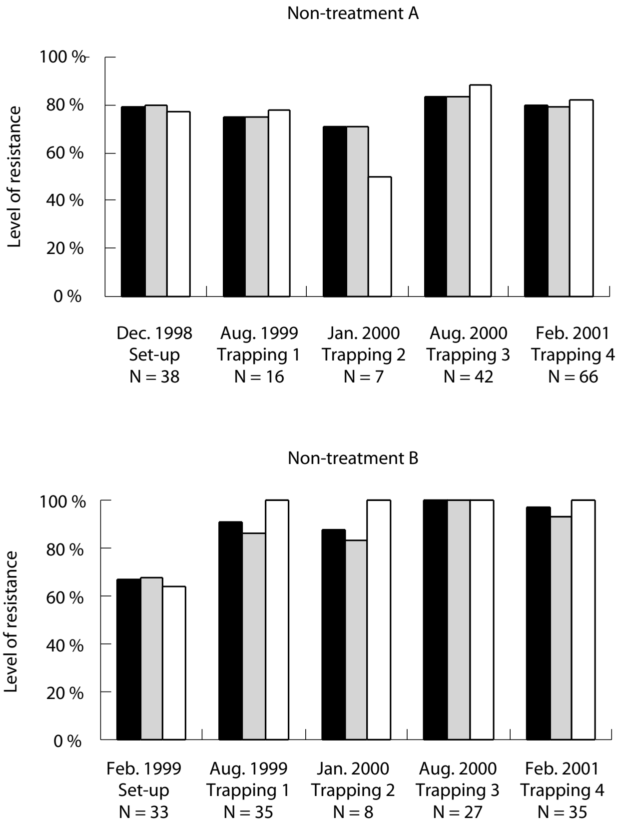

Figure 1. Level of observed phenotypic resistance within the two non-treatment populations, A and B. R_{total} (black bars) is the proportion of rats that were defined as bromadiolone resistant using the blood clotting response (BCR) test. R_{females} (grey bars) and R_{males} (white bars) are the proportions of females and males, respectively, being defined as bromadiolone resistant. N is the number of rats tested using BCR.

Between the different trapping sessions we found animals with haemorrhagic symptoms (Table 1). Since these animals (including those animals from the treatment populations as they were found a minimum of 2 months after the last treatment) had not been exposed to anticoagulants before their death, these symptoms were taken as an indication of vitamin K deficiency. There is a general tendency (though not significant, except in non-treatment B) for males to be younger in age than females when dying with vitamin K deficiency symptoms.

Discussion and conclusion

Environmental conditions are important when the impact of selection against traits is to be evaluated. Rats often live in environments under constant change, thus the selection pressure and relative fitness of the different genotypes of the selected trait will change likewise (Mitton 1997). The experimental conditions that were examined in this study resembled those of farm rat populations in many ways. The environment of many rodent infestations in rural areas does provide, often unintentionally, excellent conditions for maintenance of anticoagulant resistance; e.g. farm buildings allowing rats to reproduce all year and abundance of good-quality and unprotected animal feed, which may be enriched with vitamin K (Kerins et al. 2001).

The level of resistance remained unchanged in the non-treatment populations when anticoagulant selection was removed. The presence of a stable vitamin K source may have resulted in an insignificant pleiotropic effect, as the vitamin K requirement of most of the resistant rats would have been met. Another explanation for the unchanged resistance level could be the small effective population sizes (N_e) in the investigated populations. Small N_e can render the direction of selection unpredictable over few generations due to random genetic drift (Falconer and Mackay 1996).

The N_e ranged between 8 and 25 breeding individuals in all four populations (A.-C. Heiberg et al., unpublished data), with large fluctuations in N_e from generation to generation. Knowing this, we simulated (a Wright-Fisher model) how genetic drift in 1000 populations with different N_e affected the frequency of the sensitive allele over 1, 2, 4, 6 and 10 generations given the relative fitness components of Partridge (1979) (absence of anticoagulant selection). For non-treatment A, we could ascribe the unchanged level of phenotypic bromadiolone resistance to the effects of random genetic drift, whereas the level of

Table 1. Animals found dead within the breeding pens between trapping/anticoagulant treatments with symptoms indicating vitamin K deficiency or antagonism. N_{dead} is the number of dead animals removed in total. $N_{\text{A.S}}$ is the number of animals with visible anticoagulant poisoning symptoms. The average age of individuals showing vitamin K deficiency was estimated based on the approximated age of the individuals. Age differences between males and females were tested with the non-parametric Kruskall–Wallis, Statistical Analysis System (SAS).

Treatment[a]	N_{dead}	$N_{\text{A.S}}$	$N_{\text{dead/A.S}}$	female $_{\text{dead/A.S}}$	male $_{\text{dead/A.S}}$	Average age (months ± sd)		Kruskall–Wallis
						female	male	P
Non-A	39	21	0.54	0.57	0.56	8.6 ± 5.6	5.8 ± 3.6	0.505
Treat-A	34	13	0.38	0.44	0.31	14 ± 5.0	8.6 ± 6.7	0.163
Non-B	74	39	0.53	0.39	0.63	9 ± 3.4	4.3 ± 2.9	0.001
Treat-B	49	23	0.47	0.36	0.52	6.8 ± 6.0	4.2 ± 1.3	0.737

[a] Non-A = rats from population A, not treated with bromadiolone; Treat-A = rats from population A, treated with bromadiolone (0.005%) twice a year; Non-B = rats from population B, not treated with bromadiolone: Treat-B = rats from population B, treated with bromadiolone (0.005%) twice a year.

resistance in non-treatment B could not be explained by the forces of drift or by selection. However, given the environmental conditions, the relative fitness components of Partridge (1979) might have been too low for both the homo- and heterozygous resistant rat in this experiment, indicating that selection against the resistant rats is weak.

Conversely, large numbers of rats died with haemorrhagic symptoms without being exposed to anticoagulants and, furthermore, the diet supplied to the rats contained 3 mg vitamin K_3/kg. These signs of vitamin K deficiency do suggest that bromadiolone resistance may have some marked disadvantages.

Homozygous resistant males from treatment populations A and B later showed that they were sensitive to a low vitamin K content diet (M.D.K. Markussen et al., unpublished results) whereas the resistant females showed moderate to no response to the vitamin K deficient diet. The haemorrhagic symptoms do, however, indicate that their vitamin K requirements were not met. The role of aging has not been investigated, but it could be speculated that the process of aging played a role when considering vitamin K requirement. Older rats may become more vulnerable to various diseases, which hypothetically could reduce their ability to fully utilise the vitamin K supplied in the diet.

We found that females dying with signs of vitamin K deficiency were generally older than males and that many of the females originating from the treatment populations had survived earlier treatments. The fact that females generally are less prone to vitamin K deficiency than males may explain the observed age difference, but most of the rats lived in the population for at least half a year before becoming vitamin K deficient. Thus it can be hypothesised that the death of these rats may be due to a reduced ability to utilise the vitamin K or that older resistant individuals experience a further increase in vitamin K requirement. However, conclusions on the importance of the aging process in the context of vitamin K requirement cannot be made based on these studies. More studies focusing on that aspect have to be done.

Though we were not able to see a reduced population level of bromadiolone resistance, the animals that apparently died due to vitamin K deficiency provide evidence for a pleiotropic effect of being resistant. The relatively short time span of the study (two years, ≈ 4–5 generations) may have been responsible for the fact that we did not see a reduction of bromadiolone resistance. Genetic drift in the relatively small populations could also explain why selection has no clear effect. We do, however, believe that the primary factor leading to the lack of response is a very weak selection resting upon the heterozygous resistant rat. Thus, removal of the anticoagulants alone as an alternative resistance management strategy will have no or only very limited effect.

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Warfarin susceptibility in the lesser bandicoot rat (*Bandicota bengalensis*)

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Abstract. Warfarin is a first-generation anticoagulant that relies on multiple feeding events to achieve lethality in susceptible rodents. For the bandicoot rat, warfarin-susceptibility baselines were established using the lethal feeding period (LFP) test methodology. Against a 0.003% warfarin formulation, LFP_{50} values of 2 and 4 days, and LFP_{99} values of 16 and 10 days were obtained for males and females, respectively. However, consumption of rodenticide was significantly reduced after the 4th and 5th day of test, at a time when animals would be expected to experience symptoms of warfarin toxicity. This would seriously compromise the Probit analysis, particularly for estimates of higher percentiles. Although the majority of animals were highly susceptible to warfarin, one female animal that survived a high dose of active ingredient (79.1 mg/kg) may bode for future resistance

Introduction

A number of rodenticides, including the anticoagulants brodifacoum, bromadiolone, chlorophacinone, diphacinone, and coumatetralyl, are registered in Pakistan, and are being marketed under different formulations and trade names. Total annual consumption of rodenticides (both acute and anticoagulants) during 1989–98 was reported to be between 0.1 and 45.6 t, according to the Pakistan Agricultural Pesticide Association.

The use of anticoagulant rodenticides is considered highly effective and safe due to their delayed mode of action and the availability of the complete antidote, vitamin K_1. The delayed action prevents the association of cause (the rodenticide) and effect (symptoms of toxicity), and as a result, conditioned bait aversion (or bait shyness) does not occur. The main drawback for these compounds was the development of physiological resistance, particularly in Norway rat (*Rattus norvegicus*) and house mouse (*Mus* sp.), which developed in populations following prolonged exposure (see Greaves 1994). Resistance has also been reported in other rodent species (i.e. *Rattus rattus*, *R. tiomanicus*), although the genetic basis of the resistance differs from that of Norway rat and house mouse (Chia 2000). The emergence of resistance motivated researchers to develop methods for its detection and monitoring in rodent populations. The lethal feeding period (LFP) test (WHO 1982) is commonly used for detection of resistance, and has been included by the European Plant Protection Organization (EPPO 1995) in their guidelines for testing rodents for resistance to anticoagulant rodenticides.

Like other South Asian countries, a complex of rodent species is responsible for indoor and outdoor infestations in Pakistan. The bandicoot rat is widely distributed in the region and is one of the more prominent pest species. Efficacy of a number of rodenticides (including anticoagulants) has been tested against this species in the field and under laboratory conditions (Mathur et al. 1992). Sensitivity to warfarin in the bandicoot rat has been reported to vary between geographically distinct populations: in Bombay, India (Deoras 1967; Renapurkar et al. 1973); in Karachi, Pakistan (Greaves and Rehman 1977); and in Rangoon, Burma (Brooks et al. 1980).

The present work was initially conducted to establish warfarin-susceptibility baselines for the bandicoot rat using the LFP test methodology (EPPO 1995). The baseline data could then be used as a basis to detect the emergence of physiological resistance in field populations.

Materials and methods

The study was carried out following the EPPO (1995) guideline for testing rodents for resistance to anticoagulant rodenticides. The rats were live-trapped from the crop and non-crop areas of the National Agricultural Research Centre (NARC), Islamabad, Pakistan (33°42'N, 73°07'E) between September 1995 and May 1996. The prevalence/status of anticoagulant resistance was unknown in this population, although they had not been exposed to an anticoagulant for at least 2 years before this study.

The animals were sexed, weighed and caged individually, with food and water freely available. The laboratory maintenance diet comprised locally milled wheat flour (40%), corn flour (40%), fishmeal (10%), full-cream dry powdered milk (5%), crude sugar (2%) and sunflower oil (3%). No supplementary vitamin K was provided. Animals were maintained in the laboratory for at least 3 weeks before testing. During this time, daily food and water consumption was monitored and the animals were kept under observation to ensure they were healthy and to acclimatise them to the test conditions. Animals that were pregnant, sick, poor feeders, or were outside the body weight range of 150–350 g were not included in the study. The room temperature was maintained at 23–25°C with a natural day/night light regime.

The warfarin baits were prepared from 1% powdered concentrate (Sorex Ltd, St Michaels Trading Est., Widnes, Cheshire WA8 8TJ, England), and the bait concentrations (0.003%, 0.005% or 0.025%) were freshly formulated as required for each test.

In the light of earlier reports on warfarin susceptibility in the bandicoot rat (Deoras 1967; Brooks et al. 1980), feeding tests were initiated using 0.005% warfarin bait. In an initial ranging study, two animals of each sex were presented the bait for feeding periods of 2, 3, 4, 5 and 6 days. Complete mortality was achieved with the exception of four animals that survived feeding periods of 2 and 3 days. Survival was insufficient for effective Probit analysis (Finney 1971).

In accordance with the EPPO (1995) guidelines, the warfarin content of the test formulation was reduced to 0.003%, in order to provide sufficient feeding periods with incomplete survival. Subsequently, the group sizes for critical feeding periods were increased to 10 male or 10 female animals (EPPO 1995). For each test animal, either survival or the day of death was recorded. Survivors were observed for a further 21 days post-test observation period, and animals that died were examined for evidence of haemorrhage.

Surviving bandicoot rats were allowed to recover for 30 days, and subsequently subjected to a field-strength warfarin formulation (0.025%) for a 4-day no-choice feeding test. Animals that survived the field-strength formulation (plus the 21-day post-test observation period) were again offered the field-strength formulation in a no-choice feeding regime until death.

The lethal feeding period response data were subjected to Probit analysis, using Proc Probit (Probit – log days) in SAS (release 6.8) for WINDOWS. Other statistical analyses were performed using computer-based packages MINITAB (32 bit, release 10.51 Xtra) and Microsoft EXCEL.

Results and discussion

The feeding test results for bandicoot rats given 0.003% warfarin bait for feeding periods of between 1 and 7 days are summarised in Table 1. Complete mortality was achieved following a 6 and 7 day feeding period for males and females, respectively. As the response of males differed significantly from that of females ($\chi^2 = 5.0$, df = 1, $P = 0.025$), Probit analysis was performed and lethal feeding period percentiles were calculated separately for

Table 1. Mortality in the bandicoot rat after no-choice feeding on bait containing 0.003% warfarin for various numbers of days.

Sex/Feeding days	Body weight (g) mean ± se	Mortality (dead tested)	Amount of active ingredient (mg/kg) consumed		Daily intake of warfarin (mg/kg/day) mean ± se (*n*)	Mean days to death
			Survivors mean ± se (range)	Non-survivors mean ± se (range)		
Males						
1	289.8 ± 9.3	3/10	2.2 ± 0.2 (1.6–2.8)	2.9 ± 0.5 (2.2–3.9)	2.61 ± 0.12 (61)	6.7
2	261.2 ± 17.7	5/10	4.2 ± 0.3 (3.1–5.1)	4.8 ± 0.3 (4.0–5.7)	3.01 ± 0.16 (51)	7.6
3	255.5 ± 19.9	7/10	6.6 ± 0.6 (5.4–7.6)	9.3 ± 1.2 (6.0–15.3)	3.18 ± 0.18 (41)	7.0
4	230.0 ± 13.6	6/10	14.6 ± 2.7 (11.0–22.7)	14.1 ± 2.1 (9.2–23.5)	3.05 ± 0.21 (31)	8.8
5	211.8 ± 16.2	9/10	12.4	16.0 ± 1.5 (9.0–25.8)	2.28 ± 0.21 (20)	7.7
6	265.9 ± 9.2	11/11	–	13.2 ± 0.9 (7.1–17.3)	1.79 ± 0.35 (8)	7.0
Females						
2	240.5 ± 9.0	1/10	4.8 ± 0.2 (3.9–5.7)	7.0	2.78 ± 0.11 (60)	4.0
3	235.0 ± 11.9	3/10	8.9 ± 0.9 (6.6–12.7)	8.7 ±1.1 (7.2–10.9)	3.02 ± 0.14 (50)	8.7
4	220.0 ± 17.8	8/10	13.7 ± 3.1 (10.7–16.8)	11.5 ± 1.3 (7.4–16.8)	2.90 ± 0.13 (39)	7.4
5	227.8 ± 11.3	8/10	11.6 ± 0.7 (11.1–12.1)	13.3 ± 1.3 (9.3–21.4)	2.57 ± 0.14 (28)	7.4
6	228.4 ± 10.9	8/10	22.1 ± 1.4 (20.8–23.5)	16.1 ± 1.1 (13.5–22.6)	2.05 ± 0.23 (19)	8.0
7	241.4 ± 16.6	11/11	–	14.3 ± 2.4 (3.4–30.3)	0.98 ± 0.38 (9)	7.5

each sex. Against a 0.003% warfarin formulation, LFP_{50} values of 1.9 and 3.4 days, and LFP_{99} values of 15.5 and 9.1 days were obtained for males and females, respectively. EPPO (1995) recommend the use of the LFP_{99} (rounded up to the next whole day) as the discriminating feeding period to identify anticoagulant resistance (the resistance checking test). On this basis, the discriminating feeding period for warfarin resistance in the bandicoot rat is 16 days and 10 days for males and females, respectively.

The mean time from initial feeding on the warfarin formulation to death was 7.7 ± 0.25 days (n = 41) and 7.6 ± 0.30 days (n = 39) for males and females, respectively. No significant difference between the sexes was observed (F = 0.2, df = 79, P = 0.72). Of the 122 rats tested, 88 (72.1%) were affected by the poison (with external bleeding and/or the 'stop feed' effect) and of these, 80 animals died and 8 animals recovered completely and survived the test. Of the 80 animals that died, three developed symptoms of poisoning (the 'stop feed' effect) on the third day of the test.

For the bandicoot rat, males would appear more susceptible to warfarin than females. Of animals dying after the consumption of less than 5 mg/kg of warfarin, 14.6% (6/41) were males and 5.1% (2/39) were females; and the maximum warfarin dose survived by females (23.5 mg/kg) was greater than that survived by males (22.7 mg/kg). A similar sex difference has been reported for the Norway rat (Greaves and Cullen-Ayres 1988).

The results for the screening of the survivors of the LFP test against field-strength warfarin (0.025%) are summarised in Table 2. The only survivor was one female that consumed a warfarin dose of 79.1 mg/kg. In this study, the maximum warfarin dose consumed by all other animals that survived a feeding test was 23.5 mg/kg. The above female has survived a dose more than three times greater than that survived by all other animals tested.

Considerable variation in sensitivity to warfarin for different populations of bandicoot rat has been reported (Deoras 1967; Renapurkar et al. 1973; Greaves and Rehman, 1977; Brooks et al. 1980). Previous studies on warfarin susceptibility in the bandicoot rat showed two levels of susceptibility. In Rangoon, there was high mortality after a 6-day feeding period with single male and female survivors consuming 3.0 and 2.7 mg/kg warfarin, respectively (Brooks et al. 1980), while in Karachi, male and female survivors consumed maximum doses of 97 and 87 mg/kg warfarin respectively (Greaves and Rehman 1977). The present population would appear to be more tolerant to warfarin than the Rangoon population but more susceptible than the Karachi population. Brooks et al. (1980) considered these variations in susceptibility to be attributable to the selection pressure resulting from the consistent use of first-generation anticoagulants, to geographical variations, and to the distribution of bandicoot rats as isolated races in both urban and agricultural environments.

In the present study, one can speculate that survival of the female animal and its potential descendants following a prolonged warfarin treatment could initiate a resistance focus. The amount of warfarin consumed by this female rat is similar to that consumed by survivors in the Karachi study (Greaves and Rehman 1977).

In this study, using a 0.003% warfarin formulation, complete mortality was achieved with a feeding period of 6 and 7 days for males and females, respectively, thus demonstrating that bandicoot rats are highly susceptible to warfarin. However, Probit analysis calculated LFP_{50} values of 1.9 days and 3.4 days, and LFP_{99} values of 15.5 days and 9.1 days for males and females, respectively. The LFP_{99} values are much longer than expected, particularly for male animals.

Consumption of test bait (and thus active ingredient uptake) was reduced as the test progressed (Table 1). Among the 88 affected rats, 9 males and 14 females exhibited the 'stop feed' effect, and the majority of these belonged to test groups that were fed warfarin for 5 days or more. This 'stop feed' phenomenon has also been recorded and described in both the Norway rat and the house mouse (Rowe and Redfern 1964; Drummond and Wilson 1968; Lund 1988).

In the analysis of the susceptibility baseline data, Probit analysis will assume that the incremental increase in feeding period will be equal throughout the test period. However, in the present study (Table 1), the incremental increase of bait consumed was reduced on the 5th, 6th and

Table 2. Mortality in the bandicoot rat after no-choice feeding on bait containing 0.025% warfarin for 4 days.

Sex	Body weight (g) mean ± se	Mortality (dead/tested)	Amount of active ingredient (mg/kg) consumed	
			Non-survivors mean ± se (range)	Survivor
Males	353.0 ± 17.2	6/6	63.1 ± 11.3 (54.6–81.1)	–
Females	308.4 ± 13.5	12/13	60.9 ± 7.7 (43.8–72.4)	79.12[a]

[a] Subsequent feeding till death on warfarin (0.025%) resulted in mortality on day 8 after consuming 82.77 mg/kg. Daily intake was: 8.75, 14.29, 16.79, 14.46, 12.77, 8.30, 7.23 and 0.18 mg/kg.

7th days. This would seriously compromise the Probit analysis, particularly for estimates of higher percentiles. The problem would appear to be greater for males than for females, and would account for the lower LFP_{50} value and higher LFP_{99} value of males compared to females, despite the fact that dose mortality data indicates that males are more susceptible to warfarin than females.

The test procedures suggested by WHO (1982) and EPPO (1995), requiring the strength of the anticoagulant rodenticide to be adjusted so that some of the susceptible population will survive after 4 to 6 days feeding on anticoagulant, is considered flawed, because of the ‘stop feed’ effect. One possible option might be to assess mortality on the basis of active ingredient intake rather than duration of the feeding period. However, a reduced anticoagulant strength could undermine the efficacy of the compound in use due to possible metabolic clearance of low daily doses of anticoagulant—an aspect that may not be related to genetic resistance.

Lethal feeding period tests are a useful tool for the assessment of physiological resistance, and can be used to provide a realistic assessment of the likely impact of resistance in the field situation. However, where feeding periods extend beyond 4 days, the ‘stop feed’ effect can affect results, either by causing an overestimation of the LFP_{99} discriminating dose for susceptible animals, or by misclassifying a susceptible animal as resistant in the subsequent application of the resistance checking test.

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Factors influencing the occurrence of rodent infestations in an inner city area of Manchester

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Abstract. Cheetham Hill is an inner city area of Manchester, England. A study area that was typical of other areas of the city was defined which contained 253 domestic properties. The area has a diverse mix of domestic properties ranging in age and type from pre-1919 terraces to more recently built detached/semi-detached dwellings in public and private ownership. Tracking plates were used to detect rat activity externally, but little evidence was found. Only two properties in the area were found to have indoor rat activity. A qualified surveyor gained access to 117 properties to undertake a thorough constructional survey. Fifty per cent of the properties had indoor mouse infestations. The factors associated with these indoor infestations were examined. Variables that were significantly associated with indoor mouse infestations were screened and allocated to one of four models. Binary logistic regression was used to explore the ability of these models, including a total model, to predict the likelihood of indoor mouse infestations. All five models significantly improved the ability to predict indoor mouse infestations in the study area. Whilst the model which had all variables included was the most reliable in predicting infestation, those which relied on general factors (tenure of the property, date of construction, and type of dwelling) or the external structure (state of the damp-proof course, external front and back overall assessment, gaps on the door thresholds, and the presence of airbricks) also proved useful. These models could be used to investigate other urban areas to confirm their reliability in predicting indoor mouse infestations. The need for a review of the way in which rodent control services are resourced and delivered in the United Kingdom is discussed.

Introduction

The two main commensal rodent species in the United Kingdom (UK) are *Mus domesticus* and *Rattus norvegicus.* Both pose a potential threat to public health through the diseases they may carry and, therefore, an understanding of their distribution and potential contact with man is important in trying to estimate the actual risks posed. The English House Condition Survey (EHCS) is undertaken every 5 years and examines the state of the housing stock in the UK. The 1996 survey form included questions relating to rodent infestations and provided an important indication of the levels of rodent infestations associated with domestic properties. This survey reported modest infestation rates of 1.83% for mice living indoors, 0.23% for rats living indoors, and 1.6% for rats living outdoors (Langton et al. 2001).

Colvin and Jackson (1999) emphasised the need to define the characteristics within a habitat that favour infestation and Advani (1995) demonstrated that, in urban environments, areas with inadequate sanitary and building maintenance measures had higher numbers of rats. Socio-economic factors were also found to influence the ecology of commensal rodents (Childs et al. 1991).

In the UK, a plethora of organisations is involved in controlling commensal rodents in the urban environment (Murphy and Oldbury 2002). Local authorities in the UK have powers to enforce statutory instruments to protect public health, and although there is no statutory requirement for them to undertake treatments to control rodents in domestic premises, many local authorities do provide such a service. The way in which this service is operationalised varies across the UK with local political pressures and sensitivities determining decisions regarding whether charges are levied for the service. Charging is often related to historical (and often erroneous) views about rats and mice, with rats being classified as public health pests (and therefore usually treated free of charge in domestic premises) and mice as nuisance pests (with a charge made for domestic treatments). Some local authorities attempt to offset the cost of their public health pest control activities by charging commercial rates for treatment of nuisance pests such as wasps, garden ants and mice. In addition to the services that may be offered by local authorities, private pest control companies offer services to eradicate pests in domestic properties, and householders are able to purchase rodenticides for personal use.

Local authorities that do undertake domestic infestation treatments are often hampered in their efforts to effectively control domestic mouse infestations. Whilst rigorous legislation relating to food premises exists which provides authorised officers of the local authority (usually

Environmental Health Officers, EHOs) with powers of entry, the law relating to commercial non-food and domestic premises is relatively weak. The main piece of legislation used in these settings is the *Prevention of Damage by Pests Act 1949* (PDPA). This legislation was introduced primarily to protect agricultural crops against rodent damage and its fundamental weakness is that it does not furnish EHOs with powers of entry. Although some local authorities have introduced local legislation to provide such powers of entry (for example, the *Greater Manchester Act 1981*), many do not have such legislation in place. Thus, if an infestation is confirmed within a terraced property, EHOs are often unable to gain access to all properties to treat the block if the owner refuses entry.

A tool to predict the likely presence of domestic mouse infestations would prove useful in two ways. Firstly, it could be used as supporting evidence to convince a Magistrate of the need to issue a warrant allowing access to properties to confirm the presence of an infestation and specify measures to eradicate the infestation. Secondly, and more importantly, it would provide evidence to those who set the resource levels available for pest control work that there is a need to undertake block treatments in certain situations to ensure long-term and cost-effective control. Meyer and Drummond (1980) raised concerns about the effectiveness of pest control services that only react to public reports of infestations. By treating individual premises in an infested block, the likelihood of re-infestation from neighbouring properties is high. While they acknowledged that the initial costs of undertaking block treatments was significant, they found that once the infestation had been reduced by the first systematic treatment, the extra cost of keeping it low was financially justified.

This paper examines the reliability of using external and internal factors in predicting the likelihood of the presence of indoor mouse infestations.

Materials and methods

The research area in Cheetham Hill, Manchester, is a typical inner city residential area with a mixture of privately and publicly owned domestic properties ranging in age from pre-1919 terraces to post-1964 detached and semi-detached properties. The research area encompassed 253 residential properties. A qualified surveyor gained access to 117 properties and surveyed them internally and externally. Only 2 of the 253 properties in the area had evidence of rats inside the property, and only 4 of the196 tracking plates placed externally throughout the study site showed evidence of rats outside the properties (see Taylor and Quy 1973 for techniques used). The analysis presented is, therefore, based on evidence of mouse activity inside the properties.

The surveyor inspected each property internally and externally and scored the general area with regard to four general aspects of the properties (described below). The surveys were undertaken between January and May 2002. Residents either volunteered or were recruited during contact with the research team and appointment times convenient to the resident were agreed. As the same surveyor undertook all of the surveys, consistency was assured. He did not attempt to estimate the size of the population but recorded evidence (presence of rodent droppings, hairs, gnawing, runs, smells, damage to goods, footprints/tail swipes) of internal mouse infestations. In addition to searching for signs of rodent infestation, he also asked the resident whether he/she thought the property was infested and to show him the signs of infestation. A survey report for each property was completed, and data were compiled in an SPSS electronic database. Cross-tabulations were carried out against presence or absence of indoor mouse infestations, and where significant associations were found, the variables were screened and spurious results excluded. Variables that were significant, plausible and relatively easy to assess in the field were grouped into four categories (see Table 1 for details of the characteristics included in each model):

- general characteristics of the property;
- external structure;
- general food hygiene within the kitchen area; and
- general environment external to the property.

Using these categories, four models were tested using binary logistic regression to examine the goodness of fit in predicting indoor mouse infestations. In addition, all variables used in the models were entered into a total model.

Results and discussion

Fifty per cent of the properties surveyed were found to be infested with mice indoors. This is significantly higher than the levels of indoor mouse infestations reported in the EHCS ($\chi^2 = 933$; $p < 0.001$). Whilst the sample size in Cheetham Hill is modest, this difference may highlight a potential problem with the way in which the EHCS data were collected and weighted. Meyer and Drummond (1980) reported the effects of clumping in mouse infestations, and the EHCS, whilst giving a good indication of infestations across the UK, may miss the clumping effect, particularly in urban areas with a high proportion of older terraced properties.

The relationship between specific variables and the presence of mouse infestations was explored using a chi-square analysis (Table 1). Whilst individually these associations are valuable and provide important information about the factors which may influence the presence of an indoor mouse infestation, using them within a model provides a mechanism to examine the relative importance of difference characteristics within the environment. Results from the four models plus the total model showed that for each model the drop in the –2 log-likelihood statistic was significant (Table 2), confirming that each significantly improved the ability to predict the presence of domestic mouse infestations. The Hosmer and Lemeshow test statistics were all non-significant, confirming a good fit between the logistic equation and the observed data.

Table 1. Variables related to four general aspects of the properties surveyed with χ^2 statistics, significance levels and percentage mouse infestation for each variable (df = degrees of freedom, n = number in sample, LA = local authority).

GENERAL CHARACTERISTICS (Model 1)		
Tenure of the property ($\chi^2 = 9.04$, 2 df, $p = 0.011$)		
Variable	n	% infested
Privately owned	84	48
Privately rented	23	71
LA rented	10	20
Date of construction ($\chi^2 = 42.14$, 3 df, $p < 0.001$)		
Pre-1919	60	77
1919–1939	6	67
1940–1964	3	67
Post-1964	48	15
Dwelling type ($\chi^2 = 31.7$, 1 df, $p < 0.001$)		
Detached/semi-detached	43	16
Terraced/flats	74	70
EXTERNAL STRUCTURE (Model 2)		
Damp-proof course (front and back) ($\chi^2 = 25.58$, 1 df, $p < 0.001$)		
Satisfactory	72	32
Unsatisfactory	45	80
External front and back overall assessment ($\chi^2 = 5.4$, 1 df, $p = 0.02$)		
Satisfactory	100	46
Unsatisfactory	17	76
Gaps on external door thresholds ($\chi^2 = 14.11$, 1 df, $p < 0.001$)		
Gaps present	30	80
No gaps	87	40
Airbricks ($\chi^2 = 11.86$, 1 df, $p = 0.001$)		
No airbrick present	50	32
Airbrick present	67	64

KITCHEN (Model 3)		
Kitchen food storage ($\chi^2 = 15.85$, 2 df, $p < 0.001$)		
Variable	n	% infested
Good	34	23
Satisfactory	69	58
Poor	14	79
Kitchen refuse storage ($\chi^2 = 20.52$, 2 df, $p < 0.001$)		
Good	34	23
Satisfactory	69	55
Poor	14	93
Kitchen under-cupboard access ($\chi^2 = 9.77$, 1 df, $p = 0.002$)		
Yes	73	62
No	44	32
Kitchen overall hygiene ($\chi^2 = 14.35$, 2 df, $p = 0.001$)		
Good	34	23
Satisfactory	64	59
Poor	19	68
GENERAL ENVIRONMENT (Model 4)		
Vacant properties $\chi^2 = 19.09$, 1 df, $p < 0.001$)		
Little problem	51	27
Substantial problem	66	68
Industrial waste/rubbish ($\chi^2 = 19.09$, 1 df, $p < 0.001$)		
Little problem	51	27
Substantial problem	66	68
Domestic waste/rubbish ($\chi^2 = 19.09$, 1 df, $p < 0.001$)		
Little problem	51	27
Substantial problem	66	68
Evidence of residents feeding pigeons ($\chi^2 = 17.57$, 1 df, $p < 0.001$)		
Little problem	50	28
Substantial problem	67	67

Table 2. Statistics for binary logistic regressions (models 1–4 and total model).

	Model 1	Model 2	Model 3	Model 4	Total model
Initial –2 log-likelihood	162.2	162.2	162.2	162.2	162.2
Model –2 log-likelihood	104.1	123.7	130.5	141.9	74.2
Chi squared	58.1	38.5	31.6	20.32	88.0
Significance	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Hosmer Lemeshow test	$p = 0.992$	$p = 0.838$	$p = 0.997$	$p = 0.964$	$p = 0.858$
R_L^2	0.358	0.237	0.195	0.125	0.542
% sample correctly classified	82.1	72.6	69.2	70.1	83.8

The R_L^2 statistic (the proportional reduction in the absolute value of the log-likelihood) confirmed that whilst the total model was best at predicting the outcome variable, model 1 provided the next best predictor of internal mouse infestation. The ability of the models to correctly classify each case ranged from 69.2–83.8%, with the total model again proving to be the most reliable.

Although the total model was the most reliable, the collection of all the data specified in this model is resource intensive and in some instances, where access to the property is denied, impossible. The use of external characteristics that are relatively easy to assess may provide a useful indication of the likelihood of internal mouse infestations. The high prevalence of infestations in older, privately rented, terraced properties with external indicators of poor general maintenance concurs with previous studies and these may be more useful indicators of infestation than internal hygiene measures. The problems of leaving potential pockets of infestation within blocks are well recognised (Rennison and Shenker 1976). However, the constraints of the current legal framework in the UK, together with the variability in charging policies, result in operational difficulties when attempting to treat whole blocks.

The failure of those charged with setting public health budgets within local authorities to recognise the long-term advantages of block treatments results in a reactive service dominating the approach to treating domestic infestations in the UK. This is further complicated by the vexed issue of charging for domestic mouse infestation treatments. Indeed, some local authorities are scrutinising their pest control services and deciding whether to privatise them. This is unlikely to improve the coordination and delivery of public health services related to urban rodent control.

These models have provided a reliable indicator of the likelihood of infestation, but caution must be applied to their applicability in other urban areas. The sample size used in the models is modest and the factors found to influence indoor mouse infestations may be unique to Cheetham Hill. Further rigorous testing of the models in other urban settings is required to confirm their reliability and to enable others to use them as a tool for arguing for the need to undertake block treatments. More intensive analyses of the results will also refine the relative importance of the variables included in each model.

Conclusions

The fragmented approach to urban rodent control in the UK is cause for concern. The primary aim of local authorities is to protect public health, but the current legislative framework for rodent control and the manner of resourcing the service make it difficult to ensure that treatments are effective in protecting human health. This is further complicated by a lack of coordination between those providing pest control services in the public and private sectors. The results of the Cheetham Hill study confirm the need for a holistic approach to block treatments. Meyer and Drummond (1980) emphasised the need for such an approach over two decades ago, but little progress in implementing such a policy has been made. Urban pest control is often viewed as a low priority, and there is, therefore, little hope of a review of the legislative framework. Sadly, a serious outbreak of rodent-borne disease within an urban setting is likely to be the only driver to provide the impetus for such a review. Although no evidence of behavioural or physiological resistance to rodenticide baits was found in the mouse populations in Cheetham Hill, resistance has been confirmed in other mouse populations within the UK (Humphries et al. 1992), and if these resistant populations increase, their avoidance of bait and bait stations may further hamper control measures.

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Investigating residents’ perceptions of urban rodents in Manchester, UK

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Abstract. The need to understand and explore the perceptions about urban rodents in communities is an important and often neglected area of urban rodent control programs. This study investigated the perceptions of a group of residents living in an inner city area of Manchester about urban rodents. The study area contained 253 domestic properties, and a questionnaire was sent to all these properties. A response rate of 88.5% was achieved. Forty-four per cent of residents stated that they currently had mouse infestations in their property, 44% stated they did not, and the remaining 12% were unsure. Residents were asked to indicate their levels of agreement with nine statements about rodents. The vast majority clearly understood the potential risks to health posed by rodents and that infestations were likely to spread through blocks. The majority of respondents agreed with the statement that poisons were the best way to get rid of mice (65%) and rats (71%), suggesting that they may overestimate the efficacy of such an approach and underestimate the impact of environmental management. This view was supported by analysis of their approaches to treatments, with a heavy reliance on the use of poisons and little attempt to undertake environmental management. Significant differences in opinions were found when the sample was split into those with and without experience of domestic mouse infestations. This study underlines the importance of providing communities with clear, consistent advice on the biology of urban pests and coordinated approaches to control. The need for fundamental research on the biology and control of rodents in the urban environment is acknowledged.

Introduction

The need to understand and explore the risk perceptions of communities is an important and often neglected area of urban rodent control programs. Only by establishing these factors can effective risk communication with the public be successfully undertaken. Previous attempts to involve local residents in control programs have reported varying degrees of success (Margulis 1977; Colvin and Jackson 1999; Lambropoulos et al. 1999). However, if communities are not centrally involved by ensuring their beliefs and perceptions of urban rodents are incorporated into control programs, then they may believe that rodent control is someone else’s responsibility and that they have little to contribute to control programs. A small, but growing, body of empirical work in risk communication and related fields has investigated the effects of different message formats. No single presentation format has been found to be unequivocally the best, and the preferred format appears to vary depending on whether the purpose of the risk communication effort is to educate, to affect risk perceptions, or to motivate people to take appropriate actions. Characteristics such as the audience’s level of knowledge and education; their mental models, attitudes and beliefs about the issue at hand; their level of receptivity and openness to the ideas being communicated; and their concerns about the issue will also affect the way in which risks are communicated (Bier 2001).

Rowan (1991) identified five possible goals of risk communication: building trust in the communicator; raising awareness (e.g. of the potential disease hazard of rodents); educating; reaching agreement (e.g. on a particular strategy for ensuring long-term control of rodent infestations); and motivating action (e.g. encouraging residents to adopt an integrated control strategy to reduce levels of infestation). Because of this multiplicity of purposes, different strategies of risk communication may be appropriate for different goals.

The success of both *Mus domesticus* and *Rattus norvegicus* can be largely attributed to their ability to live in close association with man (Rowe 1973; Shenker 1973; Childs et al. 1991). Although rats and mice have been found to harbour a wide array of pathogens, the actual magnitude of the public health threat posed by rodents remains unclear (Gratz 1994; Childs et al. 1998). An understanding of the distribution, behaviour and potential contact of urban rodents with humans is essential in trying to estimate this public health risk. Different perceptions in the attitudes of the public to rats and mice may influence the way in which they implement their own control strategies and such actions may inadvertently facilitate the establishment of chronic infestations. This study examined the perceptions of residents to rodents and examined the beliefs they have about approaches to treatments.

Materials and methods

Cheetham Hill is an inner city area of Manchester with a history of pockets of chronic mouse infestations, which local residents regularly reported to the politicians representing that area. However, a review of Manchester City Council's pest control section records found little evidence of the reporting of these infestations. The charging policies of local authorities on rodent treatments vary throughout the United Kingdom (UK) and are often related to historical (and often erroneous) views about rats and mice, with rats being classified as public health pests (and therefore usually treated free of charge in domestic premises) and mice as nuisance pests (with a charge made for domestic treatments). Whilst Manchester City Council's pest control section does undertake domestic mouse infestation treatments, up until May 2002 a significant charge was levied for such treatments (apart from those occurring in Council-owned properties) and may partly explain the low numbers reported to them.

A site within Cheetham was selected and the boundaries were defined to ensure that the study area reflected a 'typical' inner city Manchester area in terms of property types (including terraced, semi-detached, detached and cottage flats ranging in age from pre-1919 terraces to post-1964 semi-detached houses), ownership (public/private) and the demographics of the population. The study site contained 253 residential properties. Community events before the fieldwork commenced, followed by regular newsletters, ensured that the residents within the study site were aware of the aims of the project. All householders in the research area were asked to complete and return a questionnaire that sought general and specific information on personal details, experience of mouse infestations and general beliefs about rodents. All data from the questionnaire were entered into a SPSS database for analysis.

Results and discussion

Two hundred and twenty-four questionnaires were returned, giving a response rate of 88.5%. This high response rate was achieved by sending out further questionnaires to non-respondents and by the efforts of community members in encouraging non-respondents to complete and return them.

Mouse infestations

Forty-four per cent of respondents reported that they currently had a mouse infestation in their property, 44% stated that they did not, and 12% reported that they did not know. Those respondents who did not currently have an infestation were asked whether they had experienced mouse infestations in the past and 41% stated that they had. The reliability of this information was validated by comparing it with the results from mouse tracking plates left in 202 properties, which confirmed mouse activity in 73 (36%). Whilst lower than that estimated by the residents, it does show that the data provided by the residents are reasonably reliable. The overall level of mouse infestation is considerably higher than that quoted by Langton et al. (2001) of 1.83%. Whilst the two studies have fundamental differences in the sampling techniques used, the differences in infestation rates are striking and suggest that the random sampling of properties reported by Langton et al. (2001) may miss concentrated pockets of mouse infestation.

Rat infestations

Although the project focused primarily on mouse infestations, several questions related to rats. Respondents were asked whether they thought rats had been present in the research area during the previous 12 months. Forty-eight per cent thought rats had been present, 45% did not know and only 7% believed there were no rats present. They were asked to clarify what information they had used to come to this view. The most common evidence, cited by 59% of respondents, was that someone else had told them. Fifty six per cent stated that they had seen rats, 15% stated they had heard them, and 3% gave other reasons. Residents were asked to indicate on a map the areas where they had seen rats. Of the 274 rat tracking plates were placed in the study area (6.65 ha) for four days (see Taylor and Quy 1973 for techniques), only four plates showed positive rat activity. This would suggest that residents may overestimate the presence of rats and may amplify the risks posed by rats. Only 31% of those who believed rats were present had reported it to anyone, despite the fact that the local authority provides free treatments to control domestic infestations.

Concerns about the presence of rodents

Respondents' concerns about rodent infestations were explored. Residents were asked to indicate their level of concern about mouse and rat infestations. Seventy per cent indicated that they were very concerned about mouse infestations, 20% reported they were concerned, and 4% reported they were not concerned. Eighty-one per cent stated they were very concerned about rat infestations, 15% stated they were concerned, and 3% reported they were not concerned. There was a significant relationship between levels of concern about rats and mice ($\chi^2 = 107.6$, df = 4, $p < 0.0001$). Results from intensive tracking show little evidence of rats in the area, but high levels of mouse infestations, yet high levels of concern about both species were found.

Respondents were asked to specify why they were concerned about mouse infestations ($n = 132$) and the largest group (47%) cited diseases or that they were unhealthy. Fifteen per cent mentioned that they were concerned about the problems they brought to the area and 14% stated that they did not like them.

Respondents were asked to consider nine statements and to indicate on a four-point scale their agreement with each statement (Table 1). The analysis that follows was based on the valid responses, and missing cases were ignored.

The link between the presence of rodents and the transmission of disease was well understood by respondents with 96% and 99%, respectively, agreeing or completely agreeing that people could catch diseases from mice and rats. However, anecdotal evidence suggests that residents are unclear as to the nature of these risks and may be overestimating the actual risks posed. Cheetham Hill has suffered from chronic pockets of mouse infestations for many years and it was, therefore, predictable that the majority of respondents (73%) would acknowledge the difficulties of eradicating such infestations.

The high levels of agreement that if their neighbour has mice then they are likely to get mice (94%) suggests that respondents appreciate the importance of constructional features in facilitating infestations and the need to treat all properties in a block.

There was a fairly even split between those who agreed (52%) and disagreed (48%) with the statement that mice are more likely to live in dirty houses, which suggests that not all of the respondents may appreciate the need for high levels of hygiene when attempting to eradicate mouse infestations.

Chemical poisons will usually form an essential element of a rodent control strategy, but analysis of the responses on whether using poisons is the best way to get rid of rats (71%) and mice (65%) suggests that residents may overestimate their efficacy in controlling rodent populations. The importance of environmental improvements may need to be emphasised.

Whilst the majority of respondents believed that poisons should be removed when mice were not present, over a third (35%) agreed or completely agreed that leaving poisons down all the time was a good strategy to adopt. Respondents may not be aware that leaving poisons down may result in the poison losing potency and may also encourage the development of resistant mouse populations.

There was clear confusion about where rats are likely to live, with 71% agreeing that rats live inside houses. This may have been influenced by media reports, which frequently cite rodents gaining entry to premises via toilets etc. This may also partially explain the high levels of concern regarding the presence of rats in the area.

To investigate whether views varied between those respondents who had experience of infestations (either currently or previously) and those who had not, the respondents were split into two groups: those with (n = 154) and without (n = 64) infestation experience. The responses to the nine questions were collapsed into two categories (completely agree/agree and disagree/completely disagree) and chi-squared tests applied. No significant differences were found to the responses for: disease transmission from mice (p = 0.174) and rats (p = 0.843); risk of infestation from neighbouring property (p = 0.0550); leaving poisons down all the time (p = 0.913); using poisons is the best way to get rid of rats (p = 0.218); or that rats live inside houses (p = 0.55). Significant differences between those with and without previous experience of mouse infestations were found in the responses to: easy to get rid of mice (χ^2 = 6.45, df = 1, p = 0.011); mice more likely to get live in dirty

Table 1. Analysis of the responses to nine statements about rodents (n = 224; CA = completely agree, A = agree, D = disagree, CD = completely disagree). The percentages presented relate to valid cases; the number of missing cases is shown below each statement.

Statement	CA	A	D	CD
People can catch diseases from mice	137	61	7	1
(Missing cases = 18)	66%	30%	3%	<1%
People can catch diseases from rats	153	51	3	0
(Missing cases = 17)	74%	25%	1%	–
It is easy to get rid of mice	14	41	100	48
(Missing cases = 21)	7%	20%	49%	24%
If my neighbour has mice I will get mice too	99	93	13	0
(Missing cases = 19)	48%	45%	6%	–
Mice are more likely to live in dirty houses	50	54	77	20
(Missing cases = 23)	25%	27%	38%	10%
Using poisons are the best way to get rid of mice	48	78	55	14
(Missing cases = 28)	25%	40%	28%	7%
Using poisons are the best way to get rid of rats	73	66	37	20
(Missing cases = 28)	37%	34%	19%	10%
Always leave poisons down, even if you don’t have mice at the moment	27	39	73	50
(Missing cases = 35)	14%	21%	39%	26%
Rats live inside houses	70	68	49	6
(Missing cases = 31)	36%	35%	25%	3%

houses ($\chi^2 = 4.16$, df = 1, $p = 0.041$) and using poisons is the best way to get rid of mice ($\chi^2 = 6.7$, df = 1, $p = 0.01$).

Respondents were asked how they thought the mice had got into their property ($n = 132$). The largest proportion (48%) stated that they did not know. Other reasons included via floorboards (15%), outside doors (11%), general holes (7%), and the cavity walls (5%). Residents were also asked where they thought the mice were coming from ($n = 149$). The largest proportion thought that mice were coming from the garden or outside (34%). Thirty-two per cent thought mice were coming from next door and 20% stated that they did not know where the mice were coming from.

Control measures

Analysis of the approaches adopted by those in the study area to control mouse infestations was undertaken. Of the 154 respondents who had experienced infestations either currently or previously, 77% had attempted to get rid of the mice themselves. Respondents were given four options (use of live-traps, snap-traps, poisons and 'other' methods) and asked to indicate all the methods they had used. Results are presented in Table 2. Poisons were used by 62% of the respondents, traps (either live or snap) by 56% of respondents and other methods by 13%. Only two respondents mentioned the need for improved hygiene and maintaining the fabric of the building. Thirty-six respondents reported that they had not attempted to control the infestation. It is unclear what influenced their decisions not to undertake treatments themselves.

Table 2. Control strategies adopted by respondents ($n = 116$).

Control measure	*n*	%
Poison only	36	31
Poison and snap-trap	18	15
Snap-trap only	16	14
Live-trap only	10	9
Other combination	7	6
Poison and live-trap	9	8
Live-trap, snap-trap and poison	9	8
Other methods only	8	7
Live-trap and snap-trap	3	3

Conclusions

Colvin and Jackson (1999) emphasised the importance of coordinated efforts supported by technical leadership at the local level in promoting successful urban rodent control programs. The results of this study underline the importance of clear, consistent information from those coordinating urban rodent control. Misconceptions regarding the risks posed by rodents, the most effective strategies for control and the importance of environmental management need to be fully explored and appropriate educational material developed and delivered. However, without the underpinning research to establish the actual risks posed by urban rodents, it is difficult to communicate these risks effectively.

Inconsistencies in the approach to the control of rats and mice as a result of political pressures mean that residents receive mixed messages about the risks rodents may pose and the most appropriate approaches to control. If residents believe that the use of poisons is the best way to gain control, then they will put little effort into environmental management—therefore they need information that is reliable and consistent on integrated rodent pest management and the contributions they can make to long-term control. If they do not feel any sense of ownership to the problems associated with infestations, then approaches to coordinated control will remain piecemeal and rodent populations will continue to exploit the plethora of niches available in the urban environment.

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Effects of the addition of L-histidine on the toxicity of zinc phosphide in laboratory rats and mice

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Abstract. The efficacy of rodenticidal compounds can be enhanced greatly if the acceptance or palatability is improved. In this study, the effect of the addition of L-histidine (which yields histamine, a very active substance physiologically for decarboxylation and a useful acid-secreting stimulant) on the toxicity of the rodenticide zinc phosphide was determined using laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*). The animals were fasted for 0, 6, 12, 18 or 24 h and then fed *ad libitum* with baits containing zinc phosphide (2%) alone or zinc phosphide (2%) plus L-histidine (0.004%).

Feeding of zinc phosphide alone resulted in 100% mortality in rats ($n = 8$) and mice ($n = 8$) when the fasting period was less than 24 or 18 h, respectively. One of eight rats fasted for 24 h, and one of eight mice fasted for either 18 or 24 h, survived. There was 100% mortality in all rats and mice fed zinc phosphide plus L-histidine. Uptake of this bait by rats was significantly greater and the time to death shorter than in the groups fed zinc phosphide only.

Introduction

In rodent pest management programs, poison baiting is the most widely used technique throughout the world (Gratz 1973; Muktha Bai 1996). Although rodenticides can be incorporated either in bait, dust or water formulations (Pratt 1983), they are generally included in food baits to achieve good control. Much effort has been made to improve the palatability of rodent baits to ensure maximum ingestion by the target rodent pests and thereby improved efficacy. A survey of the literature indicates that several attempts have been made to improve the palatability of various rodenticides, including alpha-chlorohydrin (Ericsson et al. 1971), alpha-chlorolose (Greaves et al. 1968; Cornwell 1970), norbormide (Greaves et al. 1968; Cornwell 1970; Jackson 1974), strychnine (US Patent 1960), warfarin (Cornwell 1970; Abrams and Hinkes 1974), and zinc phosphide (Cornwell 1970; El-Sebae et al. 1978; Anonymous 1986). These studies have involved a variety of methods such as encapsulation and micro-encapsulation. The results obtained have shown, in most cases, some improved palatability, but mortality was reduced. However, there is limited information available regarding the effect of compounds/additives having different pharmacological or physiological modes of action on the palatability of rodenticides.

Recent outbreaks of hantavirus pulmonary syndrome (HPS) and resistance to second-generation anticoagulant rodenticides have demonstrated a need for use of acute rodenticides in rodent pest management programs (Childs et al. 1994). A more effective formulation of these acute rodenticides would be appropriate. In this study, the responses of laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*) to zinc phosphide (2%) (an acute rodenticide) were determined after they had been deprived of food for different periods of time (0–24 h). These responses were compared with those of fasted rats and mice fed zinc phosphide bait (2%) also containing L-histidine (0.004%). In the stomach, the histidine is decarboxylated to yield histamine, which stimulates acid secretion and aids the liberation of the phosphine gas.

Materials and methods

Baits

Zinc phosphide (technical grade, 94% purity; Tata Fison, Bombay) and L-histidine (Fluka Ag, Switzerland) were used. These were mixed thoroughly with the basal diet (wheat flour, 26.6%; ragi flour, 26.6%; chickpea flour, 26.7%; peanut oil, 10%; casein, 6.7%; calcium carbonate, 0.7%; shark liver oil, 0.7%; and common salt, 2%) to the required concentrations of (i) 2% zinc phosphide or (ii) 2% zinc phosphide plus 0.004% L-histidine.

Animals

Adult albino rats (*Rattus norvegicus:* CFT-Wistar strain; males, 180–220 g; females, 160–190 g) and adult albino mice (*Mus musculus*: males, 25–35 g; females, 18–30 g) were maintained under 12 h dark and 12 h light periods at 25°C ± 5°C in the animal house at the Central Food Technological Research Institute. Ten groups of eight rats (four males and four females) each were housed individually in polypropylene cages (410 × 282 × 150 mm) and were provided with food and water ad libitum. Similarly, mice were also divided into ten groups of eight animals each but were housed in groups of four per cage (290 × 220 × 140 mm). All the animals were acclimatised for a period of 7 days. These experiments were approved by the Institute's Animal Ethics Committee.

Test procedure

All animals were held on a standard diet with water *ad libitum* for 5–7 days before the experiment commenced. The 10 groups of rats and mice were then deprived of food for a specific period (0, 6, 12, 18 or 24 h). For each period, two groups of animals (for both rats and mice) were used, and at the end of the fasting period they were given either baits containing 2% zinc phosphide alone or 2% zinc phosphide plus 0.004% L-histidine. The baits were placed in the cages for one night only and the next morning the residues were weighed and intakes calculated. The animals were closely monitored for symptoms (such as restlessness, heavy breathing, ataxia, paralysis of hind limbs etc.), mortality and time to death throughout the experimental period. The survivors were observed further for a period of 3 weeks while they were maintained on stock diet and water *ad libitum* and the results obtained were statistically analysed. The results of rats fed zinc phosphide and zinc phosphide plus L-histidine for different fasting periods were compared for parameters such as body weight, bait intake, and active ingredient intake using analysis of variance, followed by Duncan's new multiple range test whenever significant results were obtained (Douglas 1991).

Results

Laboratory rats (*R. norvegicus*)

Although at 'zero' h of fasting the mean ingestion of the bait was low (1.06 ± 0.5 g/rat) compared to the previous day's food intake of 15.2 ± 0.9 g/rat, all rats died within 8 h (range: 6–7.30 h) (Table 1). For fasting periods of 6, 12, 18 and 24 h, the mean ingestion of bait per rat was greater (2.6 ± 1.2, 3.5 ± 1.3, 4.1 ± 2.0 and 3.25 ± 1.6 g, respectively), and mortality was 100%, except in the group fasted for 24 h before exposure to the bait, where one rat survived. The time to death ranged from 4–20 h (Table 1).

The groups of rats given the baits containing zinc phosphide plus L-histidine after the period of fasting ingested almost twice as much of this bait. This was significantly different from the corresponding values of animals given zinc phosphide alone. The average time to death was reduced to approximately 6 hours and all rats died (Table 1).

Table 1. Response of laboratory rats (*Rattus norvegicus*) to baits containing zinc phosphide (2%) either alone or with added L-histidine (0.004%) (values are mean ± se of eight rats in each group). Means of the same column followed by different letters differ significantly ($p < 0.05$) according to Duncan's new multiple range test (** = very highly significant ($p < 0.001$), * = highly significant ($p < 0.01$), ns = not significant ($p > 0.05$). The parameters were also compared with the corresponding values of zinc phosphide (2%) fed animals using student's *t*-test.

Body weight (g)	Fasting period (h)	Food intake before fasting (g)	Poison bait intake (g)	Intake of active ingredient (mg/kg body weight)	Mean time to death (h) (range)	Mortality (%)
Zinc phosphide (2%)						
208.5 ± 10.7a	0	15.2 ± 0.9a	1.06 ± 0.5a	102.7 ± 47.5a	7.10 (6–7.30)	100
210.5 ± 13.8a	6	16.1 ± 2.0a	2.62 ± 1.2b	241.7 ± 121.4ab	12.20 (6–15)	100
207.2 ± 8.6a	12	17.4 ± 2.4a	3.50 ± 1.3b	330 ± 124.5bc	12.20 (7–20)	100
208.1 ± 6.3a	18	16.5 ± 2.2a	4.12 ± 2.0b	397.7 ± 192.7c	14.0 (4–20)	100
207.9 ± 5.5a	24	18.7 ± 5.8a	3.25 ± 1.6b	309.6 ± 148.2bc	12.0 (4–20)	87.5
sem: ±3.26		±1.13	±0.49	±47.97		
Zinc phosphide (2%) plus L-histidine (0.004%)						
169.9 ± 14.1a**	0	16.0 ± 2.9a*	3.62 ± 0.9a**	399.7 ± 195a**	4.0 (2.30–8)	100
170.2 ± 14.8a**	6	17.6 ± 2.6a*	7.12 ± 1.1b**	834.6 ± 80.2b**	6.16 (3–12)	100
166.8 ± 11.9a**	12	16.0 ± 2.3a*	6.2 ± 1.5b**	745 ± 142.2b**	6.0 (4–12)	100
168.8 ± 13.2a**	18	17.0 ± 2.0a*	7.2 ± 1.5b^{ns}	841.8 ± 118.4b**	6.32 (3–12)	100
167.9 ± 12.3a**	24	16.9 ± 1.6a*	7.2 ± 1.1b^{ns}	851.2 ± 93.5b**	6.45 (4–10)	100
sem: ±4.80		±0.82	±0.44	±40.64		

Albino mice (*M. musculus*)

The responses of the mice to baits containing zinc phosphide were similar to those of the rats. All mice died in the groups fasted for 12 h or less, and the time to death ranged from 5–11 h. One mouse survived in each group where the fasting period was longer than 12 h (Table 2), and time to death ranged from 8–24 h. While the bait intake of individual mice could not be recorded, as they were housed in groups of four per cage, it was noted that in all the groups, all of the bait (10 g/group) was consumed. For the groups of mice fed baits containing zinc phosphide plus L-histidine, all animals died and the time to death ranged from 4–12 h (Table 2).

Table 2. Response of laboratory mice (*Mus musculus*) to baits containing zinc phosphide (2%) either alone or with added L-histidine (0.004%). (Values are mean ± se of eight mice in each group). Mice were kept in groups of four/cage, therefore bait intake by individual mice could not be recorded.

Body weight (g)	Fasting period (h)	Mean time to death (h)	Mortality (%)
Zinc phosphide (2%)			
26.9 ± 1.2	0	8.52 (8–10)	100
26.9 ± 1.5	6	7.0 (5–7)	100
26.9 ± 1.2	12	10.0 (8–11)	100
27.4 ± 1.9	18	12.30 (8–16)	87.5
28.8 ± 4.0	24	22.0 (22–24)	87.5
Zinc phosphide (2%) plus L-histidine (0.004%)			
29.0 ± 2.2	0	7.50 (4–10)	100
30.4 ± 2.4	6	8.0 (4–10)	100
29.8 ± 0.7	12	10.0 (6–12)	100
30.2 ± 2.0	18	10.0 (6–12)	100
33.2 ± 3.0	24	11.0 (10–12)	100

Discussion

This study has demonstrated that fasting animals before testing the efficacy of new bait formulations may not necessarily lead to increased consumption of baits or a reduction in the time to death. This phenomenon has been observed previously (Hollander 1955; Bell et al. 1965). For research and development studies of new formulations of rodenticides, it may be wise to undertake a pilot experiment to determine the most appropriate period of food deprivation before full evaluation of new compounds.

When zinc phosphide baits have been used in large-scale rodent control programs, a common criticism has been the level of bait consumption by free-living rodent populations in the presence of alternative food sources. In such situations, rodents may be expected to consume smaller quantities of toxic bait and survivors may develop ‘bait shyness’ (Muktha Bai et al. 1980; Prakash 1988). While the success of baiting programs is always closely associated with consumption of toxic baits, it is reasonable to assume that the higher the bait consumption, the higher the level of mortality. However, the results of our present studies have also clearly indicated that addition of L-histidine to zinc phosphide improves significantly the palatability, reduces the time to death, and enhances the mortality of rats and mice. This could be a significant achievement in the development of a new formulation of zinc phosphide and its wider application, because other methods like encapsulation or micro-encapsulation (El-Sabae et al. 1978) or coating with paraffin wax or steric acid (Chyun 1973) have not improved the mortality, although acceptance/palatability was enhanced.

It is well known that the toxicity of zinc phosphide, which is hydrolysed by the acid present in the stomach of animals which have ingested zinc phosphide baits, is due to the liberation of phosphine (Hayes and Laws 1991). In our studies, the rats with no fasting period before being fed with zinc phosphide bait showed 100% mortality with a mean time to death of 7.1 h. However, feeding rats (0 h fasting) with zinc phosphide plus L-histidine resulted in a higher intake of bait/rat (3.60 ± 0.9 g) and also reduced the mean time to death to 4 h. This could be attributed to the action of L-histidine plus the presence of food in the stomach and the secretion of acid in the animals (Feinburg et al. 1950; West and Todd 1961, pp. 1113–1115; Bell et al. 1965; Muktha Bai 1979). This was further corroborated in our experiments by the results observed for the shorter time to death of rats given histidine in bait compared to those given bait without histidine.

In rodent pest management programs, much emphasis has been placed on increasing acceptance of toxic zinc phosphide baits in the absence of improving the efficacy of rodenticides by adding compounds/additives which help to release the toxic gas phosphine. In the present studies, the results indicate the beneficial effect of adding L-histidine (0.004%) to zinc phosphide (2%) baits. There was a significant improvement in palatability as measured by bait consumption, an increase in mortality, and a decrease in the time to death after bait consumption. The addition of L-histidine could minimise the secondary hazards arising from consumption of carcasses of poisoned rats due to the presence of unreacted toxicant in the rodent's stomach. Indeed, Rudd and Genelly (1956) have reported that several days are required for the complete breakdown of zinc phosphide in the stomach. Thus, the possibility of secondary poisoning occurring during that time could be prevented by the addition of L-histidine.

Thus, adding L-histidine (0.004%) to zinc phosphide (2%) baits may be more effective for both rats and mice living in free conditions with access to alternative food sources, because there will be an increase in the efficacy of baits through a reduction in the time to death and a minimisation of secondary effects on non-target species.

Acknowledgments

The author thanks Dr V. Prakash, Director, Central Food Technological Research Institute, Mysore, for his keen interest in this investigation, and B.S. Ramesh for helping with the statistical analysis.

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Roof rat invasion of an urban desert island

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Abstract. Roof rats have invaded the Phoenix metropolitan area. Although the desert surrounding Phoenix is formidable to roof rats, residential and urban development has probably sufficiently altered habitat to render it suitable for roof rats. Ongoing community and government campaigns are reducing the resources necessary for rat survival and are working to suppress rat populations. Whether these efforts will be adequate to eradicate roof rats from the area is unknown. Rat activity has declined over the past several months. However, it is difficult to assess whether this reduced activity reflects decreased rat numbers or if rats have become less active during the summer heat.

Introduction

Roof rats (*Rattus rattus*) first arrived in the contiguous United States on sailing vessels along with early explorers and colonists (Lowery 1974). Their distribution had expanded considerably along routes of commerce by the late 1700s (Jackson 1982). Subsequently, roof rat distribution declined, particularly from northern and inland areas, as their populations were gradually displaced by Norway rats (*Rattus norvegicus*) (Jackson 1982). The current distribution of roof rats within the continental United States is along the lower half of the East Coast, throughout the Gulf States, and along the Pacific Coast. States located within the interior of the United States are generally free of roof rats. However, infested cargo may produce isolated infestations (Marsh 1994).

Roof rats have appeared sporadically in Arizona. The first known roof rat in Arizona occurred during 1890 with dual invasions of Tucson and along the Colorado River near Yuma (Cockrum 1960). Two years later, roof rats were reported in Cochise County (Hoffmeister and Goodpaster 1954). Roof rats did not appear again until a series of small invasions during 1900 in Yuma and Tucson and towns located in the San Pedro and Santa Cruz valleys, and then a brief emergence near Miami during 1922 (Cockrum 1960). They did not persist after these initial invasions. Their failure to establish is most likely attributable to poor habitat—specifically, sparse availability of desirable vegetation and limited water resources. Cockrum (1960) reported Arizona to be roof rat free in his book on Arizona mammals. However, an increasing human population and associated urban and residential development is changing the Arizona landscape. Introduced plants and increasing irrigation are probably leading to an increase in rat habitat. During the 1970s, an outbreak of roof rats occurred in the warehouse district of Globe, Arizona. An eradication program implemented by local authorities continued for 3 years before Globe was claimed to be roof rat free (Hoffmeister 1986).

In early December 2001, a resident notified the Maricopa County Environmental Services Department that he had seen a rat outside his home in Phoenix, Arizona. The Department's Vector Control Program responded by placing live-traps in the vicinity of the resident's home. Shortly thereafter, a rat that had been electrocuted while crossing a power-line in the same neighborhood was positively identified as a roof rat. Subsequently, a live roof rat was captured on 19 December 2001. Expanded rat trapping and neighbourhood reports suggested roof rats occupied approximately 15 km^2 by early January 2002. This area was expanded to include 41 km^2 a couple of weeks later.

The objective of this paper is to describe why the current rat infestation may be more problematic than those occurring before it, initial reactions to the infestation, and preliminary results of control measures.

Rat infestation of Phoenix

Human emigration into Arizona has significantly altered resource availability over the past few centuries, often expanding suitable roof rat habitat. Early rat populations probably faded because necessary resources were sparse. Several changing environmental attributes in the Phoenix metropolitan area may be enhancing the potential for current invading rats to establish successfully. Water is probably no longer a limiting factor across most residential and agricultural areas of Arizona. For example, irrigation channels and ditches, flood irrigation of crops and lawns, drip irrigation of flowerbeds, sewers, leaking faucets, and pet dishes—among other avenues—provide excellent water sources for rats.

Plant communities also have been significantly altered. Roof rat distribution has been correlated with introduced plants. Rat populations on the west coast have expanded considerably because rats have utilised blackberry (*Ribes* spp.) associated with old mining camps (Jameson and Peeters 1988), and the lush vegetation planted along freeways and urban housing developments (Jackson 1982). Exotic plants were first introduced to the Sonoran Desert by the Spanish in 1540 when wheat and other crop seeds were distributed to Native Americans (Tellman 2002). Today, many plants introduced for landscaping or agricultural production provide at least adequate, if not excellent, food and cover for roof rats. At present, an estimated 233 non-native plant species contribute to the flora composition (Wilson et al. 2002). Introduced ornamentals used for landscaping further contribute to a changing plant community. Citrus and nut trees in yards, and interlocking hedges and vines draping over fences are common within the residential neighbourhoods most recently infested by roof rats. Other sources of rat food commonly found include poorly stored food, pet food and garbage. These readily available food sources combined with improved cover and water greatly increase the potential for the new invaders to become established as compared to opportunities afforded rats during prior invasions.

Altered fauna populations also may benefit roof rat establishment. Natural predators and species normally competitive with roof rats may be less abundant. Snakes have been largely displaced, or populations suppressed, in urban neighbourhoods (Rosen and Schwalbe 2002). Domestic cats have contributed to the disappearance of many wildlife species, including competitive rat species (Rosen and Schwalbe 2002). Roof rats do not compete well with Norway rats (Jackson 1982), and most likely do not compete well with wood rats (*Neotoma* spp.). Roof rats may fare better where populations of these species are sparse. The arboreal nature of roof rats may make them less vulnerable to cats and other urban predators than some other rat species.

Potential problems inflicted by roof rats also have increased as the Sonoran Desert has been developed. Foraging roof rats can inflict significant negative impact on citrus and nut crops (Marsh 1994). Acreage devoted to citrus and nut production in Arizona continues to increase. Mean annual production over the past five years is valued at nearly US$150 million. If roof rats became established within these orchards, subsequent consequences could be devastating to these industries. Another potential problem is contamination of stored feeds or animal facilities. Rats living in attics, walls, and basements commonly gnaw on electrical wiring, causing communication and power disruptions. Exposed and frayed wires then pose threats for electric shock or fire (Cogelia et al. 1976). Rats also serve as vectors and reservoirs for diseases communicable to humans (Chin 2000). Therefore, public health is always a concern when rat infestations occur in residential neighbourhoods.

Initial response

Successful urban rodent control needs to focus on long-term strategic, comprehensive approaches that incorporate multiple tactics and partnerships among government agencies, community groups and pest control companies (Colvin and Jackson 1999). Whenever possible, such control programs should focus on altering habitat and reducing its potential for attracting and supporting pest species. Otherwise, benefits derived from control measures will be short-lived and frequently repeated (Davis 1972).

Government agencies, primarily county, began formulating a response plan soon after officials suspected a potential roof rat infestation. The first response to the rat sighting was to identify the species. Once roof rats were confirmed, efforts were initiated to confirm boundaries of the area infested by rats. This area quickly expanded from 15 km^2 to 41 km^2, centered on the Arcadia–Camelback Mountain area of Phoenix. Whether this expansion reflected increased rat dispersal or merely better surveys is unknown. A contingency plan addressing an influx of roof rats to the Phoenix area did not exist. In retrospect a plan would have been beneficial.

The Maricopa County Vector Control Office sponsored a series of meetings during January 2002 to gather agency support, share information, and begin developing a response plan. A wide spectrum of interested groups and agencies were represented at these meetings. Subsequently, Maricopa County assumed a lead role in developing and implementing a plan to address real and perceived problems caused by roof rats.

Maricopa County issued a news release that urged citizens to cover trash containers, use rat-proof containers to store food items, eliminate rat access to pet foods, pick up fallen citrus, and harvest fruits remaining on trees. The release also announced an upcoming public meeting scheduled to explain the situation and to address public questions. At the meeting, hundreds of local residents were provided an overview of roof rat ecology and management, and advised to clean up yards, remove citrus fruits from their property, and to use traps or baits to manage local rat populations. Residents also were told that the City of Phoenix would haul away unwanted citrus and assist in organising campaigns to clean up public and common-ground areas.

Direct measures to combat roof rats were implemented by mid-February 2002. More than two-dozen groups participated in the rat eradication effort. The City of Phoenix provided bulk trash bins for residents. The Arizona Department of Health Services, in cooperation with Maricopa County Environmental Services, began testing roof rats for hantavirus, bubonic plague, and tularemia. Food banks and family assistance programs accepted undamaged discarded citrus from clean-up campaigns. Several neighbourhood groups were organised to clean common areas or assist those residents less capable of picking fruits or cleaning debris from their properties. Personal-use bait stations and snap-traps were distributed by county and volunteer groups until supplies were depleted. Home-owner associations sold additional bait stations at the cost of materials. Educational programs continued, ranging from leaflets to group meetings, urging residents to take necessary steps to deny rat access to cover and food.

Maricopa County Vector Control implemented a baiting program to suppress and hopefully eliminate rat populations. Their target area, including a buffer zone, was approximately 60 km^2. Certified County employees, assisted by volunteer apprentices, affixed approximately 6000 bait stations 2–2.5 m above the ground on utility poles. Utility poles were spaced 30–60 m apart and were located primarily along alleys. Stations were initially installed in areas considered ‘hot spots’ and in the 0.75 km buffer zone established along the outside perimeter of the infested area. Bait stations were constructed of polyvinyl chloride (PVC) pipe (30 cm long and 10 cm diameter) capped on both ends, and a hole drilled in the middle to permit rat access, but minimise non-target exposure. Each station was treated with 225 g of bait containing 0.005% bromadiolone. The Vector Control group monitored stations at least once a month, replacing any bait that had been removed.

Preliminary results and discussion

An integrated plan was developed to eradicate, or at least abate, roof rat establishment in the Phoenix area. Numerous community groups banded together to remove potential rat food and rat habitat. One optimistic volunteer considered the “rats a blessing, not a curse, in that they have brought us closer as a community…and are pushing us in a direction we need to go, and that’s cleaning up our properties.” The ‘NEIGHBOR to NEIGHBOR’ campaign picked, and donated to food banks, approximately 31.5 t of citrus through their efforts to rid neighbourhoods of rat food. Their future goal is to collect and donate more than 750 t of citrus next season. Resident and volunteer groups deposited almost another 100 t of waste citrus and debris in dumpsters distributed and serviced by the city. These efforts have greatly decreased availability of food and cover for rats. Unfortunately, some residents have not participated in the clean-up campaign, leaving pockets of citrus and other desirable rat habitat attributes. It is unknown whether these havens will enable rats to establish and disperse throughout the community in the future. Community organisations also have worked with residents to set bait stations and traps on private land inaccessible to county officials.

City, county, state, and federal governmental agencies have all contributed to roof rat eradication. Public awareness programs have greatly enhanced public involvement in rat proofing their homes, installing traps and bait stations on private land, and monitoring for rat activity. The Arizona Department of Health Services has tested rats and has thus far not found evidence of disease communicable to humans. Maricopa County Vector Control has taken the lead role to suppress roof rat populations. Over 1 t of bait has been distributed through approximately 6100 bait stations mounted on the utility poles. Few stations (less than 0.5%) have been vandalised or otherwise damaged. Vector Control also has set rat traps in areas believed to contain high rat populations or where bait stations may pose perceived problems. Other agencies have enhanced control efforts by contributing funds, labour, equipment, and expertise.

The efficacy of these programs to eradicate roof rats is largely unknown. Rat activity appears to have declined, according to indicators such as bait disappearance, trapped rats, and residential calls to hotlines. Whether this reduced activity means suppressed populations or merely reflects less movement by rats during the higher summer temperatures is difficult to ascertain. A more accurate measure of program success will occur next winter, when temperatures drop and citrus trees bloom and begin producing fruit.

Conclusions

Roof rats and other rodents have been introduced to new localities throughout the world. Invading roof rats have established and wreaked havoc on many island ecosystems (Atkinson 1989). Urban and residential development may be creating islands of habitat suitable for roof rat survival. While ships were required to transport invasive species among islands, their movement across inhospitable terrestrial sites should be relatively easy, given the rapid transport of goods and constant movement of vehicles. Therefore, municipalities may need to consider whether development is creating habitat for invasive species and the likelihood these species will be introduced. If conditions favour a species capable of causing devastating impacts to a region, then contingency plans may need to be considered. Under some conditions, it may be reasonable to establish monitoring programs for early detection, e.g. a monitoring program for early detection of roof rats in Arizona citrus orchards. However, it is understandable why government agencies are hesitant to extend limited resources to address concerns with species supposedly non-indigenous to their locality.

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SYMPOSIUM 8: TAXONOMY

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Evolutionary biology of the genus *Rattus*: profile of an archetypal rodent pest

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Abstract. *Rattus*, with at least 61 valid species, is the single largest genus of mammals. It belongs to a much larger assemblage of 'modern' murines, known informally as the 'new endemics', and distributed from South Asia to Indonesia. The first members of the genus *Rattus* probably evolved in the late Pliocene, around three million years ago. Early forms of *Rattus* underwent a rapid dispersal across the greater part of island Southeast Asia, despite the presence of a well-established rodent fauna in most areas. Today, the descendants of these early invaders survive on various islands and on scattered high mountain peaks. *Rattus* species probably colonised Australia only within the last 1–2 million years; nevertheless, they succeeded in colonising all major habitats including sandy desert. Within *Rattus*, the Norway rat (*R. norvegicus*) appears to have few, if any, immediate relatives. In contrast, the black rat (*R. rattus*) has numerous close relatives spread across mainland and island Southeast Asia. Three or more distinct species are probably included within the *R. rattus* complex. At least 15 species of *Rattus* are significant agricultural pests. Five of these are true commensals and three species now exist solely within the human environment. The role of these species in causing agricultural damage and in the dispersal and transmission of both human and wildlife pathogens is discussed.

Introduction

Species of the rodent genus *Rattus* have probably been responsible for more human suffering than any other group of vertebrates (with the exception of *Homo sapiens*!), not only through their destructive impact on food crops, but also through their role in the transmission of fatal or debilitating diseases such as plague, leptospirosis and typhus. However, the genus also contains species of immense scientific and clinical significance, such as the familiar Norway or laboratory rat (*R. norvegicus*), as well as a host of lesser-known but presumably beneficial species that inhabit a wide range of natural habitats from mangrove forests to sub-alpine grasslands. In matter of fact, the genus *Rattus*, with a total of 61 currently recognised species, is not only the single largest mammalian genus of all, but also arguably among the most complex and least well understood.

In this paper, we will give a brief summary of current thinking regarding the content and relationships of *Rattus*. We will also summarise the geographical distribution of *Rattus* and its closest allies, and examine the evidence for the geographical origin of the genus as a whole and of some of the economically more important species. Finally, some key biological attributes of the genus will be reviewed, including the role of various *Rattus* species as agricultural pests and as agents of disease transmission. All of these components will help us to frame one final question of profound evolutionary biological significance—why is *Rattus* so remarkably successful as a genus? We cannot promise any profound response to this question. However, we do believe that the act of framing the question is, in itself, worthwhile, and perhaps takes us one step closer to a better understanding of this most remarkable of mammalian genera.

Content and relationships of *Rattus*

Although *Rattus* was once considered to consist of more than 550 distinct forms (Ellerman 1941–1949), contemporary reviews list roughly one-tenth as many species in the genus (Corbett and Hill 1992; Musser and Carleton 1993). Many of the species formerly included within *Rattus* have been transferred to other genera such as *Maxomys*, *Berylmys*, *Leopoldamys*, and *Niviventer* (see references in Musser and Carleton 1993). However, even more have been grouped together to form fewer, widely distributed species (the *Rattus rattus* group alone has more than 150 synonyms, currently grouped under two species).

Despite these considerable advances, the boundaries of *Rattus* are by no means finally decided. The type species of *Rattus* is actually *Mus decumanus* Pallas 1778, a junior synonym of *R. norvegicus* (Berkenhout 1769), the familiar

Norway or laboratory rat. The other species often thought of as lying at the 'heart' of *Rattus* is the black or ship rat, *R. rattus*. The Norway rat is morphologically distinctive and appears to have few, if any, close relatives (Chan et al. 1979; Baverstock et al. 1986; Verneau et al. 1998). In contrast, the black rat is often confused with other Asian *Rattus* species and appears to have numerous close relatives. Musser and Carleton (1993, p. 649) listed 21 species in their *R. rattus* group, including the major agricultural pest species *R. argentiventer*, *R. nitidus*, *R. losea* and *R. tiomanicus*.

Several groups of species may still need to be excised from *Rattus*. These include members of the *R. xanthurus* group from Sulawesi; the '*Stenomys'* group from New Guinea and Seram; and the 'native Australian' group. Musser and Carleton (1993, p. 650) listed 10 individual species that they consider to be on the periphery of *Rattus*; many of these species are of special biogeographical interest (see below).

The evolutionary relationships of *Rattus* to other murid genera remain somewhat enigmatic. Musser and Heaney (1992) included *Rattus* among a group of essentially modern and progressive rodents that they termed the 'new endemics'. This group is widely distributed across mainland and island Southeast Asia, and includes the following genera: *Paulamys*, *Hooijeromys*, *Papagomys* and *Komodomys* of the Lesser Sunda Islands (Nusa Tenggara); *Bunomys*, *Paruromys* and *Taeromys* of Sulawesi; *Abditomys*, *Bullimus*, *Limnomys*, *Tarsomys* and *Tryphomys* of the Philippine Islands; and *Palawanomys*, *Sundamys* and *Kadarsanomys* of the Sunda Shelf Islands. Three mainland Asian genera (*Berylmys*, *Bandicota* and *Nesokia*) probably also belong to this group (Musser 1981; Musser and Brothers 1994).

The notion of a 'modern and progressive' 'new endemic' murid assemblage is supported by information from chromosomes (Yosida 1980 and refs; Baverstock et al. 1983a; Gadi and Sharma 1983), albumin immunology (Watts and Baverstock 1996 and refs), DNA/DNA hybridisation (Ruedas and Kirsch 1997), DNA sequencing (Suzuki et al. 2000) and analysis of LINE-1 retrotransposons (Verneau et al. 1998 and refs). Although none of these methods has yet been applied across the full range of relevant genera, the combined results strongly support the notion that *Rattus* evolved somewhere within the South to Southeast Asian region.

Just how recently this might have occurred is indicated by molecular estimates of divergence times between *Rattus* and other genera. These place the origin of *Rattus* at around 2–3 million years ago (Watts and Baverstock 1996; Verneau et al. 1998)—a remarkably young age for such a large and diverse genus. However, these dates are consistent with the fossil record of *Rattus*, which begins in Thailand with an extinct species of possible late Pliocene age (c. 3 million years ago; Chaimanee 1998) and includes Pleistocene records from India (Gaur 1986), Java (Musser 1982) and China (Zheng 1993; cited in Chaimanee 1998). *Rattus* is conspicuously absent from Pliocene and early Pleistocene fossil faunas of Europe (van de Weerd 1976) and Australia (Aplin 2002), and appears to have been confined to the Asian region through much of its early history.

Unresolved taxonomic problems within *Rattus*

Several species groups within *Rattus* are clearly still in need of taxonomic revision: notable examples are the *R. everetti* group in the Philippines; the *R. niobe* group in New Guinea; and the *R. sordidus* group in Australia. In each case, there are additional species that will be recognised following completion of more detailed morphological and genetic studies. However, in no group within *Rattus* is the need for taxonomic revision so glaringly and embarrassingly obvious as it is in the *Rattus rattus* complex.

Many authors have attempted to make sense of the morphological diversity among the black rats. Most attempts have been regionally based (e.g. Hinton 1918–1919 for the Indian subcontinent; Chasen 1933 for Malaysia) and the few broader-based attempts at revision have been defeated at the outset by a failure to distinguish *R. rattus* from other *Rattus* species, including *R. argentiventer*, *R. tiomanicus* and *R. sikkimensis* (e.g. Ellerman 1941–1949; Schwarz and Schwarz 1967). In addition, all but a very few attempts have placed too great an emphasis on belly fur colour, despite clear evidence dating back at least to Bonhote (1910) that this is highly polymorphic within populations and under relatively simple genetic control (see also Tomich and Kami 1968).

The first significant breakthrough in understanding the *R. rattus* complex came with Yosida's (1980 and refs) studies of chromosomal variation. Over a period of a decade, he documented 11 chromosomal variants that resolve into five major groups: (i) Asian black rats with $2n = 42$ chromosomes and high C-banding; (ii) Japanese black rats with $2n = 42$ chromosomes and low high C-banding; (iii) Ceylonese black rats with $2n = 40$ chromosomes; (iv) 'Oceanian' (also European) black rats with $2n = 38$ chromosomes; and (v) Mauritius black rats with $2n = 42$ (secondarily derived from the $2n = 38$ karyotype). Yosida found regional variation within the Asian black rat group in the frequency of minor Robertsonian rearrangements and in serum transferrin polymorphism. Laboratory F_1 hybrids were obtained between all major chromosomal variants but these invariably proved semi-sterile, with low yield of F_2 offspring. Natural hybrids were detected in four areas, either involving Asian and Oceanian types (Eniwetok Atoll, Marshall Islands; Chichijima Island, Japan; Karachi, India) or the Ceylonese and Oceanian types (Anaradhapura and Colombo, Sri Lanka).

Baverstock et al. (1983b) examined genetic differences between each of the chromosomally distinct populations, using isozyme electrophoresis and micro-complement fixation of albumin. The results show a major genetic division between the Asian and Ceylonese + Oceanian populations, with lesser differentiation between each of the Japanese versus mainland Asian and between Ceylonese versus Oceanian types. As expected, the Mauritius black rats were genetically indistinguishable from the general Oceanian type. The level of genetic divergence between the two major groups within *R. rattus* was only slightly less than that separating *R. rattus* from other undisputed species of *Rattus* (e.g. *R. losea*) and this led Baverstock et al. (1983b) to conclude that the *R. rattus* complex could be validly divided into at least two species.

Musser and Carleton (1993) indeed listed two species of the *Rattus rattus* complex in their influential checklist, using the names *R. rattus* (Linnaeus 1758) for the 'Oceanian' group and *R. tanezumi* Temminck 1844 for the Asian group. This usage has gained some acceptance, however the lack of a comprehensive morphological review of the group has left many field workers uncertain as to whether they are catching *R. rattus*, *R. tanezumi* or possibly even both. An earlier morphological study by Schwabe (1979) had revealed some apparent differences in cranial proportions between European and Asian populations, but this finding requires broader-scale confirmation.

Our preliminary studies of the mitochondrial cytochrome b gene indicate that the taxonomy of the *R. rattus* group may be rather more complex than suggested by the chromosomal and electrophoretic data sets. In particular, we have found a fundamental genetic division *within* the Asian region between an endemic Southeast Asian taxon (recorded from Vietnam, Cambodia and southern Laos) and a northern and South Asian taxon (recorded thus far from Japan, Hong Kong, northern Vietnam, northern Laos, and Bangladesh). These taxa are probably regionally sympatric in parts of Vietnam and Laos. The Oceanian type *R. rattus* appears to be more closely related to (although probably specifically distinct from) this latter group than to the endemic Southeast Asian taxon. Until further analyses are completed, and the results fully published, it would be premature to speculate on the appropriate names for each of the two Asian taxa. However, the apparent extension of the northern Asian taxon (which probably includes Japanese *tanezumi*) through to the Indian subcontinent raises the possibility that *tanezumi* may not be the earliest available name for this group. Rapid resolution of these taxonomic and nomenclatorial problems is clearly of high priority given the agricultural and clinical significance of the *Rattus rattus* complex.

The geographical distribution of *Rattus*

The contemporary geographical distribution of *Rattus* is amongst the widest of any rodent genus, rivalled only by *Mus*. However, the greater part of this range is clearly due to commensalism on the part of a small number of species, namely, members of the *Rattus rattus* complex, *R. norvegicus* and *R. exulans*.

At a broad scale, the number of native *Rattus* species is highest on the island of New Guinea, followed by Australia, mainland Southeast Asia and Sulawesi. However, the true number of native *Rattus* species on mainland Southeast Asia and on the larger islands of the Sunda Shelf (e.g. Borneo, Sumatra and Java) is somewhat uncertain due to doubts over the original distribution of various commensal and agricultural pest species (see below).

Island endemics

Two groups of endemic species are of special interest. The first are the 'island' endemics (Table 1, Figure 1). As noted previously by Musser and Heaney (1985), the majority of these species are found on *oceanic* islands that are separated by deepwater straits from adjacent major islands or continental landmasses. The important feature of oceanic islands is that they remained isolated through the glacial periods when sea levels fell by as much as 140 m below the present level (Lambeck and Chappell 2001)—any *Rattus* species on these islands must have reached them by crossing water barriers at some time in the past. As shown in Figure 1, the majority of the island endemics are found in two geographical areas: (i) around the perimeter of the Southeast Asian continental shelf (the Sunda Shelf); and (ii) in the Moluccan and Nusa Tenggaran island groups, situated in the tectonically active zone between Sulawesi and New Guinea.

In phylogenetic terms, the island endemics can be divided into two broad categories, namely an *archaic* group and a *modern* group. Members of the 'archaic' group generally show no close relationship to other *Rattus* species in adjacent geographical areas; these may be descendants of early waves of dispersal through the region. Three of the archaic taxa are found on islands lying to the south of Sumatra: *R. enganus* of Pulau Enggano, and *R. macleari* and *R. nativitatus* of Christmas Island. Two are found in the Moluccan region: *R. morotaiensis* of the Halmahera Island group, and *R. ceramicus* of Seram; and two in the Nusa Tenggaran group—*R. hainaldi* of Flores and *R. timorensis* of Timor. One final member of this group, *R. jobiensis*, is found on the islands of Cenderawasih Bay of north coastal New Guinea.

Members of the 'modern' group are more obviously related to (and presumably immediately derived from) species found on nearby major islands or landmasses. For example, *R. pelurus*, found on Pulau Peleng, to the immediate east of Sulawesi, is a member of the otherwise endemic Sulawesian *R. xanthurus* group (Musser and Holden 1991). Similarly, *R. remotus* of Koh Samui and nearby islands in the South China Sea is very similar to (perhaps even conspecific with) *R. sikkimensis* of mainland Southeast Asia.

Eight members of the 'modern' group may be related specifically to *R. tiomanicus* of the Sunda Shelf, itself a close relative of the *R. rattus* complex (Musser and Newcomb 1983). One of these species is *R. mindorensis* from Mindoro Island in the central Philippines (Musser and Holden 1991). Another is *R. tawitawiensis* from the Sulu Archipelago, off the north-eastern corner of Borneo

(Musser and Heaney 1985). The remaining six species of this group are found on islands that lie to the south and west of Sumatra and the Malay Peninsula: *R. adustus* of Pulau Enggano; *R. lugens* of the Mentawi Islands; *R. simalurensis* of the Simalule Island Group; *R. burrus* and *R. palmarum* of the Nicobar Islands; and (less certainly) *R. stoicus* of the Andaman Islands (Musser and Heaney 1985). Several of these taxa are quite specialised in different ways, yet each shows a basic similarity in dental and cranial structure to *R. tiomanicus* and its close allies. Another possible member of this group is *R. hoffmani*, a widespread and common forest rat of Sulawesi (Musser and Holden 1991).

Three members of the 'modern' group are broadly clustered in the Moluccan region: *R. feliceus* from Seram; *R. koopmani* from Pulau Peleng; and *R. elaphinus* from the Sula Island group. The affinities of these species are not quite so obvious, however Musser and Holden (1991) suggest possible links to the native *Rattus* of New Guinea.

Table 1. Island (I) and montane (M) endemics within the genus *Rattus*. Species marked as 'I,M' are found in montane habitats on islands. Morphological groups are: A = archaic and M = modern.

Species	Habitat	Morphological group	Locality
adustus	I	M	Pulau Enggano, Indonesia
burrus	I	M	Nicobar Is group, India
elaphinus	I	M	Pulau Taliabu, Indonesia
enganus	I	A	Pulau Enggano, Indonesia
feliceus	I	M	Seram, Indonesia
jobiensis	I	A	Japen, Biak and Owi Is, Irian Jaya
koopmani	I	M	Pulau Peleng, Indonesia
lugens	I	M	Mentawi Is group, Indonesia
macleari	I	A	Christmas Is
mindorensis	I	M	Mindoro Is, Philippines
morotaiensis	I	A	Halmahera Is Group, Indonesia
nativitatus	I	A	Christmas Is
palmarum	I	M	Nicobar Is group, India
pelurus	I	A	Pulau Peleng, Indonesia
remotus	I	M	Koh Samui Is, Thailand
sanila	I	A	New Ireland, Papua New Guinea
simalurensis	I	M	Simalur Is group, Indonesia
stoicus	I	M	Andaman Is group
tawitawiensis	I	M	Tawitawi Is, Philippines
baluensis	I,M	M	Mt Kinabalu, Sabah
bontanus	I,M	A	Gunung Lamphobatang, Sulawesi
ceramicus	I,M	A	Seram, Indonesia
giluwensis	I,M	M	Mt Giluwe, Papua New Guinea
hainaldi	I,M	A	Flores, Indonesia
hoogerwerfi	I,M	A	Gunung Leuser, Sumatra, Indonesia
korinchi	I,M	A	Gunung Kerinci, G. Talakmau, Sumatra, Indonesia
marmosurus	I,M	A	Gunung Masarang, Sulawesi, Indonesia
mollicomulus	I,M	A	Gunung Lamphobatang, Sulawesi, Indonesia
montanus	I,M	A	Sri Lanka
omlichodes	I,M	A	Mt Jaya, Papua, Indonesia
richardsoni	I,M	A	Papua Province, Indonesia
timorensis	I,M	?	Gunung Mutis, Timor, Indonesia
vandeuseni	I,M	M	Mt Dayman, Papua New Guinea
osgoodi	M	M	Langbian Mts, Vietnam

Montane endemics

A second group of major interest are the ‘montane’ endemics. These are typically confined to forested or sub-alpine habitats on the highest peaks of the continental areas and larger islands (Table 1, Figure 1).

Somewhat surprisingly, there is only one montane endemic *Rattus* on mainland Asia. *R. osgoodi*, a rare species from the Langbian Mountains of southern Vietnam, is morphologically similar to *R. losea* and *R. argentiventer* (Musser and Newcomb 1985). The absence of other montane endemics on mainland Southeast Asia may reflect a lack of survey effort in appropriate habitats. However, recent surveys of montane habitats in northern Vietnam have produced specimens of the widespread taxa *R. sikkimensis* and *R. nitidus*, but no local endemics (Tam et al., this volume).

Three *Rattus* species are endemic to isolated upland areas on the Sunda Shelf: *R. hoogerwerfi* and *R. korinchi* from Sumatra; and *R. baluensis* from Mt Kinabalu on the island of Borneo. The Bornean endemic is probably a close relative of *R. tiomanicus* (Musser 1986). The two Sumatran taxa retain a suite of primitive characteristics (Musser 1986).

R. montanus from the highlands of Sri Lanka is said by Musser (1986, p. 22) to resemble *R. korinchi* but the molar pattern is overall more primitive. This poorly known taxon clearly lies at the periphery of *Rattus*.

The extensive mountain habitats of New Guinea support four endemic *Rattus* species (Flannery 1995a). *R. vandeuseni* is confined to the upper slope of Mt Dayman in south-eastern Papua New Guinea; it replaces the closely related but more widespread *R. verecundus* at around 1300 m elevation. *R. giluwensis* is confined to mossy forests and sub-alpine habitats above 2195 m on Mt Giluwe and the adjoining Lamende Range in Papua New Guinea. *R. richardsoni* and *R. omlichodes* are found in areas of sub-alpine to alpine habitat in the Indonesian province of West Papua. The higher altitude species are all small-bodied and the two West Papuan taxa retain many primitive dental features.

Interestingly enough, three of the island endemics would also qualify as montane endemics; these are currently confined to montane forests on Seram (*R. ceramicus*), Flores (*R. hainaldi*) and Timor (*R. timorensis*). These taxa are also similar to the majority of the other montane endemics in displaying numerous primitive morphological features (Kitchener et al. 1991a,b).

The survival of relatively archaic forms of *Rattus* on remote islands and in high mountain regions is not totally unexpected. What is perhaps surprising is the fact that the majority of these are found through the archipelagic portion of the range of *Rattus*, with few examples in what might be regarded as its core area of distribution on mainland Southeast Asia. As noted before, this might be a function of inadequate sampling of these areas. However, the presence of such taxa in the far-eastern Moluccan Islands and in New Guinea points to a wide and probably rapid dispersal of a small number of relatively archaic *Rattus* species through the region. The absence of any relictual species of *Rattus* in montane or rainforest habitats of Australia is consistent with the notion of a more recent invasion of this continental area.

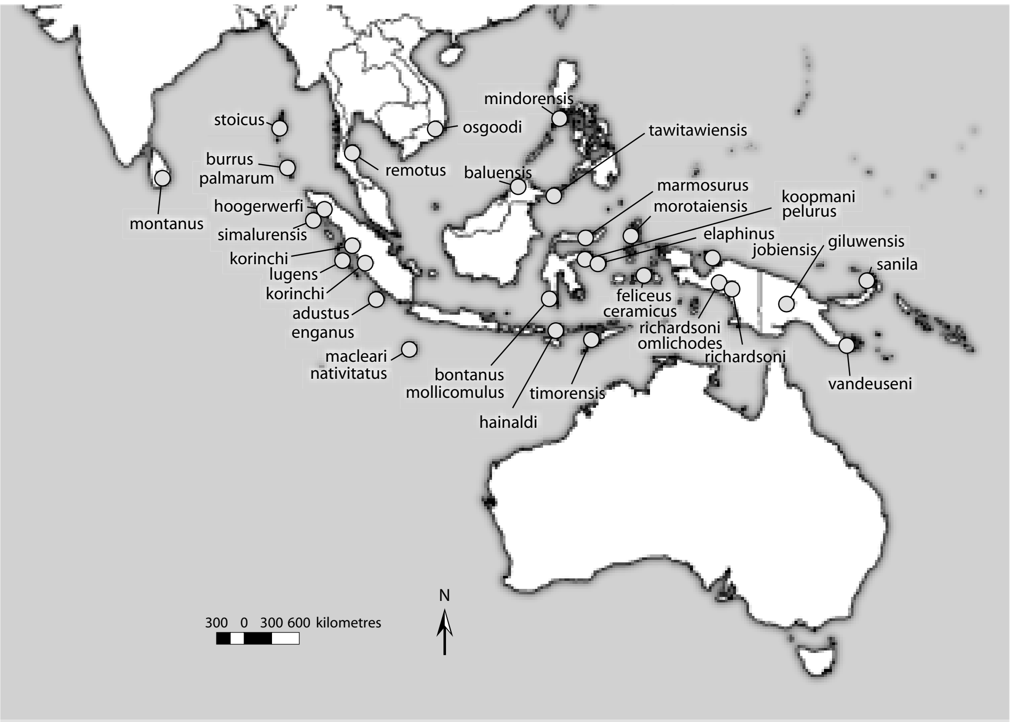

Figure 1. Distribution of island and montane endemic species within the genus *Rattus*.

Recent range expansions

Some species of *Rattus* have undergone huge recent expansions in geographical range. The best known examples are, of course, *R. norvegicus* and members of the *Rattus rattus* complex, both of which are now present on all continents except Antarctica, and on the great majority of the world's larger islands. As noted above, members of the *Rattus rattus* complex are widely distributed across Southeast and South Asia. A representative of this group (presumably the $2n = 38$ 'Oceanian' rat variety) is first recorded in the Middle East during the Upper Pleistocene (c. 20,000 years BP; Tchernov 1968), however it does not appear to have reached western Europe until much later, and did not enter the British Isles until shortly before the Roman Period (Somerville 1999). The later history of the species in Europe suggests that it was initially confined to the major commercial routes, and that its geographical coverage increased mainly through the 11th–13th centuries AD during the period of rapid urban growth (Audoin-Rouzeau and Vigne 1994).

The natural range of the Norway rat, *R. norvegicus*, is generally assumed to be south-eastern Siberia and northern China (Musser and Carleton 1993, p. 657). In northern Asia today, it is more typically associated with urban and agricultural landscapes (e.g. Won and Smith 1999). The Norway rat evidently spread out from Asia much later in time than the black rat—it does not appear in the European record until the Middle Ages. However, following the arrival of *R. norvegicus* in Britain, the black rat declined to a state of rarity. *R. rattus* is now largely confined to buildings, whereas the Norway rat occupies many different habitat types (Meehan 1984).

Other members of the *Rattus rattus* complex have expanded into the Pacific region, presumably through accidental transport with human traffic. This probably occurred during the prehistoric period to as far as the Philippines and Sulawesi. Later European activity in the Pacific probably led to the further dispersal of one or more Asian varieties of *R. rattus*, and to the introduction to many islands of the European black rat. On some Pacific islands (e.g. Eniwetok Atoll in the Marshall Islands) Asian and European forms of the black rat occur together, with some evidence for hybridisation and introgression (Yosida 1980).

The Pacific rat, *R. exulans*, has a huge geographical range that extends from Bangladesh and the Andaman Islands in the west, to New Zealand and Easter Island in the east. Throughout its range it is closely associated with human activities (Marshall 1977; Musser and Newcomb 1983, p. 523–524). *R. exulans* is absent in the fossil record of New Guinea (White 1972) and Nusa Tenggara (Glover 1986) until the last few thousand years, and it is presumed that it came from somewhere to the west. Musser and Newcomb (1983, p. 523–524) remarked on the morphological uniformity of *R. exulans* across its range and postulated a possible origin somewhere on mainland Southeast Asia.

The wide dispersal of *R. exulans* over the last few thousand years is clearly linked to the spread of Austronesian language speaking peoples; indeed it has been suggested that the rat may have been transported deliberately as a food item (Roberts 1991a). Matisoo-Smith et al. (1998) examined the pattern of mitochondrial DNA variation among Polynesian populations of the Pacific rat to document the course of its dispersal. Similar studies of Indonesian and Southeast Asian populations are now required to document its place of origin and pattern of spread in the western part of its range.

One final species that has evidently been carried by people into the Pacific region is *R. praetor*, a common species of lowland to mid-elevation habitats of northern New Guinea (Flannery 1995a). This species was probably introduced to the Bismarck Archipelago during late Pleistocene times and, more recently, to the Solomon Islands, Vanuatu and even to Fiji (White et al. 2000). In the Bismarck Archipelago, the introduction of *R. praetor* may have contributed to the extinction of an endemic species, *R. sanila* (Flannery and White 1991).

Several other species of *Rattus* have made somewhat less impressive inroads into island Indonesia and beyond. One of these is the Himalayan rat, *R. nitidus*, with a probable natural range somewhere in the belt of upland country that extends from north-eastern India through Myanmar, Thailand and Laos, to southern China and Vietnam (Musser and Holden 1991). In southern China, *R. nitidus* is a major agricultural pest (Yang et al. 1999), however in Southeast Asia it is variously recorded in forested habitat and as a house rat in upland villages (Marshall 1977, p. 463). Outside this area, *R. nitidus* occurs on Seram in the northern Moluccas; on northern Luzon in the Philippines; in the Palau Islands, south-east of the Philippines; and on the Bird's Head Peninsula of western New Guinea (Musser and Heaney 1985). The species is not present in sub-fossil faunas from either Sulawesi (Musser 1984) or the Bird's Head Peninsula (Aplin et al. 1999) of New Guinea; it is presumably introduced in these contexts. On mainland Asia, *R. nitidus* does not generally occur in lowland habitats or around ports, hence the circumstances of its accidental transport are somewhat mysterious.

R. tiomanicus may have also reached various island groups through human agency. This species occurs on many of the islands that ring the Sunda Shelf, often with endemic species derived from earlier invasions of a *tiomanicus*-like taxon (Musser and Califia 1982; Musser and Heaney 1985). Some of these populations appear to be subspecifically distinct, but others may have been introduced in recent times.

The two major pest species of lowland rice crops on mainland Southeast Asia are the rice-field rat, *R. argentiventer*, and the lesser rice-field rat, *R. losea*. Both species have probably undergone range expansions as a consequence of the widespread conversion of forest and swampland habitats to paddy over the last few thousand years or less (Khush 1997). Musser (1973) attributed populations of *R. argentiventer* on Sulawesi, in the southern Philippines and in southern New Guinea to human-assisted dispersal and further commented on the morphological uniformity of this species throughout its range. In Malaysia, *R. argentiventer* is always encountered in one of two anthropogenic habitats, either rice fields or *Imperata* grassland (Harrison 1951). Marshall (1977, p. 468) also observed that "*Rattus argentiventer* is unknown in the wild state; that is all known populations are commensal with man, living in rice fields or adjacent lalang, oil palm plantations etc.". In rice fields, the onset of breeding in *R. argentiventer* appears to be cued to the maximum tillering stage of the crop (Leung et al. 1999). This apparent physiological link to grass phenology might suggest an original wetland or grassland habitat.

R. losea presents a somewhat different case. This species does show some geographical variation in its morphology (Marshall 1977; Musser and Newcomb 1985) and it is also known from upland habitats, as high as 900 m in China, Vietnam, Laos and Thailand. Marshall (1977, p. 466) reports the discovery of this species "in the wild state … in grass beneath pine forest at 850 m in Chaiyaphum Province (Thailand)". Nevertheless, within some parts of its range, *R. losea* is clearly associated with rice fields and there can be little doubt that it has benefited from the spread of rice-growing as a way of life. Breeding activity in *R. losea* is also clearly linked to rice cropping cycles (Brown et al. 1999) but little is known regarding the precise timing of events.

These examples illustrate some of the difficulties of delimiting the place or origin or natural range of the various *Rattus* species that are either strictly commensal or else have benefited from the widespread habitat changes associated with the spread of agriculture over the last few thousand years. As a final note of caution in this regard, we would also like to stress that simply encountering a species in 'natural' habitat, far from direct human activity, is no guarantee of 'native' status. By way of example, we can report the capture of both *R. exulans* and a member of the *R. rattus* complex in mossy *Eucalyptus urophylla* forest at c. 1500 m altitude on Gunung Mutis in Timor in 1991. Both species are clearly introduced to Timor, yet these species have been able to penetrate all habitat types, presumably assisted by episodic burning and perhaps by the lack of competition following extinction of the native Timorese rodent fauna (Glover 1986). Lehtonen et al. (2001) reported a similar penetration by *R. rattus* into relatively unmodified forest habitat in Madagascar—however, in this case, the invasion has occurred even in the presence of an extant native rodent fauna.

Rattus species as commensals and as agricultural pests

At least 14 of the 61 species of *Rattus* are significant agricultural pests (Table 2). Of these, five species also can be considered true commensals in the sense that they are regularly found inside human dwellings. The most widely distributed and best-known commensals are *R. rattus* and *R. norvegicus*, both of which are virtually global in distribution. However, in many parts of Asia and the Pacific, the most abundant village rat is the smaller and generally less-offensive Pacific rat, *R. exulans* (Williams 1973). *R. nitidus* and *R. turkestanicus* (often called *R. rattoides*) are recorded as commensals in upland regions of Central and Southeast Asia (e.g. Niethammer and Mardsen 1975). As noted above, two of the commensal species, the Norway rat and the Pacific rat, are now so firmly associated with the human landscape that they are no longer known for certain in the wild state.

The agricultural pest species can be divided into what may be termed *obligate* pests and *opportunistic* pests. 'Obligate' pests are those that seem to exist across all or part of their geographical range on the basis of human agricultural production. Included here are the rice-field rat, the Pacific rat, the Norway rat, the various members of the black rat complex, and *R. turkestanicus*. The Himalayan rat, *R. nitidus*, probably qualifies as such in the northern part of its range but appears to be more typically a forest rat in the uplands of Southeast Asia.

The scale of damage inflicted by each of these species varies in accordance with the scale of the agricultural systems that they exploit. Globally, members of the *R. rattus* complex may inflict the greatest total damage to crops. Black rats are ranked among the most important pests in India (Prakash and Ghosh 1992), Thailand (Boonsong et al. 1999) and the uplands of Laos (Khamphoukeo et al., this volume). In the uplands of northern India through to southern China, they are probably replaced by *R. nitidus* and *R. turkestanicus* as the dominant agricultural pests (Zhang et al. 1999), while through much of the Pacific region this title is held by *R. exulans* (Williams 1973). The dominant pests in the major lowland rice-producing areas of Southeast Asia are *R. argentiventer* and *R. losea*. Singleton and Petch (1994) estimated annual losses of around 5–20% in lowland rice systems, with occasional higher losses during 'outbreak' years. Chronic losses may be even higher in many rainfed and upland rice production areas, and these systems are also more prone to episodic irruptions (Douangboupha et al., this volume).

The 'opportunistic' pests are those that will take advantage of human agricultural production, but are not dependent on it to maintain their geographical distributions. One Southeast Asian species, *R. tiomanicus*, is included here (Boonsong et al. 1999), but others such as *R. sikkimensis* might also warrant inclusion. Similarly, only two New Guinean species are listed, but other species such as *R. leucopus*, *R. verecundus* and *R. novaeguineae* can be trapped in and around gardens and presumably also inflict some damage to crops (Taylor et al. 1982). Among the various Moluccan Island endemics, Flannery (1995b) mentioned that *R. morotaiensis* and *R. elaphinus* have been trapped in garden habitats. Of the four Australian species listed in Table 2, *R. sordidus* is by far the most important pest in economic terms (McDougall 1947 and refs). However, *R. colletti* and *R. villosissimus* are both, in a sense, 'emergent' pests that have recently invaded new rice production areas in northern Australia. The undescribed *Rattus* sp. from central Queensland, a close relative of *R. villosissimus*, is reported to inflict local damage on wheat crops.

Rattus species as agents of disease

The role of *Rattus* as an agent of disease is most spectacularly illustrated through the example of the great plague pandemics. Black rats, or possibly just their fleas, harbouring in cloth and other trade goods, first carried the plague organism (*Yersinia pestis*) from Central Asia to the Middle East and Europe in the 5th century AD. In more recent times, shipping routes provided even more effective means of transporting plague-bearing rats around the world, leading to the infamous Black Death of the 14th century. The most recent pandemic, dating to around the turn of the 20th century, was combated to some extent by 'modern' medicine, but it still killed an estimated 10 million people, 535 of them in Australia (Curzon and McCracken 1989). Plague remains endemic in Central and Southeast Asia, many parts of Africa and South America, and across much of the United States of America (USA). In each area, rodents serve as the primary or enzootic hosts (Biggins and Kosoy 2001), with the pathogenic agent maintaining a sensitive balance between infection rate and death rate in order to persist indefinitely in the wild population.

Y. pestis has a remarkably broad host range (>200 species of mammals; Poland and Barnes 1979) and has pathogenic impacts on many species including most rodents. However, susceptibility may differ widely even between closely related taxa. Most Asian murids are highly susceptible to plague, but *R. norvegicus* and *R. rattus* both show moderate levels of resistance and may be significant enzootic hosts. The principal enzootic host of plague in Africa is the multimammate rat, *Mastomys natalensis* (Gratz 1997). However, in Madagascar, this role is taken over by *R. rattus*, which is evidently spreading as a consequence of forest destruction.

Rodents are known to serve as hosts for at least 60 zoonotic diseases (Hugh-Jones et al. 1995). Many of the clinically significant zoonoses are carried by commensal *Rattus* species (Gratz 1997). Examples include murine typhus (rickettsial disease), various spirochetal diseases (e.g. Lyme disease, leptospirosis) and some protozoal diseases (e.g. leishmaniasis, toxoplasmosis). Of these, leptospirosis is of special concern as an emergent infectious disease, with a recent upsurge in the rate of diagnosis of this previously 'hidden' disease (Singleton, Smythe et al., this volume). Commensal *Rattus* populations have been found to carry heavy leptospire infestations in widespread regions of Africa, Asia, Europe and North America (Gratz 1997).

Hantavirus infections are also of particular concern because of the high mortality rates (5–35%) associated with several of the 10 or so recorded viruses of this group (Hart and Bennett 1999). The Norway rat is a known reservoir for Seoul virus in the USA and a recent epidemiological study of this species in Baltimore showed a seroprevalence of nearly 50%; moreover, naturally infected rats did not show any reduction in reproductive capacity (Childs et al. 1989). Boonsong et al. (1999) summarised serological evidence of hantavirus infection in Thai

Table 2. Agricultural pest and commensal species of *Rattus*.

Region	Species	Primary affected crop	Economic significance	True commensal	Key references
Central + East Asia	*R. nitidus*	Cereals	++	+	Marshall 1977; Yang et al. 1999
	R. turkestanicus	Vegetables	+	+	Niethammer and Martens 1975; Hong 1989; Zhang et al. 1999
Southeast Asia	*R. argentiventer*	Rice	+++	–	Marshall 1977; Leung et al. 1999
	R. losea	Rice	++	–	Marshall 1977
	R. tiomanicus	Oil palm, vegetables	++	–	Wood and Liau 1984
Southeast Asia + Pacific	*R. exulans*	Vegetables, sugarcane	++	+	Williams 1973; Marshall 1977
Melanesia	*R. praetor*	Root crops, vegetables	+	–	Flannery 1995a,b
	R. steini	Root crops, vegetables	+	–	Flannery 1995a
Australia	*R. colletti*	Rice	+	–	Watts and Aslin 1981
	R. sordidus	Sugarcane	++	–	McDougall 1947; Whisson 1996
	R. villosissimus	Rice	+	–	Watts and Aslin 1981
	Rattus sp. (member of *sordidus* group)	Wheat	+	–	G. Gordon, Qld NPWS pers. comm.
Global	*R. norvegicus*	Various	+++	+	Meehan 1984
	R. rattus complex	Various, rice in Southeast Asia	+++	+	Meehan 1984

rodents including rural populations of *R. rattus* and *R. losea*. The likelihood of hantavirus infection is closely related to the intimacy and frequency of contact with rodents or their dried excreta—contamination of stored foods by faeces or urine poses an obvious risk in this regard. Hart and Bennett (1999) estimated a global infection rate for hantaviruses of 100,000–200,000 cases per year.

Much less is known about the potential for disease transmission between introduced *Rattus* species and native rodents. The Australian and Pacific region, where *Rattus* intruded late into an already well-established rodent fauna, provides an ideal model system in which to examine the nature of this interaction. Interestingly enough, a recent review of the helminth parasites of Australian rodents by Smales (1997) showed a marked contrast between the helminth communities of native *Rattus* species (dominated by nematodes) and native rodents belonging to other genera (dominated by trematodes). Only 13 helminth species are shared between these groups, compared with seven species shared exclusively between the recently introduced rodents (*Rattus* and *Mus* spp.) and native *Rattus*. Skerratt et al. (1995) made a strong case for an ancient transfer of trichostrongylid nematodes between native *Rattus* and other Australian rodent genera.

Another case study that documents the intensity of biotic interchange between invasive *Rattus* species and an established rodent fauna is Roberts' (1991b) study of endo- and ecto-parasites of the Pacific rat. Roberts contrasted populations of *R. exulans* that have either remained isolated from, or experienced contact with, the more recently introduced *R. rattus* and *R. norvegicus*. The evidence appears strong for cross-transfer of two nematodes, one cestode, four fleas and four mites. In a few populations, the 'new' parasites were found in isolated populations of *R. exulans*. Roberts interpreted these as reflections of unsuccessful invasion by the newly introduced *Rattus* species, where transfer of parasites had occurred quickly before the mammalian invader becoming locally extinct.

Some conclusions and some final questions

Many elements of the evolutionary history of *Rattus* are beginning to take shape as a consequence of recent morphological and molecular studies. The wider relationships of *Rattus* clearly lie among the suite of 'new endemic' murine genera, all of which are native to the Asian region. *Rattus* clearly evolved somewhere within this region, but exactly where remains uncertain. The available fossil evidence perhaps favours an origin on mainland Southeast Asia. However, two biogeographical observations point to an alternative origin in island Southeast Asia. The first is that the diversity of 'new endemic' genera is much higher in the insular region than it is on the mainland, especially on Sulawesi, in the Philippine Islands, and in Nusa Tenggara. Secondly, many of the more archaic *Rattus* species are found in these same areas, as well as in New Guinea and Australia. Archaic species are strikingly absent from mainland Asia, although they are present both on and off the margin of the Sunda Shelf.

Various biogeographical scenarios could be developed to account for these distributional patterns, however all would involve one or more early phases of dispersal by archaic forms of *Rattus*. These underwent modest to spectacular radiations in many areas. Archaic forms persisted on many smaller islands and in tropical forests, especially in montane refuges. *Rattus* may have entered New Guinea and Australia independently and perhaps at different times, leading to significant radiations in each area.

One of the most remarkable things about the dispersal and subsequent radiation of *Rattus* is that it occurred in most areas *in the presence of a pre-existing, diverse rodent fauna*. This is most striking in the case of Sulawesi, the Philippine Islands, New Guinea and Australia, each of which supports a rich and highly diversified murid rodent fauna with histories spanning 5–8 million years of local evolution (Aplin 2002). The presence of numerous, established competitors would normally represent a significant impediment to the establishment of an invasive species (Williamson and Fitter 1996). However, *Rattus* not only managed to gain a foothold in these areas, in most it was able to disperse and speciate in varied habitats from mangrove forest to sub-alpine heath; and, in Australia, extend into true deserts. Later in its history, *Rattus* was able to exploit another suite of newly created habitats—the gardens, rice fields and villages of early agricultural peoples—and then to travel with the descendants of these people to colonise many of the world's most remote islands.

To conclude this review, we should ask what it is about the genus *Rattus* that has made it so phenomenally successful? We do not pretend to know the answer to this question. However, some elements that might be included in a satisfactory answer are:

- the fact that most *Rattus* species are 'generalists'—in body size and form, in diet, in behaviour;
- the ability of at least some *Rattus* species to utilise stored abdominal fat during lean periods (e.g. Yabe 1994);
- the apparent propensity of *Rattus* species to undergo frequent chromosomal rearrangements, perhaps favouring rapid speciation in a widely dispersing group of animals (e.g. Bush et al. 1977); and
- the willingness of at least some *Rattus* species to enter water, thereby increasing their chances of dispersal and allowing them to utilise seasonally inundated habitats.

These few suggestions clearly fall well short of a satisfactory answer that should perhaps be framed in terms of physiological breadth, immunological capacity and reproductive potential. Unfortunately, knowledge of such things is too meagre at present among all but a few *Rattus* species to do more than flag these as potentially useful avenues for thought.

Acknowledgments

Fieldwork in Southeast Asia has been carried out with support from the Australian Centre for Agricultural Research (ACIAR Project AS1/98/36) and the Australian Agency for International Development (AusAID) (Capacity-building for Agriculture and Rural Development (CARD) Project ‘Enhancing capacity in rodent management in the Mekong Delta region using non-chemical methods’). Molecular studies at the Australian National Wildlife Collection were supported by funding from The Myer Foundation. We thank Henk Godthelp for his comments on a draft of this paper.

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Integrative systematics: the importance of combining techniques for increasing knowledge of African Murinae

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Abstract. The soft-furred rats of the *Praomys* group are of economic and health importance but represent one of the most difficult groups of the Murinae for systematics analyses due to a high degree of morphological similarity among species. Because neither morpho-anatomy nor morphometrics are 100% efficient, the use of cytotaxonomy and DNA sequencing is essential. We present together our recent results about taxonomy and biosystematics of the group. The distinction of two complexes, *P. jacksoni* and *P. tullbergi*, is here confirmed both by morpho-anatomy and geometric morphometrics, as well as by cytochrome b sequencing. It is also shown that the fronto-parietal crest disposition has a phyletic signal. However, these criteria cannot be applied to juvenile and very old specimens, which restricts its application. DNA sequencing of the mitochondrial cytochrome *b* gene also confirms the monophyly of the *Praomys* group. However, some incongruence is observed between molecules and morphology due to the paraphyly of the genus *Myomys*. This pattern points out the inaccuracy of external morphological characters taken as diagnostic criteria. In such a case, like in various other Murinae, the combination of different techniques appears necessary in order to better understand the taxonomy and biosystematics in the group. These results have important implications for epidemiological research.

Introduction

Systematics is the science devoted to discovery, identification, classification and interpretation of biological diversity. It is often divided into taxonomy (or description, naming and classification of taxa) and biosystematics (assessment of the evolutionary relationships between species, i.e. phylogeny). This distinction reflects different approaches and the frequent involvement of different groups of scientists. Nevertheless, the two disciplines share the phylogenetic approach and have the same fundamental aim: the production of stabilised classifications, allowing evolutionary inferences both for fundamental and applied biology. Systematics has recently benefited from a complete renewal, with the ongoing development of new methods and concepts, among them cladistics, morphometrics, molecular systematics and global genomics. The integrative application of all these tools to the same study models is now possible and this approach is developed in our research team. It provides a rich approach that leads to more complete and precise descriptions of biodiversity.

Tropical Africa supports very high micro-mammalian diversity, especially between African Murinae (Rodentia, Muridae). The soft-furred rats of the genus *Praomys* are widely distributed from West Africa (Senegal to Angola) to East Africa (Uganda to Malawi) and in both primary and secondary forest zones. The genus comprises 10 species whose geographical limits are still poorly known due to the low level of morphological differentiation among the species and a long history of confusion and misidentifications (Musser and Carleton 1993; Van der Straeten and Kerbis-Peterhans 1999). Until recently, the genus *Praomys* was broadly conceived and included members of such well recognised genera as *Mastomys*, *Hylomyscus* and *Myomys*. A revision of the genus *Praomys* also requires that we adopt a broader approach that includes these taxa, which together constitute the *Praomys* group. No phylogeny was formerly available, despite the fact that the entire group has economic and health importance (Lecompte et al., this volume). More specifically, *P. jacksoni* is a primary natural host of the arenavirus Mobala (Mills et al. 1997) and is probably a reservoir of Ebola virus (Morvan et al. 1999). Furthermore, some species of *Praomys* are almost unknown because they are restricted to some isolated montane forests. These species have special conservation importance.

Finally, the biodiversity of *Praomys* may be underestimated due to the probable existence of sibling species in various African Murinae, as suggested recently by Meester (1988) and Taylor (2000). A careful revision of all members of the genus is required, but with special attention to *P. tullbergi*, the type species of the genus. In this paper, we have applied the integrative and comparative approach to the *Praomys* group, both at specific and generic levels, in order to solve some taxonomic problems. We will highlight the perspective brought by each technique, as well as the importance of comparing results and the implications of such an approach.

Material and methods

Voucher specimens from the collections of the Museum National d'Histoire Naturelle (MNHN; Paris, France), the Natural History Museum (London, England), and the Royal Museum for Central Africa (Tervuren, Belgium) have been used for morpho-anatomical, morphometric and phylogenetic analysis. Two taxonomic levels are considered in this study. First, the initial recognition of elementary taxonomic units (OTUs) is made both at genus and species level with the help of morphometric methods; and then, the analysis of relationships within *Praomys* is performed through phylogenetic methods and assessed for their consensus.

At the intraspecific level, 208 skulls of *P. tullbergi* from MNHN have been used for morphometric analyses (to be reported in detail elsewhere). Twenty skull and mandible measurements were taken using a caliper (0.01 mm precision). Principal component analysis (PCA) and canonical variable analysis (CVA) were done using log-transformed values. Outlines of dental rows were drawn using a binocular microscope with a camera lucida and digitised using a standard orientation after preliminary tests. A total of 194 dental-row outlines of *P. tullbergi* specimens from MNHN collections—86 females and 114 males, coming from Ivory Coast (*N* = 45), Cameroon (*N* = 2), Gabon (*N* = 94), Burkina Faso (*N* = 2), Central African Republic (*N* = 31), Senegal (*N* = 6) and Togo (*N* = 14)—were digitalised using TPSDig software (Rohlf 2001) and then analysed using specially devised MATLAB V.6. routines for Elliptic Fourier analysis (Kuhl and Giardina 1982). Coefficients of elliptic Fourier were calculated for normalised and orientated contours. Four landmarks at the junction of the teeth were taken in order to superimpose the outlines. Shape and size differences were analysed using PCA and CVA of Fourier coefficients.

Seven landmarks were taken on the left anterior half of the dorsal side of the skulls of different *Praomys* species (Figure 1). Landmarks were acquired using a charge coupled device (CCD) camera with a macrophotographic device and the Measurement TV software (version 1.92, Updegraff 1990). Thin-plate spline analyses were conducted using the thin-late splines relative warp (TPSRW) analysis software of Rohlf (2001) allowing superposition of landmarks and visualisation of shape deformations in function of variance.

On the basis of good taxonomical identifications, phylogenetic analysis can be performed. A preliminary morphological phylogeny (Lecompte et al. 2002a) was completed with new characters and increased samples within the *Praomys* group. The data matrix had 51 characters on 27 species, including 24 species of the *Praomys* group. Total genomic DNA was extracted from liver, heart or muscles preserved in 70% ethanol using a CTAB protocol (Winnepenninckx et al. 1993). Mitochondrial sequences containing the cytochrome b gene (1140 pb) were isolated via the polymerase chain reaction (PCR) and sequenced directly from purified PCR products with an automatic sequencer (CEQ2000; Beckman). The sequences were entered and manually aligned using the Bioedit software. Mutational saturation was studied for each codon position for transitions and transversions separately. Both for morpho-anatomical and molecular data, the phylogenetic relationships were analysed by the maximum parsimony (MP) method using PAUP 4.0 (Swofford 1998). Twenty species of the *Praomys* group, represented by one to six specimens, were treated with other Murinae species chosen as outgroups according to Lecompte et al. (2002b). The molecular and morphological trees were compared with Treemap 1.0 software (Page 1995).

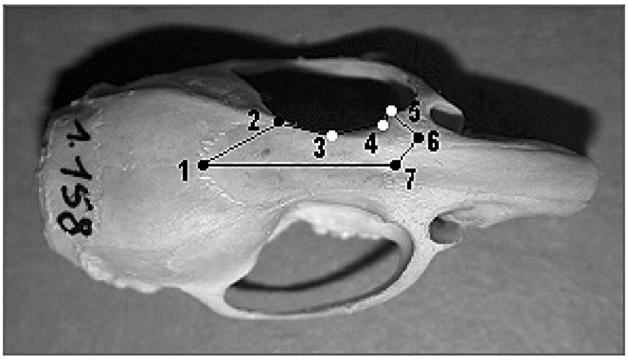

Figure 1. Dorsal view of a *Praomys* skull showing the landmarks used to analyse the shape of the frontal bone.

Results and discussion

OTU definition

Within the framework of the biological species concept of Mayr (1963), there is a need to define elementary taxonomic units (OTUs), especially when looking at 'non-natural' populations (issued from collections or systematic field inventories) where the critical tests of hybridisation cannot be made. It is also necessary in the case of sibling species (morphologically similar species but genetically structured and reproductively isolated; Mayr 1963). Classical morpho-anatomy or morphometric tools are well suited for morphospecies definition, however in the case of sibling species or a species complex, cytotaxonomic methods, especially using banding techniques, are better adapted.

Morpho-anatomy

The search for diagnostic characters is especially important for species identification. In the past, the diagnosis of species was based on external characters but this can lead to considerable confusion, especially in groups with high levels of morphological similarity and/or variability. In the *Praomys* group, most of the genera were long confused and even placed in the same genus (see Ellerman 1940–1941; Meester and Setzer 1971–1977). The first morphological revisions of the group grew out of Petter's (1965, 1975) and Rosevear's (1969) studies of skull and molar morphology, which provided some useful characters, both at the generic and specific levels. However, these authors each looked only at a few species of the genus. Around the same time, other authors reported some supplementary characters that allowed the discrimination of certain species, but comparisons were generally very limited. Our research group has, for the first time, examined all recognised species of *Praomys*, with samples of 15 to 100 specimens per species to accurately assess intraspecific variability. The selection of skull characters took into account the nature and extent of variability of the characters; all highly variable characters were rejected in devising the identification key.

The cranial characters selected for this identification key are illustrated in Figure 2. The only external character employed here is the mammary formula, because this was initially used by Thomas (1915) to separate the genera *Myomys*, *Mastomys* and *Praomys*. It is expressed as the total number of pectoral mammae and inguinal mammae. This character can be used only with adult females and consequently it is limited for purposes of species determination. We provide here an identification key for species of the genus *Praomys* (after Lecompte et al. 2001).

1. Supraorbital ridges absent or very weak (Figure 2, label a). 2.

   Supraorbital ridges present, more or less pronounced. 3.
2. Anterior limit of palatine bone extending to the level of the posterior part of M1 (Figure 2, h), nasal/frontal suture almost horizontal (Figure 2, f), zygomatic bone of the same breadth as malar process, mammary formula: 1 + 2 = 6. *P. morio*

   Anterior limit of the palatine bone extending to between M1 and M2 (Figure 2, i), nasal/frontal suture V-shaped (Figure 2, g), zygomatic bone very thin (half of the breadth of malar process), mammary formula: 2 + 2 = 8. *P. delectorum*
3. Supraorbital ridges beginning in the middle of frontals (Figure 2, b) 4.

   Supraorbital ridges very strong, straight, beginning in front of frontals (Figure 2, c) 7.
4. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M1 (Figure 2, j). 5.

   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M1 (Figure 2, k). *P. hartwigi*
5. Proportions of the teeth normal (ratio of molar row length/maximum length of skull >15%) *P. tullbergi*

   Microdonty (ratio of molar row length/maximum length of skull <15%) 6.
6. Interorbital constriction gradual and amphora-shaped (Figure 2, d) *P. misonnei*

   Interorbital constriction more sharply angular in the middle of frontal (Figure 2, e) *P. rostratus*
7. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M1 (Figure 2, j). *P. mutoni*

   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M1 (Figure 2, k). 8.
8. Four small accessory plantar pads, mammary formula: 1 + 2 = 6 *P. jacksoni*

   One or no small accessory pad, mammary formula: 2 + 2 = 8 *P. degraaffi*

Some characters must be handled carefully because of sex and/or age dependence. For instance, the 'supraorbital ridges' present some variation in relation to age—the ridges increasing in strength with the age of the animal. Thus, old *P. morio* can have similar ridges to young *P. tullbergi*, and the type of *P. morio*, a young adult, presents very weak ridges, which could be quite misleading. This illustrates the necessity of taking into account both sex

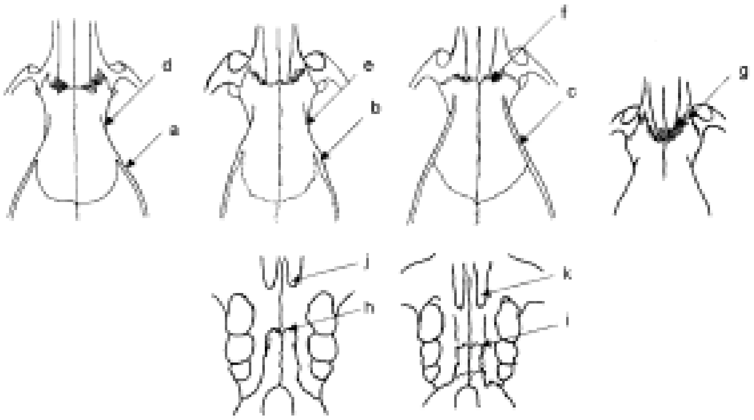

Figure 2. Morphological characters used in the identification key for *Praomys* species. See text for identification of morphological features.

and age influences on diagnostic morphological characters.

Molar teeth characters are useful for palaeontology and determination of remains in owl pellets (Denys 2002). *Praomys* teeth are characterised by an undifferentiated prelobe of the upper M1/, with t2 and t3 aligned and hardly distinguishable, low crowned teeth with well-fused cusps, a lack of deep valleys between cusps, and bunodonty of very narrow lower molars without developed cingula (Figure 3). In general, molar cusps are well united and there are few longitudinal crests.

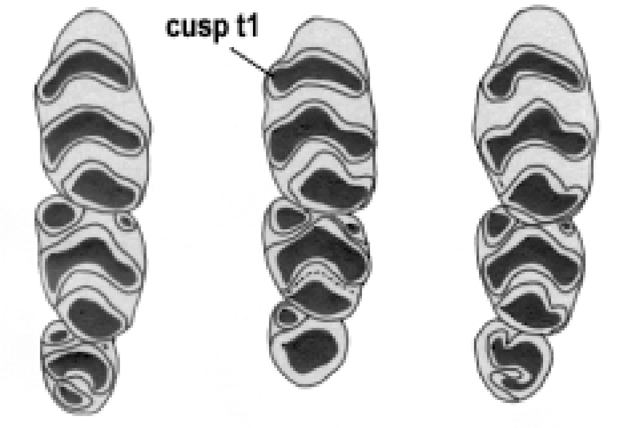

Figure 3. Variation in upper molar morphology among populations of *Praomys tullbergi*: left, Ivory Coast specimen; middle, Senegal specimen (notice the smaller size and that cusp t1 is better individualised); and right, Guinean specimen. All are left upper molar rows.

Cytotaxonomy

It has been shown recently that, in the case of African murids, cytogenetic variations provide some of the most reliable diagnostic criteria (karyospecies concept, Dobigny et al. 2002a,b). Unfortunately, cytogenetic information is lacking for some of the 10 recognised *Praomys* species. A preliminary survey of all published data indicates the existence of species complexes and of potential sibling species, especially in the *tullbergi* group, where two morphologies are known for the sexual chromosomes (Matthey 1958; Capanna 1996) (Table 1). No banding techniques have yet been applied to verify the taxonomic status of these forms. Molecular taxonomy, in this context, can also help to understand relationships within taxa and perhaps reveal cryptic species.

Morphometrics

Morphometrics is the quantitative description of size and shape of organisms (Rohlf and Marcus 1993). Initially based on distance measurements (classical morphometrics), it has been recently renewed with the use of thin-plate spline (TPS) and Fourier analysis methods which allow the analysis of shape of organisms (geometric morphometrics: Bookstein1991). Morphometric techniques are appropriate in taxonomy for species discrimination but can also help to find useful morphological characters for phylogenies or to analyse the evolution of shape by mapping onto cladograms. Classical morphometric techniques (canonical analyses) have been applied successfully to distinguish between *Praomys* taxa. For example, Van der Straeten and Verheyen (1981), Van der Straeten and Dieterlen (1987) and Van der Straeten and Dudu (1990) used these methods to define species complexes within *Praomys* and to justify the naming of new *Praomys* species. Discriminant analyses of distances have also been applied in studies of other African Murinae, both to investigate geographical patterns within species and to search for cryptic species (Taylor et al. 1993; Chimimba 1994). We present here the results of various morphometric analyses performed at different taxonomic levels, reflecting the fact that, in the case of *Praomys*, even the generic boundaries still need to be defined.

Table 1. Chromosomal data available to date for *Praomys* species (2N = diploid number of chromosomes; NFa = fundamental chromosome number; X = sex chromosome X; Y = sex chromosome Y; SM = submetacentric; M = metacentric; A = acrocentric).

Species	Chromosomal data	References
P. taitae	2N = 48, NFa = 54; X = SM	Matthey 1965
P. degraaffi	2N = 26, NFa = 24	Maddalena et al. 1989
P. jacksoni	2N = 28, NFa = 26; X = SM	Matthey 1959
P. misonnei	2N = 36, NFa = 46	Qumsiyeh et al. 1990
P. morio	2N = 34, NFa = 32; X = SM; Y = M	Matthey 1970
P. rostratus	2N = 34, NFa = 32	Gautun et al. 1986
P. tullbergi	2N = 34, NFa = 32; X = A; Y = A or X = M	Matthey 1958; Capanna 1996
Praomys sp.	2N = 42, NFa = 62; X = SM; Y = A	Matthey 1965

Morphometric methods were first applied at the population level in order to test whether the chromosomal variability observed by Matthey (1958) and Capanna et al. (1996) in *P. tullbergi* has any morphological basis (Figure 4) or if any geographical substructure occurs within the species. In Figure 4, the first canonical variate separates out *P. tullbergi* from Ivory Coast, while the second canonical variate sets Guinea and Senegal populations apart from the others. The major difference between the Ivory Coast and other populations is size—especially size of the molars. This geographical difference was also investigated by using geometrical techniques of outline reconstructions, specifically to see if changes in dental size were accompanied by any changes in their shape. Elliptical Fourier analysis shows effectively that, in addition to size, there are shape differences in upper molar outline between the Guinean and Senegal populations of *P. tullbergi* (Figure 5). These results indicate a possible taxonomic differentiation within the *tullbergi* species group for the more western part of tropical Africa. Concerning the chromosomal difference between specimens from the Central African Republic and from the Ivory Coast, the morphometrics analyses confirm some differences but much more sampling is required to investigate this problem thoroughly.

At a higher taxonomic level, there is confusion in the literature with the type of *P. lukolelae* from Central Africa. This taxon was placed in synonymy with *Malacomys* (Musser and Carleton 1993). TPS analysis using landmarks on the dorsal part of the skull confirms the distinction between the two species complexes of *Praomys* and suggest placement of *M. lukolelae* among the *P. tullbergi* complex. Combined with traditional skull and dental analysis, this strongly suggests by a quantitative method that the taxon *lukolelae* does not belong in *Malacomys* (Figure 6). Fronto-parietal crest disposition, as well as shape of the frontal part of the skull, helped to firm up the qualitative characters of Petter (1975). However, in all cases presented here, morphometrics never provided full discrimination between species or populations, hence other techniques are now required for OTU determination.

In conclusion, objective identification of OTUs requires attentive observation of large series of specimens in order to see the variability and eliminate the age differences. Good skeletal preparations and knowledge of anatomy are necessary. The discrimination methods can be applied locally with some specific identification success or at the generic level. However, in the case of *Praomys*, other molecular and karyological techniques are now needed to solve the problem of OTU definition within this group.

Phylogeny and classification

Phylogeny retraces the sister relationships of a species or a group of species. The genealogy obtained is shown graphically as a tree where the topology represents an hypothesis corresponding to the inferred evolutionary relationships between taxa. Congruent phylogenetic trees produced from different types of characters can form the basis for stable classifications (build the tree of life). Robust monophyletic groups allow us to make hypotheses about the history of characters and distributions. Phylogenetic relationships within the *Praomys* group were inferred using both morphological (Lecompte et al. 2002a) and molecular data (Lecompte et al. 2002b). By comparing the results of these analyses (Figure 7), several points of incongruency are given emphasis.

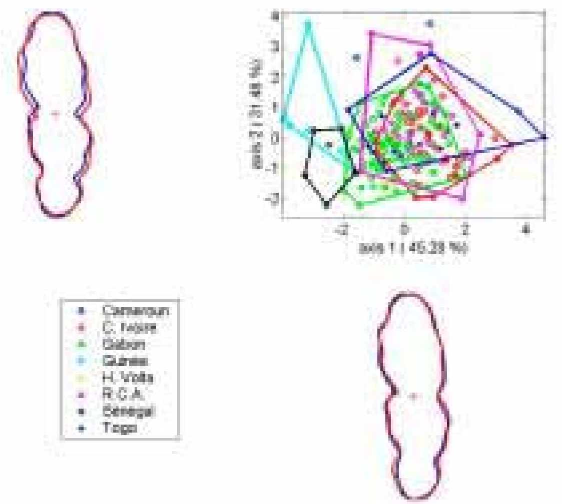

Figure 5. Canonical variable analysis (CVA) on upper molar row outlines and the representation of extreme shapes on each axis. The first canonical variable shows mainly a size difference and the second one a shape asymmetry especially on upper M1/.

A new maximum parsimony analysis is presented here for all members of the *Praomys* group. The morphology-based consensus tree displayed in Figure 7 (left), shows that the *Praomys* group is monophyletic and further confirms that the genus *Praomys* can be divided into two complexes, the *jacksoni* complex and the *tullbergi* complex. The crest character, first qualitatively identified by Petter (1975) and assessed quantitatively here (Figure 6), appears to have a robust phylogenetic value insofar as it provides an unambiguous synapomorphy for the *jacksoni* complex. The divergence between the *tullbergi* and *jacksoni* complexes is supported by a total of 13 synapomorphies. Species within

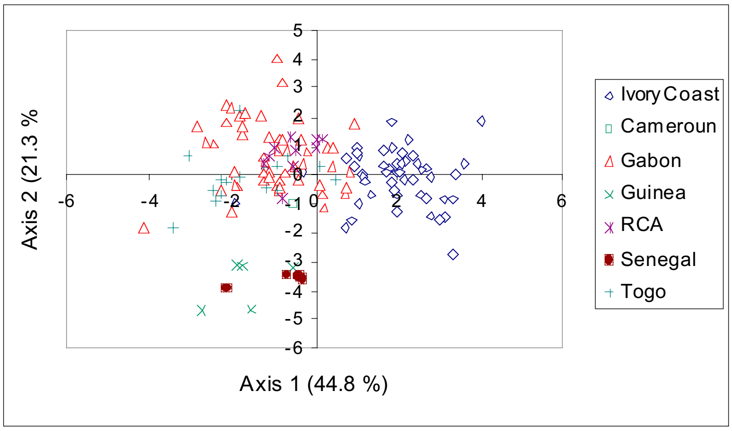

Figure 4. Results of the canonical variable analysis (CVA) based on 20 skull log-transformed measurements for 208 specimens of *P. tullbergi* from West Africa (axes 1 and 2) (RCA = Central African Republic).

the *tullbergi* group are distinguishable by up to six synapomorphies but there is no autapomorphy to define this entire group. Generally, some characters provide good local synapomorphies but they show convergence at the total *Praomys* group scale.

DNA sequencing is an important and objective source of characters usable in phylogeny (Figure 7, right). For the cytochrome b gene, the *Praomys* group is found to be monophyletic, as in the morphological tree. On the contrary, *Praomys*, *Myomys* and *Stenocephalemys* are this time paraphyletic. The cytochrome b sequences within the *P. tullbergi* group suggest the existence of a complex of species since *P. tullbergi* itself is divided into three paraphyletic units (E. Lecompte, unpublished). This pattern is consistent with previous geometric morphometrics and cytogenetic results.

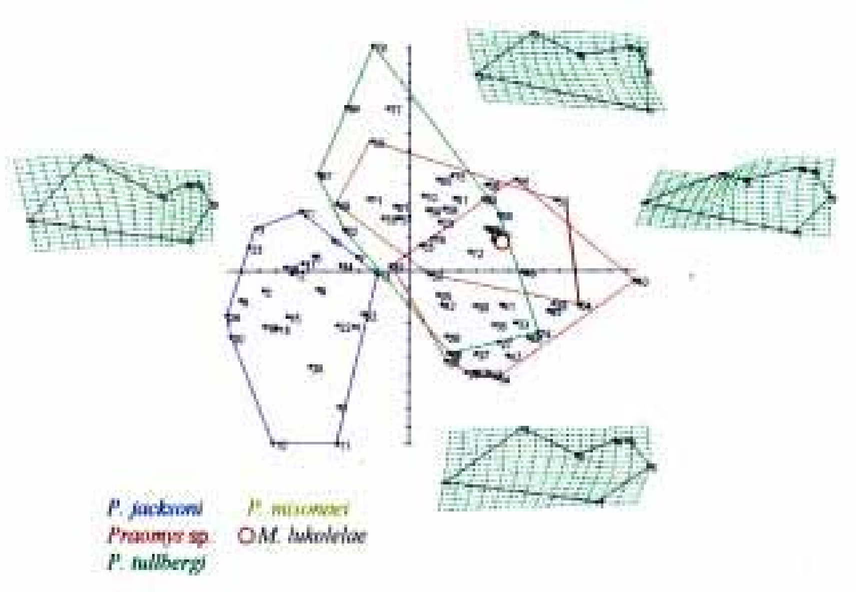

Figure 6. Thin-plate splines relative warp (TPSRW) analysis of variation in the dorsal outline of the frontal bone of different *Praomys* species. The results demonstrate the distinction of *P. jacksoni* on axis 1 and the similarity of the type of '*Malacomys*' *lukolelae* to members of the *P. tullbergi* complex.

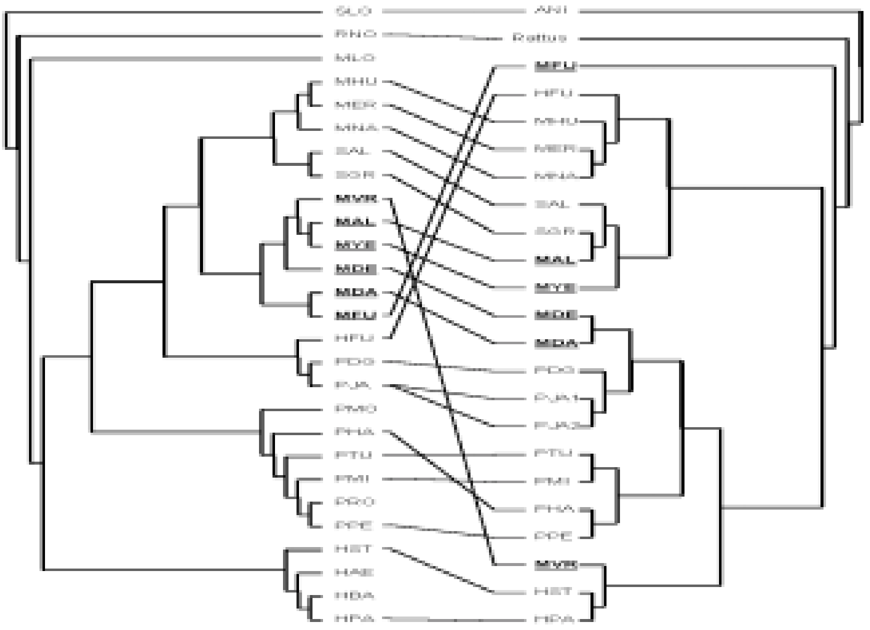

Figure 7. Morphological (left) and molecular (right) phylogenies of the *Praomys* group (after Lecompte et al. 2002a), showing the incongruence between these analyses. *Praomys* species are identified by acronyms beginning with P; *Hylomyscus* with H; *Stenocephalemys* with S; *Mastomys* are MER, MHU and MNA; *Heimyscus* is HFU; and the *Myomys* species are underlined.

In a recent article, Hillis and Wiens (1999) summarised the advantages and disadvantages of molecular versus morphological data for phylogenetic analysis. Both methods can provide useful information, especially when a range of different techniques is applied. Here, the comparison of the two trees with Treemap shows that the discrepant points are made by the *Myomys* species whose position in both the morphological and molecular trees is neither stable nor congruent. As a consequence, the morphological and molecular phylogenies are once again in conflict, especially in basal nodes and the monophyly/paraphyly of the genus *Myomys*. This conflict suggests that the genus *Myomys* is a possible cause of the wider confusion in the *Praomys* group. One classical criterion used to distinguish *Myomys* from *Praomys* or *Mastomys* species, is the number of mammae (10 in *Myomys* species), but the phylogenetic significance of this character is challenged by the molecular data that fail to support *Myomys* as a valid biological OTU. Similarly, the condition of a pure white belly may not be of phylogenetic value since this character is shared by *M. daltoni* and *M. fumatus*, which are highly divergent phylogenetically.

Similarly, morphologically divergent taxa like *Stenocephalemys* are found to be sister groups of certain *Myomys* species, and in this the new phylogeny confirms previous works by Lavrenchenko et al. (1999) and Fadda et al. (2001). The two phylogenies are congruent on the paraphyly of the genus *Praomys* (forest species): some *Myomys* (savannah species) are closer to *P. jacksoni* than to *P. tullbergi*. Interestingly, both *Praomys* species are hosts of arenaviruses (e.g. Mobala, Ippy, probably Ebola). The taxonomic results suggest that research on these viruses among related savannah taxa might prove of great interest from an epidemiological perspective.

Conclusion

In the *Praomys* group, it is now demonstrated that traditional diagnostic external morphological characters are far from effective in species identification. By combining cytogenetic, morphometric and molecular approaches in taxonomy, an accurate and stable classification can be achieved. Good species identification is still fundamental for applied research in agriculture and health. Furthermore, robust classifications that reflect the evolutionary history of the group may help in predicting the distributions of viruses and in discovering new species of potential hosts. The *Praomys* group has yielded numerous sibling species, especially in *Praomys* and *Mastomys* groups (Lecompte et al., this volume) and the biodiversity of the group is probably very much underestimated for these taxa. A similar conclusion can probably be inferred for most other genera of African Murinae. There is an urgent need to collect numerous specimens and tissues, spanning the entire geographical distributions of species within these genera. This is particularly pressing for some of the poorly known species that are under threat from drastic reduction of their primary and mountainous forest habitats.

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Landscape-dependent differentiation of deer mouse populations (*Peromyscus maniculatus*): a total-evidence approach using molecular and morphometric data

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Abstract. We employed random amplified polymorphic DNA (RAPD), microsatellite and morphometric measurements to study the microdifferentiation of five insular and four mainland populations of deer mice (*Peromyscus maniculatus)* from Lake Duparquet (Québec). Population divergence was assessed using distance comparisons and regressions were used to link the differentiation patterns to ecological and landscape variables. A significant fraction of among-population variance was detected, indicating a clear differentiation of the populations, in spite of the small size of the study area (50 km^2). Pairwise F_{st} values and Euclidean distances were computed to derive matrices of interpopulation differentiation. We found that barriers to dispersal were a key factor shaping the genetic structure of the insular populations. Indeed, three explanatory variables clearly emerged from our analyses, the *Area* of the islands, the *Remoteness* of an island from the shore, and the *Isolation index* combining the effect of *Remoteness* and *Mainland geometry.* The analysis of a total evidence matrix clarified the population differentiation pattern and allowed for a three-fold increase of the proportion of variance explained by the regression models. A multiple regression based on the ecological and landscape variables explained over 70% of the combined molecular and morphometric population divergence.

Introduction

Over the last decade, biologists have described and characterised the genetic structure of numerous rodent populations at various geographical scales (e.g. Jaarola and Tegelström 1996; Patton et al. 1996). The structure of the genetic variation can reflect historical factors related to the distribution of populations (phylogeography). However, the demography of populations and the landscape configuration can also alter the distribution of the genetic diversity within a species (Gilpin and Hanski 1991). Recently, the researches in molecular ecology and population genetics have focused on linking the genetic structure with landscape features that influence dispersal of individuals among populations and, consequently, gene flow (e.g. Mech and Hallett 2001). Investigation of the effects of these variables on population genetics will not only provide insights into microevolutionary processes operating at the ecological scale, but also extend our understanding of the effects of environmental modifications caused by human activity at the landscape level. Habitat fragmentation reduces the size of populations and increases their isolation, which accelerates genetic drift and decreases gene flow, respectively, inducing, in turn, a quick decline of the genetic variation. For these reasons, addressing the effects of landscape alteration on the spatial organisation and genetics of populations is of primary importance for management purposes and conservation biology (Berry 1986). Indeed, efficient management of the genetic diversity relies on the quantification of the population differentiation and a clear understanding of the relationship between genetic and landscape structures. From this perspective, the study of populations inhabiting insular landscapes is of great interest, since insular biotas can provide a simple yet accurate model of the long-term effects of extreme habitat fragmentation in a simplified habitat matrix (Vucetich et al. 2001).

In the present paper, we have addressed these issues by assessing the structure of the genetic variation of insular and mainland populations of deer mice (*Peromyscus maniculatus*) sampled from a single lake covering a limited geographical area (<50 km^2). Amounts of interpopulation differentiation were estimated using three classes of markers: random amplified polymorphic deoxyribonucleic acid (DNA) (RAPD), microsatellite and morphometric data. We tested whether the observed genetic structure could be explained by the landscape configuration and spatial structure of populations. The results obtained with the three data sets taken separately were compared and combined to clarify the effect of habitat fragmentation on the genetic differentiation of deer mouse populations.

Materials and methods

Sampling sites

Lake Duparquet is located at the southern edge of the Canadian boreal forest (48°30'N, 79°13'W). It covers approximately 50 km^2 and has more than 150 islands of various sizes. Deer mice were collected from five islands and four mainland sites in August 1995 and 1998 (Figure 1). Sites were selected to cover a wide range of geographical distances from each other or from the mainland (from 0.2 to 9.2 km). For the purposes of the present study, 64 specimens from nine populations were considered for both RAPD and microsatellite typing as well as for morphometric analysis (for sample sizes, see Table 1).

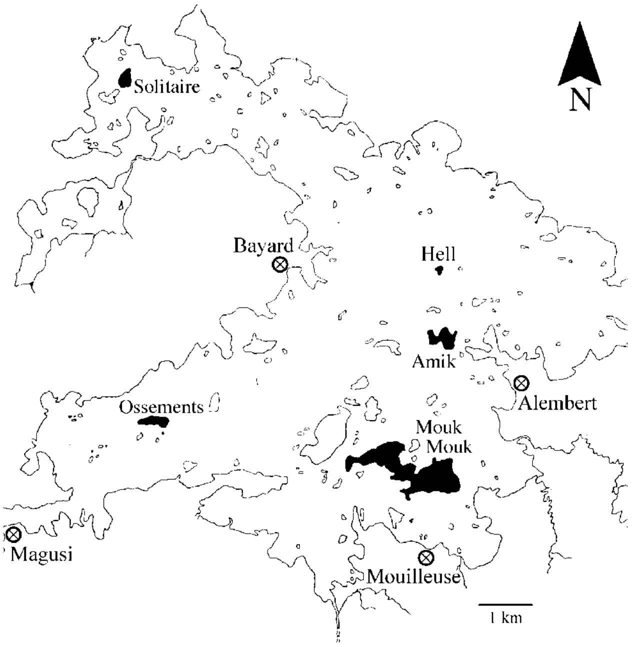

Figure 1. Map of Lake Duparquet (Abitibi, Québec) showing the five islands (in black) and the four mainland sites (crosses) analysed in this study.

Molecular data

DNA was extracted from fixed liver tissue, according to standard phenol/chloroform protocols. Three 10-mer primers were employed to derive the RAPD patterns, following the methods in Landry and Lapointe (1999), whereas microsatellite polymorphism was analysed at five loci using specific primers and polymerase chain reaction (PCR) profiles developed for *P. maniculatus* (Chirhart et al. 2000). Alleles were sized with an automated sequencer (ABI Prism 310) for microsatellites or using gel electrophoresis for RAPD typing.

Morphometric data

The morphological differentiation of populations was assessed by measuring 17 craniometric variables on each individual (see Landry and Lapointe 2001). These measurements were submitted to principal component analysis to correct for allometric growth. The first principal axis is assumed to represent a combination of the morphometric descriptors related to size, and the 16 subsequent orthogonal components were thus used to quantify morphometric differences between populations.

Population differentiation analyses

The amounts of population differentiation were calculated using an analysis of molecular variance (AMOVA; Excoffier et al. 1992). For both types of molecular data, pairwise interpopulation differentiation values were computed as linearised F_{st} values. In the case of morphometric measurements, Euclidean distances were computed between all pairs of individuals to measure population differentiation. Provided that the molecular and morphometric distances can be perfectly represented in a Euclidean space, this analytical framework applies to any type of data and was selected for the evaluation of all three distance matrices in a coherent fashion (see Landry and Lapointe 1999).

Ecological and landscape variables

The three population differentiation matrices were tested against six Euclidean distance matrices computed from the corresponding to each ecological and landscape variables (Table 1). The investigated variables were:

- *Population status*: coded 1 for island populations, and 0 for mainland populations.
- *Population abundance*: number of mice captured on each island (number of individuals/100 traps*night).
- *Island area*: for comparative purposes, the area (in ha) of all mainland sampling sites was set equal to the area of the largest island included in the analyses.
- *Remoteness*: distance (in km) separating each island from the mainland; for that matter, mainland populations have a remoteness of zero.
- *Mainland geometry*: angle of the shoreline (in degrees) at the closest distance from each island (see Landry and Lapointe 2001); small angles designate peninsulas whereas large angles indicate a flat-line shore; mainland populations are assigned a value of zero.
- *Isolation index*: combination of remoteness and mainland geometry (degrees*km); namely, an island situated close to a peninsula is considered to be less isolated than one located further away from a straight-line shore (Landry and Lapointe 2001).

Regression analyses

Contributions of the ecological and landscape variables to population differentiation matrices were assessed using a linear regression framework based on matrix comparison tests; the coefficients were tested using a permutation procedure (Mantel 1967). However, because all variables were strongly associated with population status, the effect of this descriptor was controlled with appropriate matrix treatment using a partial regression framework and population status as a covariate (Smouse et al. 1986). Ultimately, different combinations of distance matrices were evaluated in a multiple regression model.

Table 1. Details of the populations and ecological and landscape variables tested in this study.

Population	Sample size	Population status	Area (ha)	Population density (individuals/100 traps/night)	Remoteness (km)	Mainland geometry (degrees)	Isolation index (deg*km)
Amik	8	Island	13.0	35.6	0.20	60	12.0
Hell	8	Island	2.6	31.5	1.20	61	73.2
Mouk Mouk	8	Island	78.2	17.2	0.26	150	39.0
Ossements	8	Island	5.7	41.4	0.54	164	88.6
Solitaire	8	Island	6.7	9.4	0.34	90	30.6
Alembert	5	Mainland	78.2	3.1	0.00	–	–
Bayard	6	Mainland	78.2	3.8	0.00	–	–
Magusi	5	Mainland	78.2	1.6	0.00	–	–
Mouilleuse	8	Mainland	78.2	3.6	0.00	–	–

Only the matrices contributing significantly to the regression model were selected using a backward elimination procedure (Legendre et al. 1994). These analyses were computed independently from each of the three differentiation matrices as well as from a total evidence matrix averaging the morphometric and molecular interpopulation distance matrices to increase the amounts of information and maximise the explanatory power of the variables.

Split decomposition graphs

The structure of interpopulation differentiation was explored with a split decomposition graph (Huson 1998), in which the number of branches separating pairs of populations and the branch lengths are proportional to the differentiation among populations. This method allows visualisation of the multiple relationship patterns among populations by relaxing the constraints imposed by a tree representation. It also indicates alternative relationships supported by the data, combining information about historical factors and gene flow, the latter being represented by reticulated connections (parallel edges) in the graph. To evaluate the congruence among the three data sets, the topologies of the corresponding splitsgraphs were compared with a permutation test (Mantel 1967). A total evidence graph was then computed to represent the relationships among populations based on the combined data.

Results

RAPD data

Forty-eight polymorphic markers were scored from three RAPD primers and 64 individuals. No marker was unique to a particular population, and none could discriminate between insular and mainland populations. The AMOVA revealed that the sampled populations could be clearly discriminated despite the small spatial scale, with a large fraction of among-population variance (F_{st} = 21.8%, $p = 0.0001$). Interestingly, a significant fraction of intergroup variance was established between insular and mainland populations (6.3%, $p = 0.0071$). Pairwise interpopulation differences ranged from 5.56% to 29.12%, most of which exhibited significant differences at the 0.05 level (except for one pair: Bayard–Magusi).

Microsatellite data

The five loci analysed produced 72 alleles, with numbers of alleles per locus ranging from 11 to 18. The AMOVA analysis revealed a relatively large proportion of among-population variance (F_{st} = 11.5%, $p = 0.0001$). Contrary to RAPD findings, no significant differences were found among the mainland populations except for one (Bayard), which was significantly different from all the others. Similarly, no significant differences were detected between the island group and the mainland group (2.1%, $p = 0.9805$). On the other hand, all inter-island comparisons were significant at the 0.05 level, with pairwise interpopulation differences ranging from 1.1% to 40.2%.

Morphometric data

Euclidean distances among populations ranged from 0.051 to 0.617 and the analysis of variance computed from these morphometric distances indicated that populations were highly differentiated, with a substantial proportion of among-population variance (15.4%, $p = 0.0001$). The mainland populations were found to be morphometrically homogeneous, whereas the majority of insular populations were statistically different from one another at the 0.05 level. However, no significant difference was detected between mainland and insular populations (3.1%, $p = 0.2742$).

Regression analyses

Regression tests revealed that different ecological descriptors were related to the differentiation matrices. Whereas *Remoteness* ($r = 0.409$, $p = 0.047$) was significantly correlated with RAPD distances, the *Area* ($r = 0.214$, $p = 0.028$) was the only variable correlated with microsatellite differentiation. In the case of morphometric data, *Population abundance* ($r = 0.432$, $p = 0.031$), *Remoteness* ($r = 0.573$, $p = 0.034$) and the *Isolation index* (*r* = 0.727, *p* = 0.003) were all found to be significant in the simple regression models. When all distances were combined in a total evidence matrix, *Area* (*r* = 0.265, *p* = 0.018), *Remoteness* (*r* = 0.816, *p* = 0.003) and the *Isolation index* (*r* = 0.547, *p* = 0.018) were significantly correlated with the combined data. A multiple regression model including these variables revealed that 70% of the variance of the total evidence matrix can be explained by these ecological descriptors, which is more than three times the proportion of variance explained in the case of the separate data sets.

Splitsgraphs

Few features were congruent in the splitsgraphs obtained from the different data sets, as an important proportion of interpopulation distances was attributable to single population differentiation. The splitsgraphs computed from RAPD and microsatellite differentiation matrices exhibited somewhat different topologies, mainly regarding the position of the mainland populations (results not shown). Expectedly, no significant relationship was obtained when comparing the topological distances of these two graphs (*r* = 0.191, $p > 0.05$). However, restricting the analysis to inter-island comparisons revealed an exceptionally high level of congruence of the two splitsgraphs (*r* = 0.740, *p* = 0.002). Alternatively, the graph based on morphometric data was found to be remarkably congruent with the RAPD graph (*r* = 0.733, *p* = 0.001), but not with the microsatellite graph (*r* = 0.112, $p > 0.05$). Again, the incongruence was mainly caused by the mainland populations, and comparing only the islands revealed a much higher correlation (*r* = 0.883, *p* = 0.049). The splitsgraph of all populations based on the total evidence matrix combining the RAPD, microsatellite and morphometric distances is presented in Figure 2. This representation clarified and confirmed the relationships observed in the separate analyses. For one, the four mainland populations clearly formed a distinct group, separated from the five insular populations, and with shorter branches among them. Two pairs of populations (Hell–Amik and Ossements–Solitaire) also appeared to be strongly supported by the combined data. Interestingly, the same pairs were obtained in the separate analyses of the three data sets.

Discussion

Overall, the interpopulation values calculated with the three data sets consistently revealed a high proportion of among-population variance, indicative of strong population differentiation, considering the small geographical scale of the study area. The amounts of differentiation calculated from the microsatellite data were comparable to those observed from morphometric data, the main differences among data sets being attributable to mainland populations. In the case of RAPD data, our analyses underscored a clear division between islands and mainland populations, which is consistent with other results obtained for the same species using similar markers in a different insular landscape (Vucetich et al. 2001). Thus, it appears that such mainland–island disparities are likely to reflect the influence of habitat fragmentation on genetic processes. While island and mainland populations were sampled in different years, it is unlikely that variations in time could solely explain the directional changes implied by the difference observed. Indeed, the genetic structure in populations of *Peromyscus* has been shown to remain stable for six consecutive years (Baccus and Wolff 1989).

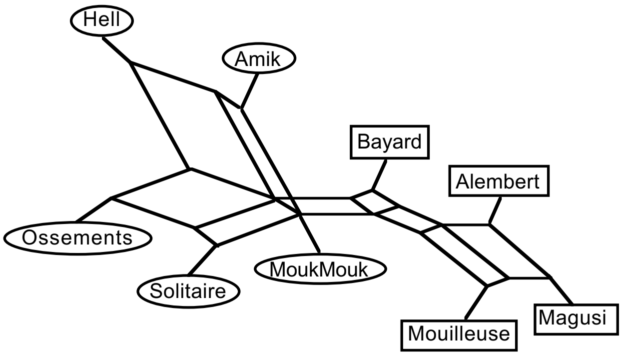

Figure 2. Split decomposition graph illustrating the relationships among nine populations of deer mice. The path-length distances are proportional to the amount of differentiation between pairs of populations from Lake Duparquet, Québec. Terminal branches are not drawn to scale to focus on the internal branches of the graph. Ellipses are used to represent insular populations, whereas rectangles designate mainland populations.

The absence of morphometric or microsatellite differentiation among mainland populations suggests extensive gene flow or large population size on the mainland. This also indicates that the interactions involving mainland populations are many times greater than those among insular populations; indeed, gene flow is expected to come mostly from the mainland. On the other hand, most insular populations were extremely divergent from one another, regardless of the data set analysed. Collectively, the substantial amounts of genetic differentiation documented here suggest that insular populations undergo reduced amounts of gene flow relative to the mainland populations. This observation is in agreement with other studies that also reported a reduction of genetic variability caused by increased genetic drift and reduced gene flow in insular populations (Vucetich et al. 2001).

Given the substantial gene flow among mainland populations, dispersal from the mainland to the islands was expected to be of primary importance in determining the amounts of island population differentiation. Three variables were related to this insular dispersal (*Remoteness*, *Area* and *Isolation*). *Isolation* is a composite index of two descriptors: *Remoteness* and *Mainland geometry.* When considered separately, these two variables contribute differentially to dispersal mechanisms. Whereas *Mainland geometry* measures the inclination of small mammals to enter the water during dispersal (Landry and Lapointe 2001), *Remoteness* measures the length of the water barrier preventing a mouse from reaching an island. These two descriptors are not collinear and can be thus used in combination to quantify the similarities among populations. The *Isolation index* was found to be the strongest predictor of population morphometric divergence and was also highly significant with the total evidence data. *Remoteness*, on the other hand, was significant in the regression models based on RAPD, morphometric and total evidence distances. These results confirmed that population differentiation could not be explained without considering the habitat spatial structure and the biology of the species. *Peromyscus* mice are rather good dispersers on the mainland, and some mice are known to be able to swim across water barriers up to 200 m (Sheppe 1965). Despite their relatively poor ability to cross water barriers, one must bear in mind that deer mice are active all winter long and could disperse when the lake surface is frozen. Nevertheless, dispersal rarely occurs during the winter months when the activity is reduced (Fairbairn 1978). Therefore, limited over-water dispersal is expected to be an important factor preventing the gene flow from the mainland to the islands.

Relationships among populations arise both from historical factors and lateral transfer, even though pairwise F_{st} values cannot separate these factors. A split decomposition graph can be used, however, to visualise the relationships among populations, as it reconciles both conceptual interpretations of F_{st} values. The model underlying split decomposition is more flexible and desirable for population analysis than the commonly used dichotomous trees (Lapointe 2000). It allows for a larger fraction of the available information to be displayed while only retaining the strongest relationships among pairs of populations. Moreover, the residual fraction of the data is not represented in a splitsgraph, a desirable feature when working at small spatial scales and when random dispersal is very likely. Few compatible associations were recovered across the three data sets. Small sample sizes and the limited numbers of microsatellite loci analysed for the mainland populations can possibly explain these discrepancies. However, further examination of the splitsgraphs, ignoring the mainland populations, revealed that the three data sets were extremely congruent. Because of their very high variability, microsatellites require more extensive sampling than other genetic markers, and it is likely that only the strongest differences could be identified in the present case. Nevertheless, the splitsgraphs jointly showed that the relationships among populations were not reflected by the geographical location of the populations (see Figure 1).

Previous studies conducted at various spatial scales have reported a reduction of within-population genetic variability in island populations of rodents (oceanic islands: Berry and Jakobson 1975; Redfield 1976; Berry 1986; Ashley and Wills 1987; Lake islands: Loxterman et al. 1998; Vucetich et al. 2001). This depletion of genetic variability is caused by increased genetic drift and reduced gene flow related to isolation (Slatkin 1985), in turn inducing a strong genetic structure among populations. Our results corroborate these earlier findings using three different classes of genetic markers. Moreover, the RAPD results suggest the existence of a difference between mainland and island populations, which was also underscored by a very similar study involving RAPD markers in *P. maniculatus* populations (Vucetich et al. 2001). Still, this differentiation could not be observed either with microsatellites or morphometric data. Nevertheless, these findings stress the need for a closer scrutiny of insular population genetics, especially in the context of population insularisation caused by habitat fragmentation (Hanski 1998).

Finally, the use of a total-evidence approach proved to be fruitful to clarify the differentiation patterns among populations. The data combination clearly increased the amount of explained variance of the differentiation matrix in the multiple regression models. This result supports the hypothesis that adding molecular and morphological information maximises the content of evolutionary information. Moreover, the use of a distance approach based on fractions of interpopulation variance allowed us to compare and combine data from very different sources, providing a highly flexible analysis framework. The residual variance could be attributed to a series of random events altering the differentiation of insular populations, including random genetic drift.

Conclusion

We have shown that the amount of population genetic differentiation is associated with landscape configuration. We used a rigorous approach involving the statistical testing of all descriptors that allowed the evaluation of the relative effects of many variables. Our results clearly indicate that ‘ecological distances’ related to the dispersal abilities of a species are important to explain the population differentiation. The combination of different data sets in a total evidence matrix provided increased resolution to understand the factors influencing the genetic structure of insular populations. These results, along with the analytical approach presented in this paper, could be used to provide guidelines and a framework for the management of rodent populations or metapopulations inhabiting any fragmented landscape.

Acknowledgments

The authors are grateful to A. Bolduc, C. Savage and D. Dubé for field assistance, to S. Roy for technical help in the laboratory work, and to P. Paquin for constructive discussions. The manuscript was improved through the valuable comments of J. Ferron, A. Bruneau, S. Gauthier, J.A. Lambert, Y. de Repentigny, J.O. Wolff, S.G. Mech and C.J. Krebs. This work was supported by scholarships from the National Science and Engineering Research Council of Canada (NSERC) and Le Fonds pour la Formation de Chercheurs et l’Aide à la Recherche (FCAR) to P.-A. Landry and S. Noël, as well as by NSERC grant OGP0155251 to F.-J. Lapointe.

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Systematics and distribution of the house mice of Russia and neigbouring countries, with special regard to zones of high genetic polymorphism

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Abstract. The taxonomy of house mice (genus *Mus*) of Russia and neigbouring countries is reviewed. Two free-living species (*Mus spicilegus*, *M. macedonicus*—both monotypic) and one commensal species (*M. musculus*—polytypic) are found in the former Union of Soviet Socialist Republics. The distribution of these species is described and the origin of zones of high genetic polymorphism in Transcaucasia and Asia is discussed. The Transcaucasian populations are interpreted as early-differentiated forms of *M. musculus* that preserve the ancestral gene pool. In Adjaria, secondary contact occurs between these forms and differentiated *M. domesticus* from Turkey. Analysis of hybrid populations of house mice in Russia demonstrates the particular significance of hybridisation in the evolution of commensal taxa.

Introduction

Karl Linnaeus described *Mus musculus* in 1758 from Uppsala. Since that time, a total of 151 morphologically defined taxa of house mice have been described (Marshall 1998). In the territory of the former Union of Soviet Socialist Republics (USSR) authors described 25 different taxa of house mice (5 species and 20 subspecies).

The systematics of the genus *Mus* have advanced during the last three decades, largely owing to the application of biochemical and molecular genetic methods. Two large, divergent groups have been identified in the *Mus musculus* species group. The first group includes the commensal speces: *Mus musculus*, *M. domesticus*, and *M. castaneus* [after Sage et al. (1993) we consider these as distinct species]. The second group includes the indigenous free-living species *M. spretus*, *M. macedonicus* and *M. spicilegus*.

The aims of this work are: (i) to review the available data concerned with the taxonomy of house mice in Russia and neighbouring countries, with emphasis on the distribution of each species; and (ii) to discuss the origin of Transcaucasian and Asian populations possessing high levels of genetic variability.

Taxonomy and distribution of house mice in Russia and neighbouring countries

Intensive systematic studies, involving the investigation of allozyme variation among more than 600 individuals, and morphological analysis of both genetically marked individuals and other museum specimens (collections of zoological museums of Moscow, St Petersburg, Kiev and others), have revealed three species of the genus *Mus* in the former USSR. One is commensal (*Mus musculus*), while two are free-living (*M. spicilegus* and *M. macedonicus*) (Mezhzherin and Kotenkova 1989, 1992; Frisman et al. 1990). Some populations of house mice had high levels of genetic polymorphism, sometimes extending across large zones (e.g. Transcaucasia and Asia) (Mezhzherin et al. 1998; Yakimenko et al. 2000).

Mus spicilegus, the mound-building mouse, is a small mouse with a grey homogeneous or contrasting two-coloured coat. The tail of *M. spicilegus* is always shorter in length than its body and it is thinner than the tails of other species. *M. spicilegus* occurs in Ukraine, Moldova and some regions of Romania, Hungary, Serbia, Macedonia, Bulgaria, and Austria (Sokolov et al. 1998; Figure 1). An isolated population was described at Ulcinj, close to the border between Montenegro and Albania (Krystufek and Macholan 1998). Attention should be paid to the easternmost as well as the northern edges of the distribution of this species. Available data do not support the occurrence of *M. spicilegus* in northern Caucasus. Across its range, *M. spicilegus* occurs sympatrically with *M. musculus*.

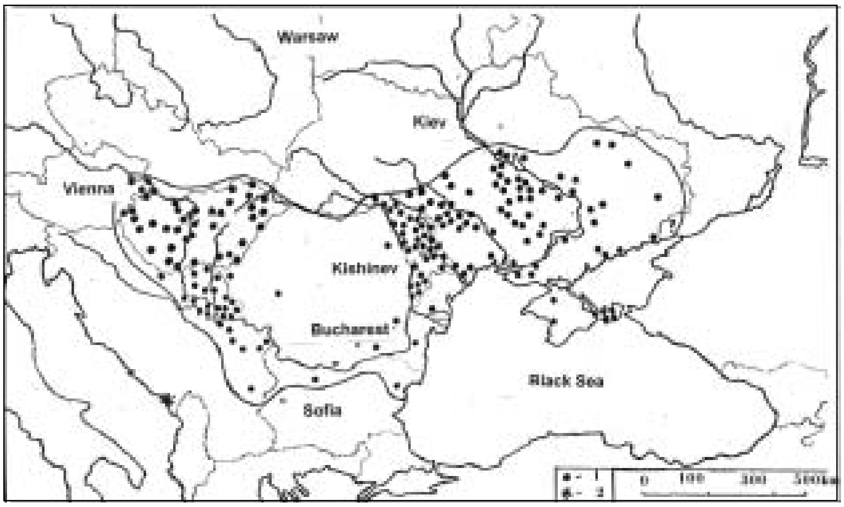

Figure 1. Distribution of *Mus spicilegus* (Krystufek and Macholan, 1998; Sokolov et al. 1998). Dots represent documented *M. spicilegus* captures or mounds; star represents an isolated population of *M. spicilegus*.

Mound-building mice inhabit a variety of agro-ecosystems and, as a rule, are locally abundant throughout their range. A distinctive characteristic of *M. spicilegus* is its grain-hoarding activity. In autumn, groups of 4–14 mice construct special mounds (kurgans) in which to store food and spend the winter. Seeds of 84 species of plants belonging to 29 families have been found within these mounds; 28 of these are major forage plants (Sokolov et al. 1998).

The mound-building mouse was supposedly first described by Nordmann (1840) as *Mus hortulanus* from a specimen collected at the Botanical Garden of Odessa, Ukraine. Nordmann did not mention mounds, which are typical of *M. spicilegus,* and indicated that the colour of *M. hortulanus* was brown. In the Zoological Museum of the Russian Academy of Science, St Petersburg, we located one skull of a mouse from Odessa (No. 4460) identified by Nordmann as *M. hortulanus*. The skull is badly damaged, but the breadth of the zygomatic process of the maxillary (>0.8 mm) suggests that the skull belongs to *M. musculus*. Gerasimov et al. (1990) used discriminant function analysis to show that this specimen can be referred to as *M. m. musculus*. Evidently, what Nordmann described was the wild form of *M. musculus*, which is widespread throughout the steppes of southern Ukraine and Moldova. In 1882, J.S. Petenyi (Chyzer 1982) described the mound-building mouse as *Mus spicilegus*. The type series is still preserved in good condition in the Hungarian Natural History Museum, Budapest; the lectotype is an adult male, mounted, No. 161.7 from Felsobesnyo, collected on 15 April 1852 (Csorba and Demeter 1991).

Mus macedonicus, the eastern Mediterranean mouse, is a comparatively large mouse with a contrasting two-coloured coat. Mice from Transcaucasia have light sandy backs and white bellies. Transcaucasia is situated between the Black and Caspian Seas to the south-east of the large Caucasus mountain ridge and includes the territories of Georgia, Armenia and Azerbaijan. The tail of *M. macedonicus* is always shorter than the length of its body. In Transcaucasia, this species occurs sympatrically with populations of commensal mice that are genetically intermediate between *M. musculus* and *M. domesticus* (Figure 2), and is found in both agro-ecosystems and natural habitats.

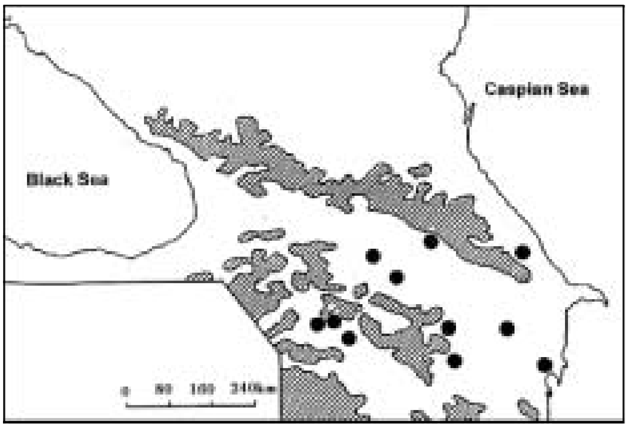

Figure 2. Distribution *of Mus macedonicus* in Transcaucasia. Dots represent documented *M. macedonicus* captures.

Mus musculus is a widespread and polytypic commensal found in eastern Europe and Asia. Considerable variation exists in coat colour and tail length. Coat colour varies from a homogeneous grey to contrasting two-coloured. The dorsal colour can be grey, reddish-grey, reddish, brownish, light-reddish, sandy and so on. Fur colour of the belly varies from grey to pure white. In some commensal populations, especially in large cities, the level of coat colour polymorphism is very high. The tail can be shorter or longer than the body. *M. musculus* occurs throughout practically all of the former USSR. The range of *M. musculus* can be divided into four ecological zones based on the level of commensalism (Prilutskaya 1984; Figure 3). In the northern zone, house mice live year-round in human dwellings. In the two intermediate zones, these rodents leave the houses in spring and spend the summer in natural habitats (in the second zone, never far from houses). In autumn, they return to human dwellings. In the southern zone, house mice are free-living but sometimes inhabit dwellings.

The former USSR supports a minimum of three subspecies, which differ in external morphology and, according to Lavrenchenko (1994), are readily distinguished on multifactorial analysis of 18 skull measurements. These can be characterised thus:

- *Mus musculus musculus* Linnaeus, 1758 (syn. *funereus*, *borealis*, *hortulanus*). Colour of back is grey, reddish-grey, reddish, brownish or light-reddish; colour of belly is light grey to whitish. The tail is usually longer than body, however in some regions, e.g. Ukraine steppe, the tail is shorter than the body. This subspecies occurs in Pribaltica, Ukraine, Byelorussia, the European part of Russia, southern Siberia, northern Pribaikalie and in some parts of Far East Russia.
- *M. m. wagneri* Eversmann, 1848 (syn. *bicolor*, *decolor*, *sareptanicus*, *severtzovi*, *oxyrrhinus*, *pachycercus*). Short-tailed; colour of back is pale straw; colour of belly is pure white or whitish. This subspecies is found in the Pricaspian lowland, Kazakhstan (except some northern and eastern regions) and Middle Asia.
- *M. m. raddei* Kastschenko, 1910 (syn. *variabilis*). Short-tailed; colour of back is brownish or reddish; colour of belly is whitish. The 17th chromosome has increased in size through addition of pericentromeric heterochromatin blocks. It is not clear how this subspecies relates to the more easterly forms *M. m. manchu* and *M. m. mongolium*. *M. m. raddei* occurs in eastern Kazakhstan, Altai and eastern Zabaikalie.

Yakimenko et al. (2000) investigated pericentromeric heterochromatin in the karyotypes of about 1000 commensal and indigenous individuals from the former USSR and divided the short-tailed house mice into four subspecies: *wagneri*, *gansuensis*, ‘*molossinus*-like’ and *musculus*. Although this division based on chromosome morphology requires confirmation, the data nevertheless support the viewpoint that *Mus musculus* is a highly polytypic species that requires additional investigation.

Zones of high levels of genetic polymorphism and the role of hybridisation in the evolution of commensal house mice

The significance of introgressive hybridisation in the evolution and diversification of mammals (including *Mus musculus* sensu lato) is an important problem of evolutionary theory. There is a narrow (16–50 km wide) zone of introgressive hybridisation between *M. musculus* and *M. domesticus* in Central Europe, and a well-studied zone of secondary contact (Sage et al. 1993) that traverses different habitats along its course through the Alpine and Balkan mountains and across the plains of Central Europe. Allozyme analysis has shown that Transcaucasian populations of commensal house mice possess an admixture of *musculus* and *domesticus* genes (Mezhzherin and Kotenkova 1989, 1998; Milishnikov et al. 1990). This region is either a zone of secondary contact between *musculus* and *domesticus*, with very wide introgression of *domesticus* genes into the genome of *musculus* (Mezhzherin and Kotenkova 1989; Frisman et al. 1990; Mezhzherin et al. 1998), or these are relict populations descended from non-differentiated forms with ancestral

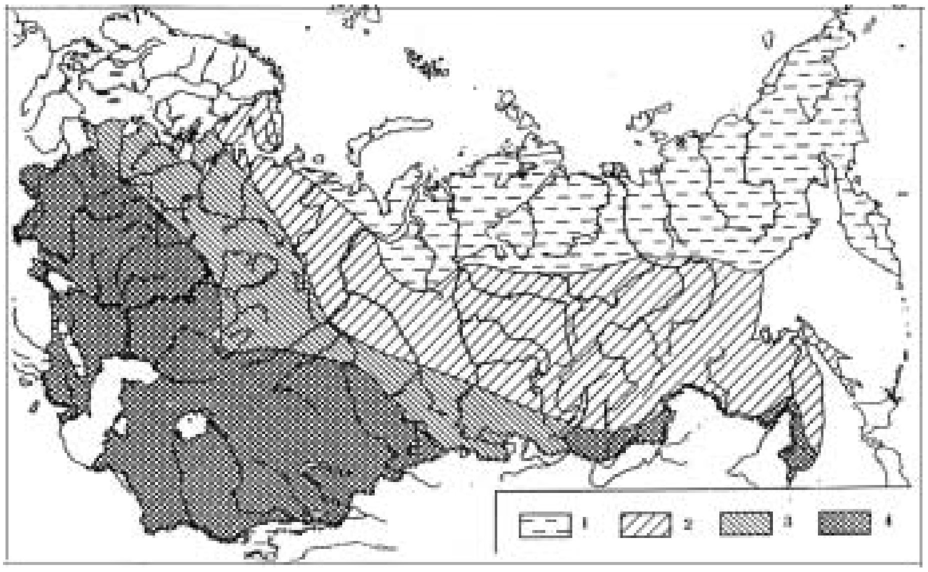

Figure 3. Distribution of *Mus musculus* in Russia and neighbouring countries. There are four ecological zones: 1 = house mice inhabit houses during all year; 2 = house mice leave houses during summer, but stay not far from houses; 3 = house mice leave houses during spring and summer; and 4 = house mice can be free-living all year round.

polymorphism (Milishnikov et al. 1990). The main feature of this zone is the unusually large extent of *domesticus* gene which occurs throughout the entire Transcaucasia region (about 300 km^2).

Within the last decade, much progress has been made in the study of populations of the *M. musculus* species group in India and Pakistan (Din et al. 1996). Populations of house mice from the northern part of the Indian subcontinent are more heterozygous than samples from any other region. They also contain the majority of the alleles that exist in the various differentiated species at the periphery of the wider geographic range of the group. According to a neighbour-joining analysis using Nei's genetic distances, and a factorial correspondence analysis of allelic composition, the Pakistani and Indian populations occupy a genetically central position with respect to the peripheral species. Din et al. (1996) interpreted these results as a retention of ancestral genetic polymorphism and identified northern India as the probable cradle of this commensal species. *M. musculus* and *M. domesticus* lineages probably started to differentiate a few hundred thousand years ago in isolated mountain areas, and they may have colonised the peripheral parts of their ranges only recently. In a related publication, Orth et al. (1996) reiterated the view that the Transcaucasian region is a zone of secondary contact between *M. musculus* and *M. domesticus*. However, a hybrid origin of Transcaucasian populations of house mice is doubtful in the light of the following facts:

1. There are no genetic gradients suggesting introgression of domesticus genes from west to east Transcaucasia.
2. Populations of Transcaucasian house mice contain some alleles that are not found in peripheral populations of *M. musculus* and M. *domesticus*. These genes are all found in northern Indian populations (Din et al. 1996), and some of them occur in populations from Turkmenistan and Tadjikistan (Milishnikov et al. 1994).
3. Populations of house mice in south-western Georgia (Adjaria, Kobuletty) possess a predominantly *domesticus* genotype but have a *musculus* morphotype according to multifactorial analysis of cranial morphology (Lavrenchenko 1994).
4. In a comparative analysis of exploratory behaviour in eight populations of different species and subspecies of house mice, the Adjarian population was similar to populations of *M. m. musculus* (Kotenkova et al., this volume).

These observations favour the view that Transcaucasian house mouse populations are relicts of an early-differentiated form of *M. musculus*, preserving much of the ancestral gene pool. The Adjarian population would then be a product of secondary contact between these forms and fully differentiated *M. domesticus* from Turkey.

Large zones of hybridisation are present also in Asia. According to Yakimenko et al. (2000) there is a minimum of three large hybrid zones in Primorie, Priamurie and Sakhalin. The taxa involved in the formation of these hybrid zones are *M. castaneus*, *M. domesticus* and various subspecies of *M. musculus*. The hybrid zone of Primorie is very young, dating to the last 30–40 years of the 19th century at a time when the territory of Primorie was settled by people from Priamurie—the European part of Russia, Siberia and China.

Analysis of hybrid populations of house mice in Russia demonstrates the particular significance of hybridisation in the evolution of commensal taxa. This enhanced role in commensals is linked to their unique ability to expand their geographical ranges through human agency and even survive as commensals in areas that are beyond their physiological tolerance. Subjects that warrant further investigation include the mechanisms of precopulatory isolation in commensal taxa and the fitness of mice from hybrid populations.

Acknowledgments

The author's research was supported by the Russian Foundation of Basic Research, Grant 01-04-48283.

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Rodents and other small mammal diversity in Lore Lindu National Park, central Sulawesi, Indonesia

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Abstract. A terrestrial small mammal survey of Lore Lindu National Park was carried out from March 2000 to July 2001, sampling 11 major vegetation types on eight land systems and at altitudes ranging from 400 to >2100 m above sea level (asl). The survey used a standardised arrangement of trap type, trap spacing and two types of bait, roasted coconut and dried fish. Forty locations were surveyed, using 200 traps at each location for a total of four nights (800 trap-nights/survey site). In all, 309 individuals of 22 species of rodents were trapped using snap-traps and cage-traps. Seven species constituted 75% of captures as follows: *Rattus hoffmani* (17.1%), *R. marmosurus* (15.2%), *Bunomys chrysocomus* (12.3%), *B. prolatus* (11.6%), *B. penitus* (9.7%), *Paruromys dominator* (9.7%) and *Taeromys celebensis* (8.1%). Significantly more rats were captured in cage-traps (171 individuals) than snap-traps (138 individuals) and dried coconut was preferred (196 individuals) to fish as bait (113 individuals).

Rodent diversity as measured by Fisher's α peaked in the altitude range 1200–1500 m asl and generally declined at higher elevations. However, a secondary peak above 2100 m in diversity reflected the very low and even abundance of upper montane species. Simpson's and Shannon–Weiner indices were relatively constant across all altitude categories. Among the surveyed vegetation types, rodent diversity was highest in cloud forest, upper montane forest, montane forest, lower montane moist forest, swamp forest and marsh habitats, and lowest diversity in lower montane forest, lowland forest and monsoon forest. Fisher's α and Simpson's diversity indices attained highest values in the Kototinggi land system and for Shannon–Weiner index in the Telawi land system.

Introduction

Lore Lindu National Park is located just south of the equator in Central Sulawesi. It lies within the intertropical convergence zone and contains high mountains rising to above 2100 m above sea level (asl) and formed during late Miocene to Pliocene times. A geographical information system (GIS) (RePPProT 1989), developed in the context of a Department of Transmigration initiative and with assistance from the United Kingdom's Overseas Development Administration (ODA), identified 10 major land systems in the park (Lore Lindu National Park 2001). The island of Sulawesi has a unique mammalian fauna that is not particularly rich in species, but features a very high level of endemism. This has resulted from its long period of isolation from other landmasses and its location in the biological region of Wallacea, situated between the rich source areas of Sahul and Sunda. Before the current survey, several important mammal populations were known to occur in this park, including: dwarf mountain anoa, *Anoa quarlesi*; babyrousa, *Babyroussa babyrusa*; tarsiers, *Tarsius pumilus*, *T. dianae*, and *T. spectrum*; giant Sulawesi civet, *Macrogalidia musschenbroecki*; and Sulawesi cuscus, *Strigocuscus celebensis*. Three species of murid rodents, *Margaretamys elegans*, *Melasmothrix naso* and *M. rhinogradoides*, are recorded only from Lore Lindu National Park (Musser and Dagosto 1987).

Despite the publications of Musser (1969a,b,c, 1971, 1991), Musser and Dagosto (1987), van Strien (1986) and Suyanto et al. (1998) on the murid rodents of Sulawesi, little is known regarding the distribution of species in relation to vegetation, habitat, altitude and land systems. This study was designed to provide detailed information on the micro-distribution of rats in Lore Lindu National Park to be used in the design of management strategies. In particular, information was sought on: habitats or areas particularly rich in numbers of species or numbers of individuals of a particular species; on habitat preferences of individual species and their location along altitudinal gradients; and on seasonal shifts in habitat requirements of particular species. The survey represents the most extensive field study of rats yet carried out in Lore Lindu National Park, and indeed anywhere in Sulawesi.

Methods

Sampling areas

The survey was carried out from March 2000 to July 2001. All 11 major vegetation types were surveyed: cloud forest, upper montane forest, montane forest, lower montane forest, lower montane moist forest, marsh, mixed garden, monsoon forest, swamp forest, lowland forest, and degraded lowland forest. These vegetation types lay on eight land systems over an altitudinal range of 400 to >2100 m asl. Geological and geomorphic characteristics of the eight major land systems are given in Table 1.

Forty sites were selected to represent the varied geography, climate and habitat of the park (Figure 1). Each trap line was geo-located using a Garmin 12 global positioning system (GPS), and the elevation of each site recorded using an altimeter.

Seven altitudinal groupings were recognised as follows: 300–599 m, 600–899 m, 900–1199 m, 1200–1499 m, 1500–1799, 1800–2099 m and above 2100 m.

Table 1. Land system types in Lore Lindu National Park sampled in this study.

Land system type	Land and rock types
Telawi	Precipitously oriented mountain ridges on acid igneous rocks, granite, granodiorite, rhyolite
Bukit Balang	Irregular mountain ridges on intermediate basaltic, volcanics, andesite, basalt breccia
Kototinggi	Moderately sloping, non-volcanic alluvial fans
Bukit Baringin	Very steep, ordered hills on acid igneous rocks, rhyolite, granite
Bukit Pandan	Precipitously oriented metamorphic ridges, quartzite, schist, gabbro, granite, serpentinite
Pendreh	Asymmetric, broadly dissected ridges on sandstone and mudstone
Batang Anai	Long, very steep ridges over metamorphic rocks
Lindu	Lacustrine plains

Capture techniques

Mammals were trapped using a standardised trapping arrangement of trap type, trap spacing and bait. Two types of traps were used: small Kasmin cage-traps made of wire with dimensions of 28 × 12 × 12 cm; and standard snap-traps of sufficient size to capture the largest rat species.

Ten transect lines were set at each survey site. Each line was comprised of 20 traps—a cage-trap alternated with a snap-trap placed every 5 m. Traps were set for four nights, giving a standard trapping effort of 800 trap nights per site. Two types of bait were used: a lightly roasted coconut and dried fish; these were placed alternately in each trap type.

Small mammal trapping results from elsewhere in Indonesia suggest a substantial reduction in rate of captures of additional species of mammal over a weekly period (Kitchener et al. 1997; Maryanto and Kitchener 1999; I. Maryanto, unpublished). Accordingly, a trapping period of 4 days was considered adequate.

Data analysis

Diversity measures variably reflect both the number and relative abundance of species in a community. Three indices of species diversity were used: Simpson’s, Shannon–Weiner and Fisher’s α (Krebs 1989). The results of the survey were entered into a Microsoft Access database linked to an Arcview 3.2 GIS. Diversity indices were calculated using an Ecological Methodology computer package. Chi-square tests were used to analyse patterns of habitat association, and to compare the effectiveness of different trap and bait types.

Observations and results

Species captured

Twenty-two species of rodents was trapped in the park, including 21 Muridae and one Sciuridae (*Prosciurus murinus*; two individuals). The murid rodents were: *Bunomys chrysocomus* (Hoffmann 1887), *B. penitus* (Miller and Hollister 1921), *B. prolatus* Musser 1991, *Lenomys meyeri* (Jentink 1879), *Margaretamys elegans* Musser 1981, *Maxomys hellwaldii* (Jentink 1879), *M. musschenbroecki* (Jentink 1879), *M. wattsi* Musser 1991, *Melasmothrix naso* Miller and Hollister 1921, *M. rhinogradoides* Musser 1969, *Paruromys dominator* (Thomas 1921), *Rattus exulans* (Peale 1848), *R. hoffmani* (Matschie 1901), *R. marmosurus* Thomas 1921, *R. rattus* (Linnaeus 1758), *R. xanthurus* (Gray 1867), *Rattus* sp. (undescribed?), *Taeromys celebensis* (Gray 1867), *T. hamatus* (Miller and Hollister 1921), *T. punicans* (Miller and Hollister 1921) and *Taeromys* sp. (undescribed?). One individual of the widespread insectivore *Suncus murinus* was also captured.

Trapping success

In all, 309 small mammals were caught in 32,000 trap-nights during the survey. Overall trap success was one animal captured on average for each 104 trap-nights or <1%. Seven species of murid rodents accounted for 75% of captures, as follows: *Rattus hoffmani* (17.1%), *R. marmosurus* (15.2%), *Bunomys chrysocomus* 12.3%, *B. prolatus* (11.6%), *B. penitus* (9.7%), *Paruromys dominator* (9. 7%) and *Taeromys celebensis* (8.1%). Significantly more rats were captured in cage-traps (171 individuals) than snap-traps (138 individuals) ($p > 0.05$, $\chi^2 = 3.524$, df = 1).

Trap and bait effectiveness

Dried coconut was preferred (196 individuals) to fish baits (113 individuals) ($p < 0.001$, $\chi^2 = 22.29$, df = 1). The combination of trap and bait type significantly influence

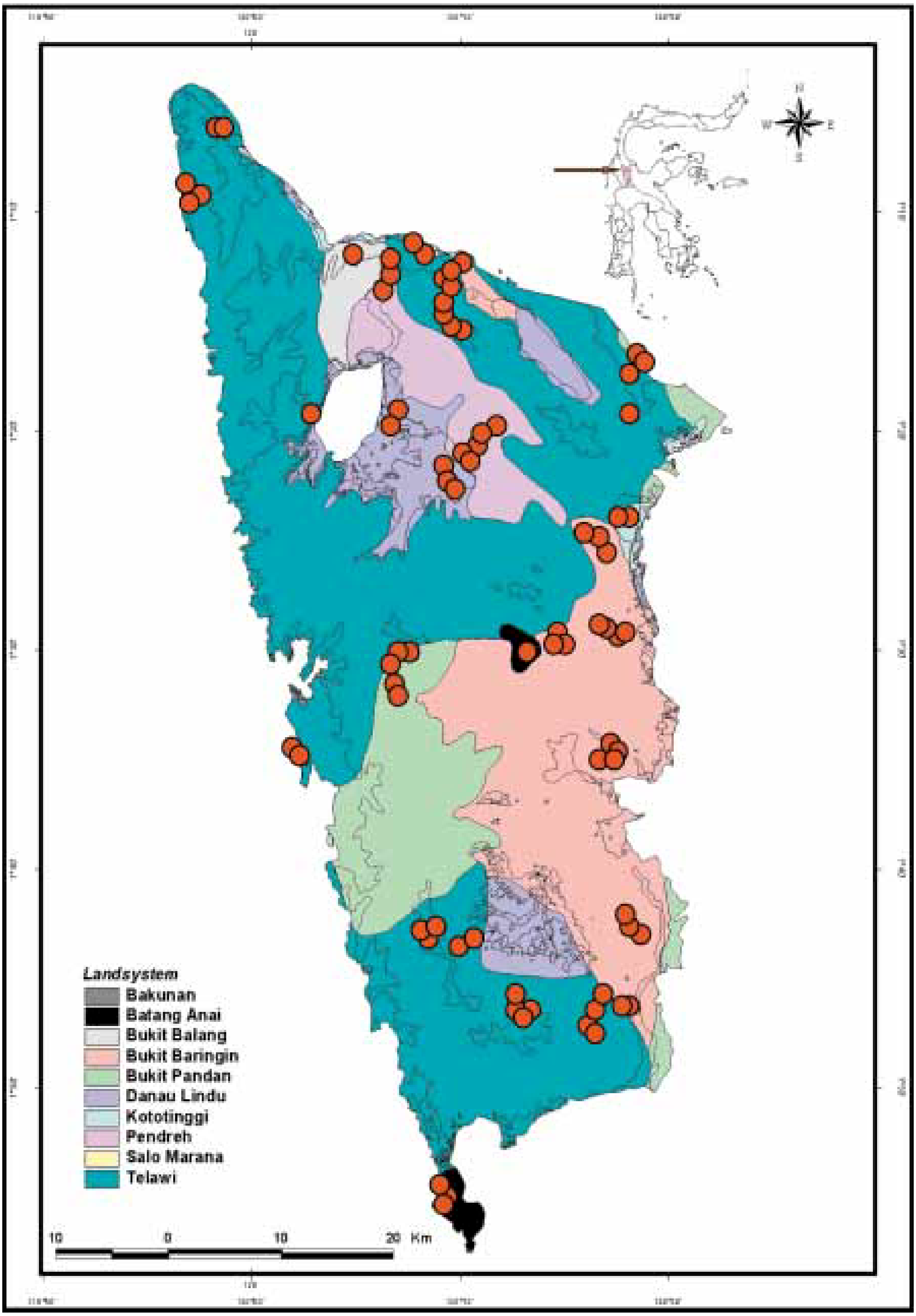

Figure 1. Map of the small mammal survey locations.

capture rates of *Maxomys hellwaldii* ($p < 0.05$, $\chi^2 = 7.149$, df = 1), *Paruromys dominator* ($p < 0.001$, $\chi^2 = 29.119$, df = 1), *Rattus marmosurus* ($p < 0.05$, $\chi^2 = 3.848$, df = 1), *Taeromys celebensis* ($p < 0.001$, $\chi^2 = 25.781$, df = 1) and *T. hamatus* ($p < 0.05$, $\chi^2 = 4$, df = 1). Among the vegetation/land system types, only captures in lower montane forest on the Pendreh land system were significantly influenced ($p < 0.05$, $\chi^2 = 5.04$, df = 1) by a combination of trap type and bait, with rodents preferring cage-traps baited with dried coconut. There were no significant associations of capture rate, trap type and bait type with either altitude or vegetation type. Only on Bukit Pandan and Bukit Balang land systems were capture rates not significantly associated ($p > 0.05$) with trap and bait type.

Species diversity

Trends in each of the three diversity indices are shown in Figure 2 (elevational zone), Figure 3 (vegetation type) and Figure 4 (land system type). All three indices show a peak in murid diversity in either the 990–1199 m or the 1200–1500 m zones, with a secondary peak above 2100 m. However, an examination of the raw data (Table 2) shows that the actual species number above 2100 m is not particularly high (8 species compared with 14 at 900–1199 m). Rather, the return to higher index values reflects the even representation of species, all of which were caught in very low numbers (total of 16 individuals). The Shannon–Weiner values remain more constant across all altitude groups but with a low point at 1500–1799 m.

Low capture rates make it difficult to recognise clear trends in diversity among vegetation types (Table 3). However, all three indices indicated that the highest murid diversity occurred in cloud forest, upper montane forest, montane forest, lower montane moist forest, swamp forest, and marsh habitats, and the lowest murid diversity occurred in lower montane forest, lowland forest and monsoon forest. Fisher's α and Simpson's diversity indices were highest in the Kototinggi land system, while the Shannon–Weiner index was highest in the Telawi land system (Table 4). Among habitat types, Fisher's α diversity was highest in Kototinggi lower montane forest and lowest in Bukit Balang lower montane forest (Table 5).

Discussion

In this study, cage-traps proved more effective than snap-traps and dried coconut better than dried fish at capturing small mammals. A similar result was obtained by Kitchener et al. (1997) in the Freeport area of West Papua province (formerly Irian Jaya) and on Gag Island, West Papua province, by Maryanto and Kitchener (1999).

Twenty-one species of murid rodents were recorded in Lore Lindu National Park. Of the 51 murids known in total from Sulawesi, the following species are recorded only in Central Sulawesi: *Melasmothrix rhinogradoides, M. naso, Lenomys meyeri, Bunomys penitus, B. prolatus, Margaretamys elegans, Taeromys hamatus*, *Maxomys wattsi*, and the unidentified *Rattus* sp. and *Taeromys* sp.

Table 2. Comparison of diversity indices based on elevation zones (m above sea level) (*N* = number of species captured, Sum = total captures).

	300–599	600–899	900–1199	1200–1499	1500–1799	1800–2099	>2100
N	1	12	14	11	7	10	8
Sum	1	83	111	33	18	46	16
Simpson		0.852	0.899	0.905	0.817	0.844	0.908
Shannon–Weiner		2.978	3.4	3.204	2.399	2.806	2.858
Fisher's α		3.851	4.238	5.773	4.205	3.934	6.365
Fisher's α se		0.622	0.756	2.691	3.762	1.132	26.845

Table 3. Comparison of diversity indices based on vegetation types (*N* = number of species captured, Sum = total captures).

	Cloud forest	Degraded lowland forest	Lower montane forest	Lower montane moist forest	Lowland forest	Marsh	Mixed garden	Monsoon forest	Montane forest	Swamp forest	Upper montane forest
N	13	1	13	4	7	6	1	4	11	8	8
Sum	54	3	131	6	20	11	5	8	35	17	17
Simpson's	0.861		0.863	0.8	0.863	0.891		0.786	0.892	0.882	0.772
Shannon–Weiner	3.058		3.76	1.792	2.633	2.482		1.811	3.128	2.749	2.396
Fisher's α	5.432		3.585	5.244	3.827	5.408		3.183	5.514	5.896	5.896
Fisher's α se	1.497		0.607	2.203	2.491	6.703		18.982	2.305	34.261	34.261

Table 4. Comparison of diversity indices based on land system types (*N* = number of species captured, Sum = total captures).

	Batang Anai	Bukit Balang	Bukit Baringin	Bukit Pandan	Lindu	Kototinggi	Pendreh	Telawi
N	4	5	12	6	9	10	7	18
Sum	4	19	49	15	28	19	27	148
Simpson's	1	0.708	0.894	0.829	0.878	0.924	0.86	0.893
Shannon–Weiner	2	1.845	3.244	2.333	2.901	3.156	2.652	3.523
Fisher's α	4	2.21	5.066	3.706	4.592	8.54	3.064	5.37
Fisher's α se	1.665	1.075	1.476	4.024	2.209	12.144	1.238	0.833

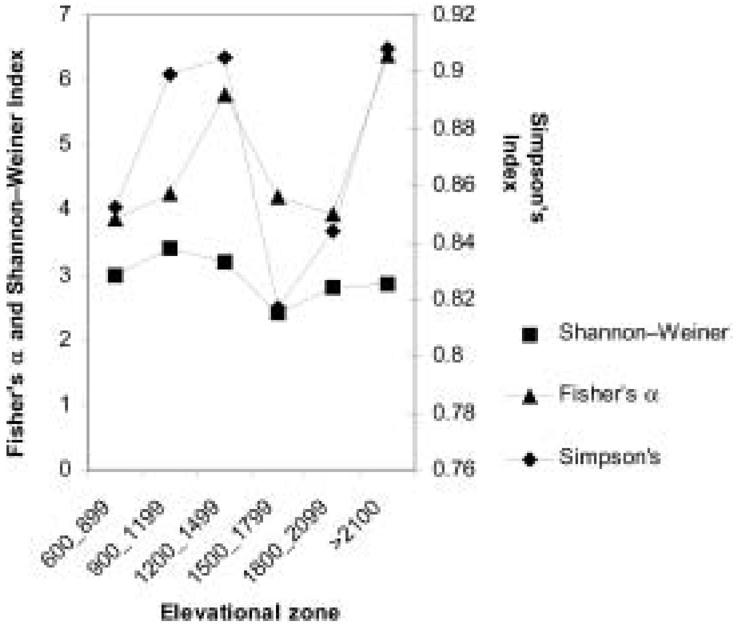

Figure 2. Comparison of trends in three diversity indices across elevational zones.

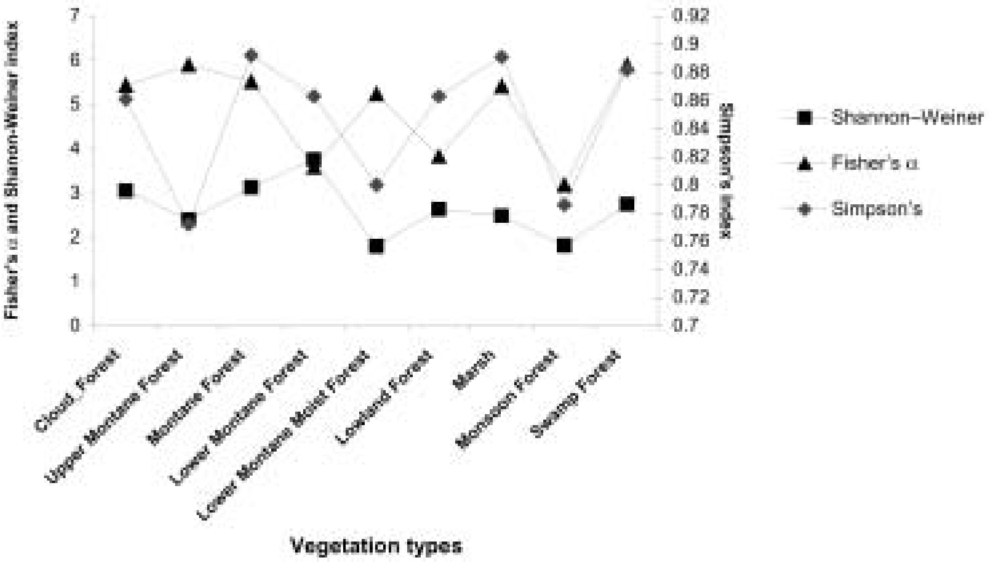

Figure 3. Comparison of trends in three diversity indices across vegetation types.

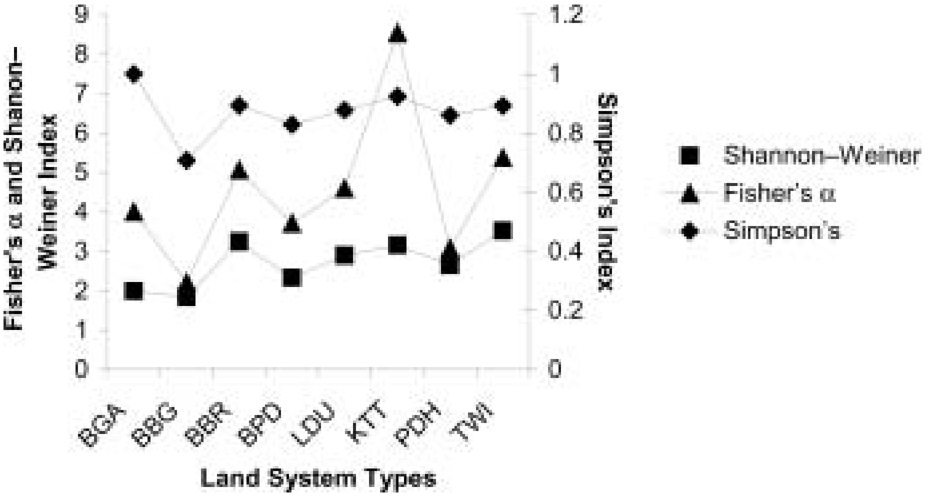

Figure 4. Comparison of trends in three diversity indices across land system types (BGA = Balang Anai, BBG = Bukit Balang, BBR = Bukit Baringin, BPD = Bukit Pandan, LDU = Lindu, KTT = Kototinggi, PDH = Pendreh, TWI = Telawi).

The three diversity indices used in this study (Fisher's α, Simpson's and Shannon–Weiner indices) did not always indicate the same trends in diversity. Indeed, correlation coefficients calculated between pairs of indices for each of the four data sets generally show weak association; R^2 values are typically below 0.3 and never exceed 0.6. The strongest association was found between the Simpson's and Shannon–Weiner indices for the elevational data set (R^2 = 0.591). Peet (1974) noted that the Shannon–Weiner index was particularly sensitive to changes in the abundance of rare species. Because rare species are probably poorly sampled by the trapping approach used in this study, the Shannon–Weiner index was perhaps the least appropriate method to apply to our data. Fisher's α method of estimating diversity is perhaps the most appropriate index for data of this kind, but in reality it may be concordance between the various methods used in this study that gives the most reliable indication of biological meaning (Krebs 1989). Whitmore (1984) observed that plant diversity in tropical rain forests generally falls with increasing elevation. Heaney et al. (1989) and Medway (1972) showed that diversity of pteropodid fruit bats also typically decreased at higher elevations. Little is known in Indonesia of changes in either species richness or species diversity of mammals with increasing altitude.

The highest estimate of rat diversity using Fisher's α was recorded at altitudes above 2100m (Fisher's α = 6.36). However, this value has a very high standard error (se = 26.845) and we have little faith in this result. Similarly, all of the highest values of Fisher's α based on vegetation, land system and habitat categories have high standard errors. Maryanto and Yani (2001) reported much lower standard errors in the estimates of species diversity of bats from Lore Lindu National Park and this undoubtedly relates to the fact that many more individuals of each species of bat were collected compared with rodents in this study.

The very low capture rates for rodents and other small terrestrial mammals pose considerable difficulties for documenting patterns of habitat association in small mammals of the park. Overall trap success was less than 1%, with one capture on average per 104 trap nights. This capture rate is comparable with the trapping figures reported by Kitchener and Yani (1998) from Gunung Ranaka, Flores, where, on average, 117 trap-nights were required to collect each small mammal (total 37,604 trap-nights). These Indonesian capture rates appear very low when compared to other tropical Asian studies. Medway (1972) reported that at 300–2400 m asl on Gunung Benom, West Malaysia, 50 trap-nights were required to capture each small mammal (total 5777 trap-nights). Heaney et al. (1989) reported that at 300–900 m asl on Leyte Island, Philippines, 30 trap-nights were required (total 3485 trap-nights), and at 0–1500 m asl, on Guisayawan, Negros Island, Philippines, 11 trap-nights were required (total 3231 trap-nights).

In summary, this study showed that species diversity of murid rodents in Lore Lindu National Park varies with altitude, vegetation, land system and habitat. It is important that future management practice in the park protects the full variety of animal habitats. In particular, the environs around Lake Lindu contain marsh habitat that is here identified as having high murid species diversity. This area also produced what may be a new murid species; hence, it is important that the marsh habitat is represented within the core zone of the park. Human encroachment onto this marshy country and its progressive conversion to paddy is of major concern. Finally, the monsoon forest vegetation/habitat type is also identified in this study as being distinctive; this habitat should also be included in the core zone of the park.

Table 5. Comparison of diversity indices based on habitat types (*N* = number of species captured, Sum = total captures).

	Cloud forest–Bukit Pandan	Cloud forest–Telawi	Degraded lowland forest–Telawi	Lower montane moist forest–Bukit Baringin	Lower montane forest–Bukit Balang	Lower montane forest–Bukit Baringin	Lower montane forest–Kototinggi	Lower montane forest–Pendreh	Lower montane forest–Telawi	Lower montane forest–Batang Anai	Lowland forest–Kototinggi	Lowland forest–Telawi	Lowland forest–Batang Anai
N	2	13	2	4	5	10	7	7	12	2	5	5	
Sum	3	51	4	6	19	21	9	27	58	2	10	10	
Simpson’s	0.667	0.865	0.5	0.8	0.708	0.905	0.944	0.86	0.844	1	0.844	0.867	
Shannon–Weiner	0.918	3.092	0.811	1.792	1.845	3.065	2.725	2.652	2.916	1	2.171	2.246	
Fisher’s α		5.629		5.244	2.21	7.478	9	3.064	4.594		3.978	3.978	
Fisher’s α se		1.641		2.203	1.075	70.057	2.497	1.239	1.162		21.233	21.233	

Table 5. Continued

	Marsh–Lindu	Mixed garden–Lindu	Mixed garden–Telawi	Monsoon forest–Telawi	Montane forest–Batang Anai	Montane forest–Bukit Baringin	Montane forest–Bukit Pandan	Montane forest–Telawi	Swamp forest–Lindu	Upper montane forest–Pendreh	Upper montane forest–Telawi	Upper montane forest–Bukit Baringin	Upper montane forest–Bukit Pandan
N	6		2	4	2	9	4	3	8		5	1	2
Sum	11		6	8	2	19	10	4	17		10	3	2
Simpson’s	0.891		0.333	0.786	1	0.912	0.733	0.8333	0.882		0.905		1
Shannon–Weiner	2.482		0.666	1.811	1	3.011	1.761	1.5	2.749		2.236		1
Fisher’s α	5.401			3.183		6.686	2.47	4	5.896		3.978		
Fisher’s α se	6.703			18.982		48.475	3.286	1.665	34.261		21.223		

Acknowledgments

We were indebted to Duncan Neville, The Nature Conservancy (TNC) Program Manager at Palu, and Dr Darrell Kitchener, TNC Director of Conservation, for their organisation of the mammal survey on Lore Lindu National Park, and to Mr Edward Polard, Manager of the conservation program, TNC Palu branch office. We also gratefully acknowledge the support of Ir. Banjar Yulianto Laban MSc, the Director of Lore Lindu National Park, who provided us with great assistance in the field.

Thanks are extended to our field assistants Mohamad Annas, Hariyanto and Thius Jacson, who assisted in developing the trapping procedures. Thanks also to Dr Martin Hadianto for his support and preparation of the Lore Lindu National Park map. Expedition costs were met by a grant to The Nature Conservancy Indonesia program from the United States Agency for International Development (USAID)/Natural Resource Management 2 (NRM2) program, Jakarta, Indonesia.

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Modelling rodent pest distributions in Mexico

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Abstract. Ecological niche models based on museum specimen data were generated to provide predictions of geographical distributions of native rodents known to be agricultural pests in Mexico. By overlapping rodent pest distributions, we found significant correlation between predicted presence of rodent species and crop damage in four main crops widely distributed nationwide. This study provides a first step for generating risk maps for crop damage due to rodent pests in agricultural regions. Museum collections may thus provide essential information for expanding these analyses to other pests.

Introduction

Mexico is an extremely varied country with a rich crop diversity. Historically, Mexico has mainly focused on agriculture, which presently occupies almost half of its area, producing corn, beans, sorghum, and sugarcane, among other crops. Mexico has a diverse rodent fauna, which has been reported as pests in crops (de Ita 1992). Most of these rodent species share the life-history traits of frequent litters, short gestation periods, post-partum oestrous, and aseasonal reproduction (Nowack 1991). In a previous study, we used novel techniques for modelling ecological niches of 17 rodent pests to determine potential species distributions, and showed that crop damage was related significantly to the predicted presence of rodent pests in the Mexican state of Veracruz (Sánchez-Cordero and Martínez-Meyer 2000). Here, we expand these analyses at a national level in four main and widely distributed crops. This approach can be used as a first approximation for generating risk maps in crop damage due to rodent pests, as well as other pests, in agricultural regions in the country.

Material and methods

Distribution data for each species were obtained from the mammal collections of the University of Kansas Natural History Museum (KU), The Field Museum of Natural History (FMNH) and the Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México (CNMA). Species names and taxonomic arrangements followed accepted authorities. Locality data were geo-referenced to the nearest 10^{-3} degree by direct consultation of maps, and reduced to unique latitude–longitude combinations. The four thematic geographical coverages used (annual mean temperature, annual mean precipitation, elevation, potential vegetation) consisted of raster grids (5 × 5 km pixels), obtained from Conabio (2002).

Rodent pest distributions

Ecological niches and potential geographical distributions were modelled using the genetic algorithm for rule-set prediction (GARP) (Stockwell and Peters 1999; see BIODI 2002). Specifically, GARP relates ecological characteristics of known occurrence points to those of points randomly sampled from the rest of the study region, seeking to develop a series of decision rules that best summarise those factors that are associated with the species' presence (Stockwell and Peters 1999). GARP includes several distinct algorithms for niche modelling in an artificial-intelligence-based approach. Occurrence points are divided evenly into training and test data sets. It works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection, choosing a method from a set of possibilities (e.g. logistic regression, bioclimatic rules) applied to the training data. Then a rule is developed or evolved. Predictive accuracy is then evaluated based on 1250 points resampled from the test data and 1250 points sampled randomly from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model—the algorithm runs 1000 iterations or until convergence. These component 'rules' are then incorporated into a broader rule-set, defining portions of the landscape as within or without the ecological niche. GARP models thus provide a heterogeneous rule-set that delimits a polygon or set of polygons within which the species is expected to be able to maintain populations, and outside of which it should not. This model of the ecological requirements of a species is the key to the inferential portion of the method (Stockwell and Peters 1999). GARP has demonstrated ability to predict small mammal species' distributions in the Neotropics (Peterson et al. 1999; Sánchez-Cordero and Martínez-Meyer 2000).

Rodent pest species previously identified to be related to crop damage (see Sánchez-Cordero and Martínez-Meyer 2000), and included in the present analyses, were (G = granivore, H = herbivore, O = omnivore): one squirrel (*Sciurus aureogaster,* O), thirteen rats and mice (*Microtus mexicanus*, H; *Oligoryzomys fulvescens*, O; *Oryzomys couesi*, O; *O. melanotis*, O; *Peromyscus aztecus*, G; *P. leucopus*, G; *P. levipes*, G; *P. maniculatus*, G; *Reithrodontomys fulvescens*, G; *R. megalotis*, G; *R. mexicanus*, G; *R. sumichrasti*, G; *Sigmodon hispidus*, H), and three pocket gophers (*Orthogeomys hispidus*, H; *Pappogeomys merriami*, H; and *Thomomys umbrinus*, H).

Crop loss and statistical analyses

We used the 1999 agricultural census data that provide reliable information on planted and harvested areas for seasonal crops of corn, sugarcane, beans, and sorghum for each of the 193 crop districts nationwide (SAGARPA 2002). We included only non-irrigated agricultural areas. Crop loss was calculated as the difference between planted and harvested area, assuming that non-harvested areas were partially related to damage by rodent pests (Table 1, Figure 1). These estimates are biased since biotic (other pests), abiotic (climatic conditions), and economic (lack of funding for harvesting) factors are also related to crop losses. We overlapped the distribution hypotheses of rodent pests with the crop districts using a geographical information system (GIS) (Arc View 3.2) (Figure 1). Forward stepwise multiple regression analyses were performed using Statistica 4.3.

Table 1. Total area cultivated and area lost (cultivated – harvested), as well as statistical significance (*P*), of stepwise multiple regression models relating areas with crop damage reported for the 1999 agricultural census data nationwide (n_1), and rodent species' presence (n_2), and numbers of granivore (G), herbivore (H), and omnivore (O) species included in the statistical analyses. In parentheses are parts of plant crops damaged by rodents.

Crop	Total area (ha)	Area lost (ha)	R^2	$F_{n2, n1}$ (*P*)	G	H	O
Corn (seeds, stems)	157,269,099	16,278	0.08	$F_{14, 184}$ (0.05)	4	3	2
Sugarcane (stems)	2,708,207	165,445	0.12	$F_{3, 89}$ (0.01)	4	3	2
Beans (seeds)	4,775,180	415,323	0.38	$F_{5, 132}$ (0.005)	6	1	3
Sorghum (seeds, stems)	155,706	16,278	0.05	$F_{3, 23}$ (0.094)	6	1	3

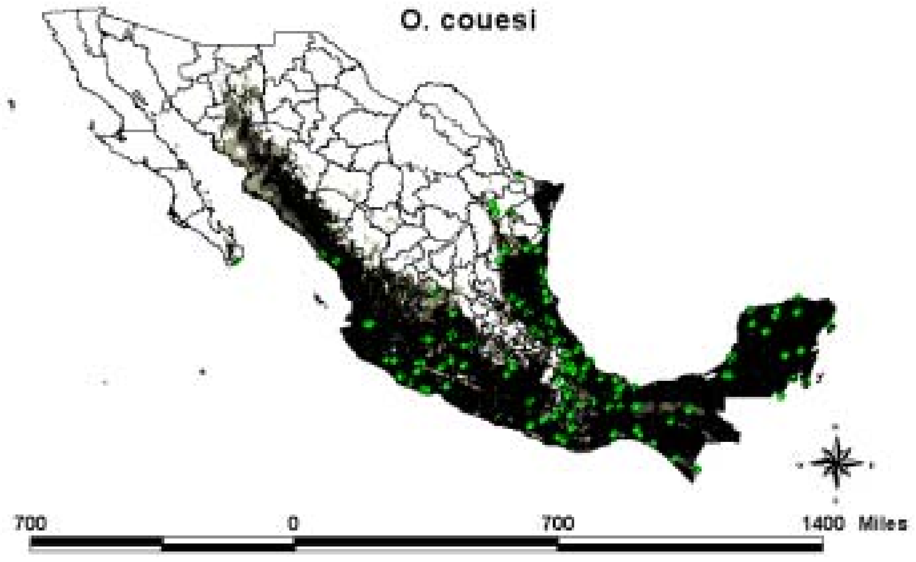

Figure 1. Map depicting the predicted distribution (in black) of the rice rat, *Oryzomys couesi*, a major rodent pest in Mexico. Green dots are known collecting localities of rice rats, and polygons represent all crop districts, where the 1999 agricultural census data for corn, sugarcane, beans, and sorghum are available nationwide.

Results and discussion

We generated ecological niche models for each of the 17 rodent species, using these models as the potential species distributions in the country (Figure 1). These rodent species identified as agricultural pests include a high taxonomic diversity, belonging to the families Muridae (rats and mice), Sciuridae (squirrels) and Geomyidae (pocket gophers). Such high rodent diversity results in a high diversity of food habits, such as granivores, herbivores and omnivores, with the potential for causing damage to a wide range of crops (de Ita 1992). In a previous study, Sánchez-Cordero and Martínez-Meyer (2000) developed a similar modelling approach for these rodent pests in the state of Veracruz, along the Gulf of Mexico in Mexico, and provided preliminary evidence of a causal relationship between predicted presence of rodent pests and crop damage. Stepwise multiple regression models predicted crop damage in each crop in the 193 crop districts nationwide (dependent variable) related to the proportional predicted coverage of that crop district by each of the 17 rodent species (independent variables). Models for all crops were statistically significant, explaining 5–38% of variation in crop damage, and rodent food habits matched food items supplied by these crops (Table 1). Interestingly, these statistical relationships were previously documented for these crops and rodent pests when analyses were conducted in the Mexican state of Veracruz (Sánchez-Cordero and Martinez-Meyer 2000). We interpret these findings to strengthen our modelling approach for identifying risk areas in other agricultural regions.

Considering the scale (the whole country) of cultivated areas used in the present study, the predicted distribution of rodent pests suggests significant economic impacts of rodent pests on large agricultural regions in Mexico; crop loss estimates were 0.1% for corn, 6.0% for sugarcane, 8.6% for beans, and 10.0% for sorghum (Table 1). These results are supported by recent studies documenting crop damage caused by the cotton rat, *Sigmodon hispidus*, and the rice rat, *Oryzomys couesi*, on sugarcane and sorghum fields in several states, such as Veracruz, Morelos, Michoacán, Tamaulipas, Sinaloa, and Sonora (de Ita 1992; Sánchez-Cordero and Martínez-Meyer 2000; SAGARPA 2002).

Conclusions

Integrated pest control programs require robust distributional hypotheses of pest species across agricultural landscapes (Prakash 1988; Buckle and Smith 1994; Singleton and Petch 1994). Our approach provides a solid baseline to launch such programs at a national level, and can serve as a useful tool with applicability to other pest taxa and agricultural regions worldwide.

Acknowledgments

Thanks to A.T. Peterson and M. Canela for comments. Support and funding was provided by the Comisión Nacional Para la Conservación y Uso de la Biodiversidad (project W036), and the Consejo Nacional de Ciencia y Tecnología (project 35472-V).

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The distribution of *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae) in South Africa

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Abstract. Although *Mastomys natalensis* and *M. coucha* are widely distributed in South Africa, the respective distributions of these medically and agriculturally important cryptic species of rodents are still uncertain. Karyotyped and/or electrophoretically identified specimens were used to clarify the geographical distributions and predict the most likely areas of occurrence of the two sibling species; and the derived distributions were compared with reported incidence of plague in South Africa. Both verified and predicted distributions show a geographical separation along the eastern escarpment of South Africa that appears to be influenced by altitude and rainfall. *M. natalensis* occurs in the low altitude/high rainfall area of the eastern coastal region, extending to north-eastern South Africa, while *M. coucha* occurs in the high altitude/moderate rainfall area of central and north-eastern South Africa. The two species were found to be either sympatric or to occur in close proximity at four localities. Statistical analyses showed significant differences between eco-geographical characteristics of localities associated with each of the two sibling species. The reported cases of plague in South Africa to some extent coincide with the distributional range of *M. coucha* rather than that of *M. natalensis*.

Introduction

Mastomys natalensis (*sensu lato*) was considered a single species until it was found to include two electrophoretically distinct cytotypes ($2n$ = 32, ‘slow’ haemoglobin electromorph; and $2n$ = 36, ‘fast’ haemoglobin electromorph) (Gordon and Watson 1986). This, together with the absence of hybrids in areas of sympatry, led to the recognition of two cryptic species referred to as the nominate species, *M. natalensis* ($2n$ = 32) and *M. coucha* ($2n$ = 36).

Although the combined geographical range of the two sibling species in South Africa is extensive, their respective geographical distributions remain uncertain. There is a critical need for more reliable delimitations of geographical ranges of these two species as they cause extensive damage to agricultural products and have been implicated in epidemiological problems.

The present investigation represents the first attempt to delimit the geographical distributions of *M. natalensis* and *M. coucha* in South Africa, based on specimens positively identified by karyotype and/or electrophoretic data. The distributions so derived are in turn used to predict the most likely areas of occurrence of the two cryptic species, and for assessment with reference to previously reported incidence of plague in South Africa.

Materials and methods

Locality data were gathered from karyotyped and/or electrophorectically identified specimens in the collections of the Transvaal (TM) and Durban (DM) Museums, South Africa, as well as from the literature (Hallett 1977; Smit et al. 2001). The prediction of the most likely areas of occurrence of the two sibling species was based on spatial analysis (Eastman 2001) using the following eco-geographical variables (EGVs): altitude; mean annual precipitation; mean annual temperature; mean daily minimum temperature for July; coefficient of variation of precipitation; mean primary production; and potential evaporation.

Analysis of variance (ANOVA), unweighted pair-group arithmetic average (UPGMA) cluster analysis, principal components analysis (PCA), and canonical variable (discriminant) analysis (CVA), in combination with multivariate analysis of variance (MANOVA), were used to test for statistical differences in EGVs between localities associated with each of the sibling species. EGV loadings derived from the PCA were used to weight each EGV’s relative contribution for the spatial analysis.

The geographical ranges derived from both verified locality data and predicted distributions were used to assess historical incidence of plague in South Africa as reported by Davis (1964).

Results and discussion

Positively identified records were located from 77 localities in South Africa, of which 31 were for *M. natalensis* and 46 were for *M. coucha*. The geographical distributions of *M. natalensis* and *M. coucha* show a distinct pattern of segregation along the eastern escarpment of South Africa. Their distributions thus appear to be largely influenced by altitude and rainfall. *M. natalensis* occurs along the low altitude/high rainfall eastern coastal region, extending up to the north-eastern corner of South Africa. In contrast, *M. coucha* occurs in the high altitude/moderate rainfall central and north-eastern parts of South Africa.

The two species were recorded either in sympatry or else in close proximity to each other at four localities, namely Pretoria and Satara (Kruger National Park) in the north-eastern part of South Africa, and Grahamstown and Addo Elephant Park in the Eastern Cape province. Interestingly, predictions of the most likely areas of occurrence for the two species also suggest a zone of overlap along the eastern escarpment. However, additional field survey is needed to determine the specific zone of parapatry between the two species in South Africa.

The ANOVA showed highly statistically significant differences ($P < 0.001$) for all EGVs associated with collecting localities of *M. natalensis* and *M. coucha* in South Africa. UPGMA cluster analysis and PCA of the EGV data showed two discrete clusters of localities which coincided in large part with the collecting localities associated with each of the two species in South Africa. Where overlap occurs, the localities in question fall in areas of potential sympatry or parapatry between the two species. A CVA and a MANOVA indicated a highly statistically significant difference between group centroids ($F_{7,69} = 20.21$, $P < 0.001$) of the species-linked collecting localities.

PCA loadings from the first two axes suggest that all of the EGVs are important in determining the species' distributions. The inverse relationship between the coefficient of variation of precipitation and the mean annual precipitation is of particular interest as it suggests that *M. natalensis* prefers relatively wet areas with a stable rainfall pattern, whereas *M. coucha* prefers relatively dry areas with a more erratic rainfall pattern. The particular importance of mean annual temperature on PCA axis 2 may further imply that *M. coucha* is more able to withstand a drier environment than *M. natalensis*—this can be tested through controlled laboratory investigations.

Geographical distributions based on both the verified locality data and the predicted distributions show that previously reported cases of plague in South Africa coincide to some extent with the distributional range of *M. coucha* rather than *M. natalensis*. Exceptional areas include the north-eastern parts of South Africa that have records of *M. coucha* but no historical records of plague, and the western parts that have no records of *M. coucha* but have reported incidence of plague. Since the discovery of the two sibling species, it has been demonstrated that *M. coucha* is susceptible, while *M. natalensis* is resistant, to *Yersinia pestis* infection. However, the imperfect match of plague incidence with the geographical range of *M. coucha* may suggest that either a complex of taxa is involved in the epidemiology of the disease, and/or that population eruptions of *M. coucha* in these areas do not attain infectious levels.

Conclusion

Geographical distributions of two medically and agriculturally important rodent species, *Mastomys natalensis* and *M. coucha* in South Africa, derived from karyotyped and/ or electrophoretically identified specimens, show a geographical separation along the eastern escarpment. This pattern of distribution seems to be influenced by altitude and rainfall whereby *M. natalensis* prefers low altitude/high rainfall regions, while *M. coucha* has a preference for higher altitude/relatively drier parts of South Africa. The two species appear to have a zone of parapatry along the eastern escarpment but are locally sympatric. The geographical distribution of previously reported human cases of plague in South Africa seems to coincide more with the distributional range of *M. coucha*, a species that is susceptible to plague infection, than with the more plague-resistant *M. natalensis*. However, there are significant exceptions that caution against any simplistic interpretation of the epidemiology of plague in South Africa.

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Identification of rodents of the genus *Bandicota* in Vietnam and Cambodia

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Abstract. *Bandicota indica* and *B. savilei* are broadly sympatric across Southeast Asia and both species can be locally abundant. *B. savilei* is not often reported in ecological or rodent management literature and is presumably misidentified either as immature *B. indica* or as other rodent species. New material from Vietnam and Cambodia helps to clarify the morphological distinction between these species. Special care is needed to distinguish adult *B. savilei* from juvenile or immature *B. indica*. The Cambodian specimens of *B. indica* and *B. savilei* represent the first records for either species in this country where so little collecting has occurred.

Introduction

Burrow systems dug by bandicoot rats of the genus *Bandicota* are one of the most conspicuous signs of rodent activity in the agricultural landscapes of South and Southeast Asia. However, with the exception of one species found chiefly on the Indian subcontinent, comparatively little is reported in the scientific literature about either their basic biology or their role as pest species in agricultural systems. Accurate field identification represents the first step towards improving ecological knowledge, but for *Bandicota* this has proven elusive.

Across most of its geographical range, the genus *Bandicota* is represented by co-occurring large and small species. The larger form is generally called *B. indica*. The smaller forms were previously treated as a single species under the name *B. bengalensis*, but are now generally divided into true *B. bengalensis* of the Indian subcontinent and *B. savilei* of Southeast Asia (Musser and Carleton 1993). Whereas *B. bengalensis* and *B. indica* differ in obvious morphological features (Musser and Brothers 1994), *B. indica* and *B. savilei* differ primarily in adult size. In this paper, we report on new material of *B. indica* and *B. savilei* from Vietnam and Cambodia that helps to clarify the morphological distinction between these species.

Materials and methods

We variously trapped and purchased *B. indica* and *B. savilei* at various localities in the north and south of Vietnam and in two provinces in Cambodia. All specimens were weighed and an external assessment made of sexual maturity and reproductive status. The following standard external measurements were taken: head+body length; tail length; pes length (without claw); and ear length. Selected specimens were prepared as voucher specimens (either whole bodies, skins, or heads). The majority of the voucher material is registered in the Australian National Wildlife Collection, the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Canberra.

K. Aplin and N.P. Tuan examined specimens of *Bandicota* in the zoological collection of the University of Hanoi (previously reported by Tien 1985).

Results and discussion

Geographical distributions of *Bandicota* species

The probable natural geographical range of *Bandicota indica* includes all or part of India, Sri Lanka, Nepal, Bangladesh, Myanmar, Thailand, Laos, Cambodia, Vietnam and southern China (Musser and Brothers 1994). This taxon was introduced historically to Taiwan and to the Kedah and Perlis regions of the Malay Peninsula, and possibly pre-historically to Sumatra and Java (Musser and Newcomb 1983). We have recorded this species in numerous localities in both the south and north of Vietnam (Brown, Tuan et al., this volume; La Pham Lan et al., this volume) and in the vicinity of Phnom Penh and in Kampong Cham province in Cambodia. It is sympatric with *B. savilei* in southern Vietnam and in both study areas in Cambodia. Musser and Brothers (1994) noted other instances of sympatry in Vietnam and Thailand.

B. savilei is recorded from scattered localities in Central Myanmar, Thailand and Vietnam (Musser and Brothers 1994). In southern Vietnam, K. Aplin, L.P. Lan and N.M. Hung collected specimens of *B. savilei* in Ho Chi Minh City province and in Binh Thuan province—no specimens were obtained within the Mekong Delta proper, despite intensive sampling (La Pham Lan et al., this volume). A. Frost collected specimens of *B. savilei* from two localities in Cambodia (Somrong commune, Kampong Cham province and near Phnom Penh). K. Aplin and N.P. Tuan recorded specimens of *B. savilei* from several northern provinces (see Table 1) in the zoological collection of the University of Hanoi. These include specimens previously reported by Tien (1985) as *B. bengalensis*. *B. savilei* is also tentatively recorded from southern Laos (Khamphoukeo et al., this volume) based on a photographic record.

The natural range of *B. bengalensis* probably includes all or part of Pakistan, India, Sri Lanka, Nepal, Bhutan, Bangladesh and Myanmar (Musser and Brothers 1994). It has been introduced to Penang Island off the west coast of Malaysia, to the Aceh region of Sumatra and eastern Java in Indonesia, to Saudi Arabia, and possibly to Kenya in East Africa. In central Myanmar, this species and *B. savilei* have been collected within 30 km of each other and they may yet be found in sympatry.

Figure 1. Adult individuals of *Bandicota indica* (top) and *B. savilei* (bottom) from the Cambodian Institute of Agricultural and Rural Development field station near Phnom Penh, Cambodia. Photographs by A. Wildman and A. Frost.

The Cambodian specimens of *B. indica* and *B. savilei* represent the first records for either species in this country where so little collecting has occurred (see Figure 1 for illustrations of live animals).

Identification of Southeast Asian *Bandicota*

Bandicota species can be distinguished from other Southeast Asian murid rodents, including members of the genus *Rattus*, by their relatively broader, heavier incisors (which exceed 3 mm in combined width, even in juveniles) and by the nature of their claws, which are straighter and more forward projecting than in typical murids. Adult *Bandicota* tend to have coarser pelage than most other rodents, with conspicuous guard hairs, but the difference between an adult *B. savilei* and a *Rattus rattus* in this regard is subtle. The tail is relatively shorter in *Bandicota* species than it is in many *Rattus* species, however there are exceptions in the latter genus (e.g. *R. argentiventer*) that negate the diagnostic value of this feature.

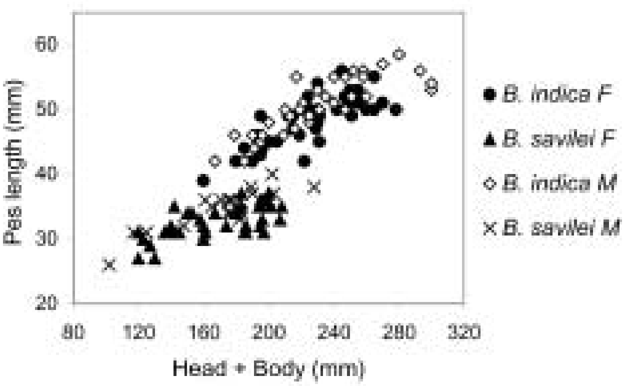

Figure 2. External measurements (head+body length, pes length) of *Bandicota indica* and *B. savilei* from Bin Thuan province, Vietnam, showing a complete bivariate separation of the two species. Slight overlap in pes length occurs between young female *B. indica* and fully adult male *B. savilei.*

Our largest regional *Bandicota* sample, comprising 82 individuals of *B. indica* and 59 of *B. savilei*, comes from Binh Thuan province in the south of Vietnam. In this area, adult *B. indica* are readily distinguished from *B. savilei* by their much larger size, overall darker colouration and more prominent guard hairs. However, immature *B. indica* closely resemble *B. savilei* in colouration and fur texture, and considerable care is needed to reliably distinguish the two species. Adult *B. savilei* often have a rust-coloured patch on the chest and throat that is rarely, if ever, seen in *B. indica*.

For both species in the Binh Thuan sample, males average slightly larger than females for all measurements (Table 1). There is considerable overlap between the species in head+body, tail and ear lengths, and in body weight. The ratio of tail to head+body does not distinguish the species or the sexes within each species. In contrast, pes length shows little overlap between the two species and no overlap when used in bivariate combination with

Table 1. External measurements of *Bandicota* spp. summarised by locality, species and sex (SVN = southern provinces, Vietnam; CVN = central provinces Vietnam; NVN = northern provinces, Vietnam). Measurements of specimens from Bac Thai, Hai Phong, Hoa Binh and Hung Yen provinces are taken from specimen labels in the Zoology Museum, University of Hanoi. Measurements for Gai Lai province are from Tien and Sung (1990; type series of *B. bengalensis giaraiensis*). All other measurements were taken by the authors on live or freshly dead specimens. Details given are mean ± standard deviation, range (where relevant) and number in sample.

Locality/Species	Sex	Head+body (HB) length (mm)	Tail length (mm)	Tail/HB%	Pes length (mm)	Ear length (mm)	Body weight (g)
Binh Thuan, SVN							
B. savilei	M	171 ± 30.6 102–228 (*n* = 21)	141 ± 23.4 90–183 (*n* = 20)	84 ± 4.6% 75–92% (*n* = 20)	35 ± 3.2 26–40 (*n* = 21)	23 ± 2.0 19–25 (*n* = 21	157 ± 65.0 45–290 (*n* = 21)
B. savilei	F	169 ± 28.5 120–228 (*n* = 37)	139 ± 20.6 95–176 (*n* = 36)	83 ± 6.5% 74–98% (*n* = 36	33 ± 2.5 27–37 (*n* = 37)	23 ± 1.4 20–26 (*n* = 37)	147 ± 58.1 55–292 (*n* = 38)
B. indica	M	231 ± 34.9 167–300 (*n* = 38)	196 ± 28.6 147–248 (*n* = 34)	85 ± 4.1% 73–91% (*n* = 34)	51 ± 4.2 42–58.5 (*n* = 38)	25.5 ± 2.1 19–29 (*n* = 34)	370.5 ± 191.0 125–870 (*n* = 37)
B. indica	F	229 ± 28.2 160–278 (*n* = 44)	190 ± 26.6 135–235 (*n* = 37)	84 ± 6.3% 73–99% (*n* = 37)	49 ± 3.9 39–56 (*n* = 41)	25 ± 1.8 21–29 (*n* = 37)	364.5 ± 130.4 110–640 (*n* = 43)
Vinh Phuc, NVN							
B. indica/savilei	M	213 ± 19.4 180–285 (*n* = 35)	197 ± 17.1 150–234 (*n* = 31)	93 ± 6.1% 82–111% (*n* = 31)	41 ± 4.6 35–54 (*n* = 35)	22 ± 3.3 18–34 (*n* = 35)	239 ± 106.3 115–600 (*n* = 35)
B. indica/savilei	F	233 ± 25.6 200–280 (*n* = 14)	212 ± 26.4 164–255 (*n* = 13)	84 ± 2.5% 95–105% (*n* = 13)	44 ± 4.2 37–50 (*n* = 14)	26 ± 4.0 19–31 (*n* = 14)	277 ± 97.9 154–473 (*n* = 14)
Hai Phong, NVN							
B.indica	M	275	270	98%	48	31	600
B.indica	F	255.0	216.0	85%	47.0	28.0	483.0
Hoa Binh, NVN							
B.savilei	M	235	195	83%	38	22	235
B.indica	M	185–205 (*n* = 2)	170–175 (*n* = 2)	83–95% (*n* = 2)	40–41 (*n* = 2)	27–28 (*n* = 2)	170–235 (*n* = 2)
B.indica	F	207	185	89%	40	28	246
Bac Thai, NVN							
B.savilei	F	220	182	83%	38	22	235
B.indica	M	258	250	97%	46	30	550
B.indica	F	240	182	76%	43	26	235
Hung Yen, NVN							
B.indica	M	285.0	260.0	91%	50.0	35.0	616.0
Gia Lai, CVN							
B. savilei	F	164–205 (*n* = 2)	136	83%	33–36 (*n* = 2)	21–25 (*n* = 2)	–
B. savilei	M	193	183	95%	33	25	–
Ho Chi Minh, SVN							
B. savilei	F	190	–	–	35	24	190
Cambodia							
B. savilei	M	120–125 (*n* = 2)	110–115 (*n* = 2)	92% (*n* = 2)	35–36 (*n* = 2)	22–23 (*n* = 2)	78–88 (*n* = 2)
B. savilei	F	120–175 (*n* = 3)	110–159 (*n* = 3)	80–95% (*n* = 3)	32.5–36.5 (*n* = 3)	19.5–25 (*n* = 3)	78–157 (*n* = 3)
B. indica	M	232 ± 32.9 175–285 (*n* = 19)	196 ± 28.6 147–248 (*n* = 18)	93 ± 6.4 84–107 (*n* = 18)	49 ± 3.0 43–54 (*n* = 19)	26 ± 1.1 24–29 (*n* = 19)	402 ± 203.2 78–830 (*n* = 18)
B. indica	F	229 ± 25.8 175–285 (*n* = 14)	218 ± 35.2 140–270 (*n* = 14)	95 ± 7.6 78–108 (*n* = 14)	48 ± 3.3 40.5–52 (*n* = 14)	27 ± 1.3 25–29 (*n* = 14)	370 ± 121.4 115–540 (*n* = 14)

head+body length (Figure 2). The very slight interspecific overlap in pes length occurs between young female *B. indica* and fully adult male *B. savilei*. The hind foot of *B. savilei* is more slender than that of juvenile *B. indica* (Figure 3) but is similar in colouration and the configuration of plantar pads.

Figure 3. Sole of the right hind foot of a juvenile *Bandicota indica* (on left) and an adult *B. savilei* (on right). Both individuals are from Binh Thuan province, Vietnam. Note the more robust nature of the hind foot of *B. indica*.

The smaller Cambodian sample also includes two clearly distinct taxa that compare favourably with the Binh Thuan samples (Figure 4). However, Cambodian *B. indica* appear to have slightly larger hind feet and a proportionally longer tail that sometimes exceeds head+body Length (Table 1). Male *B. savilei* from Cambodia also appear to have slightly larger feet than their counterparts in Binh Thuan province of Vietnam (Figure 5).

The *Bandicota* sample from Vinh Phuc province in northern Vietnam was measured over the course of an extended period of fieldwork (Brown, Tuan et al., this volume) and few voucher specimens were taken. In both sexes, the hind feet are shorter relative to head+body length than in the Binh Thuan and Cambodian samples (Figures 4 and 5). There is also a strong suggestion that two species are included within the sample, especially among the males. Without voucher material of the smaller taxon, the identity of this population cannot be resolved. However, specimens from Hoa Binh and Bac Thai provinces leave us in no doubt that *B. savilei* is present regionally in the north of Vietnam and this species may well be present in Vinh Phuc. We have not examined the type series of *B. bengalensis giaraiensis* Tien and Sung 1990 from Gia Lai province, but published measurements (repeated in Table 1) are consistent with the other material referred here to *B. savilei*.

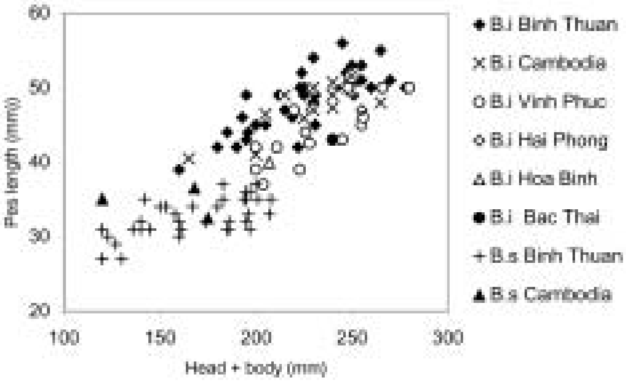

Figure 4. External measurements (head+body length, pes length) of female *Bandicota indica* and *B. savilei* (B.i and B.s in legend) from various localities in Vietnam and Cambodia. The sample of *B. indica* from Vinh Phuc in northern Vietnam probably includes some individuals of *B. savilei*.

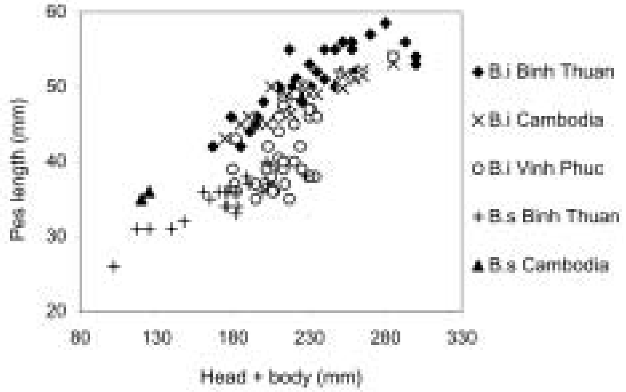

Figure 5. External measurements (head+body length, pes length) of male *Bandicota indica* and *B. savilei* (B.i and B.s in legend) from various localities in Vietnam and Cambodia. The sample of '*B. indica*' from Vinh Phuc in northern Vietnam probably includes some individuals of *B. savilei*.

Conclusion

B. indica and *B. savilei* are broadly sympatric across Southeast Asia and both species may be locally abundant. However, *B. savilei* is not often reported in ecological or rodent management literature and is presumably misidentified either as immature *B. indica* or as other rodent species. Close attention to the incisors and nature of the claws on the hind feet will distinguish *Bandicota* species from other rodents such as species of *Rattus*. Southeast Asian *Bandicota indica* and *B. savilei* are readily distinguished by the size and morphology of the hind feet, which are proportionally larger and heavier in *B. indica*. Special care is required to distinguish adult *B. savilei* from juvenile or immature *B. indica*.

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Integrative systematics: contributions to *Mastomys* phylogeny and evolution

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Abstract. The multimammate rats (genus *Mastomys*) are widely distributed throughout Africa and their interactions with human populations can have important consequences in regard to agriculture and human health. The latest results in the systematics and phylogeny of four *Mastomys* species, namely *M. coucha*, *M. huberti*, *M. erythroleucus* and *M. huberti* are presented here, combining results from morphology, morphometrics, cytogenetics and molecular analysis. In general, *Mastomys* species are morphologically similar, some of them being sibling species, thus no simple method of discrimination between the four studied species is successful. The use of morphometric analysis on skull and dental measurements does not allow complete discrimination, despite the fact that *Mastomys* species are strongly molecularly and chromosomally divergent, which allows reconstructions of their phylogenetic relationships. By comparing the different data sets, we are able to detect evolutionary patterns within *Mastomys* and to raise some new perspectives for further analyses. The use of a variety of different techniques will be necessary to resolve the systematics of the group.

Introduction

The method of integrative systematics combines results from numerous methods to improve the taxonomy and phylogenetic resolution of a group under study. This is even more important in the case of sibling species for which classical identification techniques are not efficient, and where a good attribution is fundamental for any phylogenetic work.

The African multimammate rats (*Mastomys* species) are found in all savannah areas in sub-Saharan Africa. Different populations can be morphologically very similar but chromosomally highly divergent (reviewed by Granjon et al. 1997). Some of these species are commensal, with very wide areas of distribution, and they are often found in sympatry, but not always in the same biotopes (Duplantier and Granjon 1988) since there is strong ecological structuring among *Mastomys* species. A recent review by Granjon et al. (1997) recognised seven species in the genus but indicated that the status of some forms was still to be resolved.

The interaction of certain *Mastomys* species with human populations can have important consequences, especially in regards to agriculture and human health. Several species can achieve high local population densities and outbreaks of *Mastomys natalensis* have been reported in East Africa (Leirs et al. 1996; Mwanjabe et al. 2002). The highest population density observed in Tanzania was more than 1400 rats/ha (Mwanjabe et al. 2002). At such densities, these rodents can cause seed depletion and losses in field crops, which have strong economical consequences (Mwanjabe et al. 2002). In the health domain, some *Mastomys* species are reservoir hosts and/or vectors of viruses and parasites responsible for human diseases such as bubonic plague (Green et al. 1978), Lassa fever (Wulff et al. 1975; McCormick et al. 1987), Rift Valley fever (Diop et al. 2000) and schistosomiasis (Imbert-Establet et al. 1997; Duplantier and Sène 2000). Each *Mastomys* species has its own biological properties in contact with the virus or parasites (Diop et al. 2000).

A good knowledge of the systematics of these rodents is clearly necessary and the integrative approach could be appropriate. The results obtained by the simultaneous use of morphological, morphometric, cytogenetic and molecular studies on the same individuals are presented here in order to give an overview of the systematics and evolution of one *Mastomys* sibling species complex.

Materials and methods

The *Mastomys* sibling species complex studied here comprises four species, namely *M. coucha*, *M. huberti*, *M. erythroleucus* and *M. huberti*, identifiable unambiguously only by their karyotypes (Table 1). The morphological, morphometric and molecular studies were all carried out on karyotyped specimens.

Table 1. Chromosomal characteristics and geographical distribution of *Mastomys* species (2N = diploid number of chromosomes; NFa = fundamental autosome number).

	Chromosomal data	Distribution
M. coucha	2N = 36; NFa = 54	South Africa
M. huberti	2N = 32; NFa = 44	West Africa
M. erythroleucus	2N = 38; NFa = 52–56	West Africa to southern Ethiopia
M. natalensis	2N = 32; NFa = 52–54	Sub-Saharan Africa

The skulls of all specimens were examined under a microscope, with close attention paid to the tympanic bullae, the foramina and the teeth. The characteristics of the fur were not considered because of their high intraspecific variability. The specimens were sorted by age according to their stage of dental wear (Verheyen and Bracke 1966) so that age-related variation could be ascertained. Due to the wear of their molar crown surface, older specimens of stages 5–6 were not incorporated into the analyses.

A total of 208 specimens belonging to *M. natalensis*, *M. huberti*, *M. coucha* and *M. erythroleucus* were used and 12 dental measurements taken from each (lengths and widths of the crown for the three upper and three lower molars). Log-transformed data were analysed using principal components analysis (PCA) and discriminant function analysis (DFA).

Mastomys species are cytogenetically divergent and the chromosomal characteristics can be used to infer phylogenetic relationships. Chromosome analyses were performed on preparations obtained from fibroblast cultures. Each identified structural rearrangement was considered as a character and its presence or absence scored in the various taxa (see details in Volobouev et al. 2002). The matrix of chromosomal characters was analysed by maximum parsimony (MP) using the exhaustive search option in PAUP 4.0 (Swofford 1998) for 5 taxa and 41 characters.

Total genomic deoxyribonucleic acid (DNA) was extracted from liver, heart or muscles preserved in 70% ethanol using a CTAB protocol (Winnepenninckx et al. 1993). Mitochondrial sequences containing the complete cytochrome b gene were isolated via polymerase chain reaction (PCR) and sequenced directly from purified PCR products with an automatic sequencer CEQ2000 (Beckman). The sequences were entered and manually aligned using Bioedit software. Mutational saturation was studied for each codon position, with transitions and transversions treated separately. Phylogenetic relationships were analysed by MP. The phylogenetic analyses were conducted using PAUP 4.0. The MP analysis was done with a heuristic search using stepwise addition. Robustness of trees was assessed by the bootstrap method performed by PAUP 4.0. (1000 replicates) and by the decay index (DI) using Autodecay software. The divergence dates were calculated based on transversion in the 3rd codon position. The molecular clock hypothesis was tested by relative-rate tests using RRTree and Mega programs.

Results and discussion

Results

The four *Mastomys* species considered show very similar morphology and high intraspecific variability. Thus, no qualitative characters have yet been found to discriminate between them.

The DFA of dental measurements of karyotyped specimens (Figure 1) shows that *M. erythroleucus* and *M. natalensis* are rather well discriminated both by size and shape. This is not the case for *M. huberti* and *M. coucha*, which are not very different from each other. The percentage of misclassified specimens for all species is high (between 45.86 and 57.74%) and all *M. coucha* specimens are misclassified. *M. natalensis* and *M. erythroleucus* have the best reclassification results. Axis 1 discriminates *M. natalensis* and *M. erythroleucus* on both size and shape, while *M. huberti* and *M. coucha* are indistinguishable. Overall, no complete discrimination has been found between any two of the four *Mastomys* species and wide intra-specific variability has been observed for *M. natalensis* (Denys 2002).

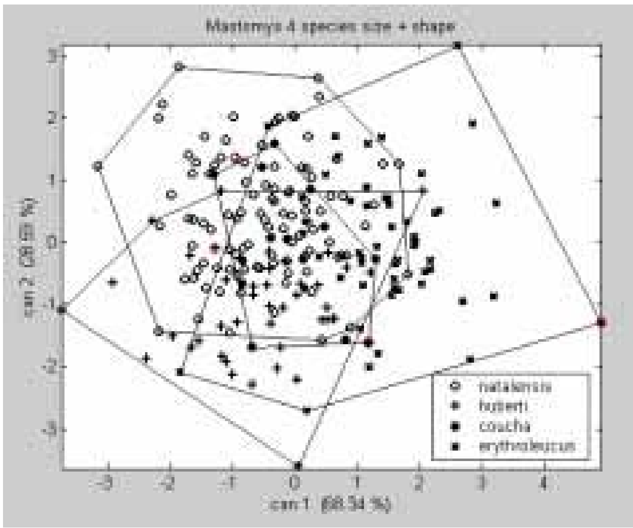

Figure 1. Discriminant analysis on 12 molar measurements for karyotyped specimens of four species of *Mastomys*. The sample consists of 101 *M. natalensis* from Senegal, Tanzania and South Africa, 43 *M. huberti* from Senegal, 14 *M. coucha* from South Africa and 54 *M. erythroleucus* from Senegal. Where possible, the type of each species has also been measured.

Phylogenetic relationships within *Mastomys* species have been inferred by chromosomal and molecular data (Lecompte et al. 2002; Volobouev et al. 2002). Figure 2 compares the results obtained from the two data sets. The cytogenetic and molecular trees are incongruent in regard to the phylogenetic position of *M. erythroleucus* and *M. natalensis*, which are sister taxa according to the molecular data set, while *M. natalensis* is closest to *M. huberti* in the chromosomal phylogeny.

With respect to the molecular data, the highest genetic distance between the four species is approximately 10%. The monophyly of this clade is strongly supported (100% of bootstrap replicates). The basal position of *M. coucha* versus *M. huberti* is less supported at 77% bootstrap support. *M. erythroleucus* and *M. natalensis* are sister species in this analysis, with high support (88%). The relative rate tests do not reject the molecular clock hypothesis for this data set, hence we are able to estimate the dates of the divergence between *Mastomys* species. The initial divergence of the four species is estimated about 3 million years which is congruent with discriminate analysis (DA) of *Mastomys* fossil at 3.7 million years (Denys and Jaeger 1986). The two first species within this terminal clade appear almost at the same time, then *M. erythroleucus* and *M. natalensis* diverge 1 million years later.

Discussion

Our analysis suggests that traditional morpho-anatomical and classical morphometric techniques do not seem very efficient at discriminating between sibling species of *Mastomys*. This confirms previous work on skulls by Duplantier (1988) and Dippenaar et al. (1993). The use of geometrical morphometrics is now required. This technique has proven successful for discriminating *Mus* species (Auffray et al. 1996) and *Praomys* species (Denys et al., this volume) but less effective in the case of sibling *Taterillus* species (Dobigny et al. 2002). When standard karyotypes fail to discriminate between taxa, cytogenetic banding analysis is required. Moreover, this banding information allows phylogenetic reconstruction, and can be integrated in a global analysis and compared with other data sets, such as morphology or molecular data. Previous phylogenetic relationships within *Mastomys* were inferred from chromosomal data (Britton-Davidian et al. 1995) and from DNA/DNA hybridisation (Chevret et al. 1994). These studies gave incongruent results and an absence of clear (robust) resolution at the interspecific level. In the case of the cytogenetic studies, *M. natalensis* and *M. huberti* were identified as sister groups, while *M. erythroleucus* was found to be most divergent (Britton-Davidian et al. 1995). In the DNA/DNA hybridisation tree, *M. coucha* was found to be the more divergent species (Chevret et al. 1994), a result that is supported by the new molecular data. The chromosomal and molecular trees are clearly incongruent in regard to the positions of *M. coucha* and *M. erythroleucus*. The DNA sequencing data allows us to solve in part the irresolution of the DNA/DNA tree, however both new analyses confirm the instability of *Mastomys* classification.

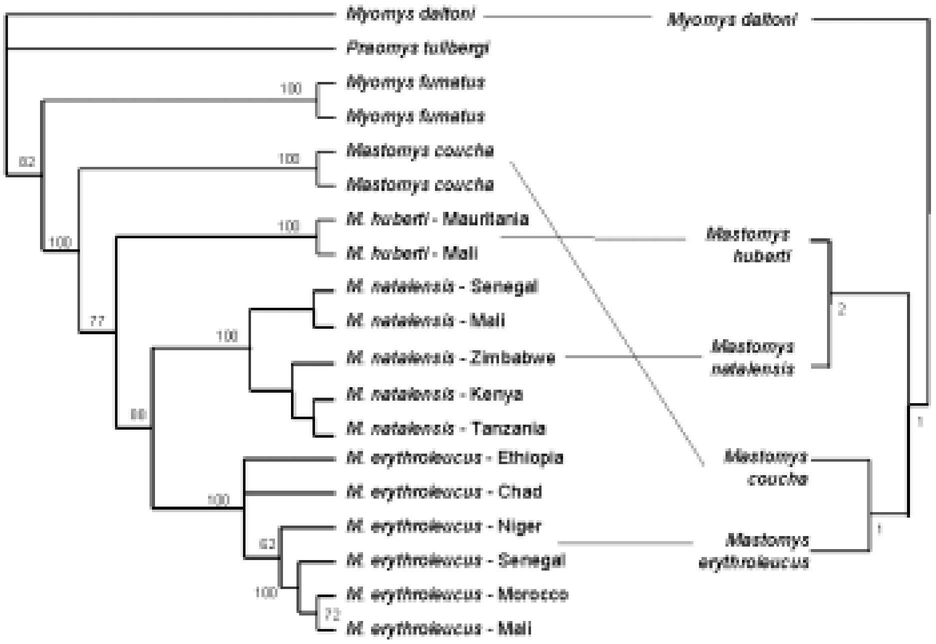

Figure 2. Phylogenetic relationships within *Mastomys* species reconstructed using molecular data (left) and chromosomal data (right) (after Volobouev et al. 2002 and Lecompte et al. 2002). The molecular phylogeny is the strict consensus of two trees (consistency index (CI) = 0.695; retention index (RI) = 0.766). The chromosomal tree is the most parsimonious tree (CI = 0.941; RI = 0.900). The values above the nodes (molecular tree) are bootstrap values; the values under the nodes (cytogenetic tree) are decay index values.

The degree of morphological stasis in the group, together with the incongruence between phylogenies, suggests that this lineage is the product of radiation that involved formation of numerous sibling species. The almost simultaneous divergence of the *M. coucha* and *M. huberti* is consistent with this hypothesis, whereas the mitochondrial phylogeny provides evidence of divergence between *M. erythroleucus* and *M. natalensis* 1 million years later. The seemingly late divergence of these taxa might result from the introgression of mitochondrial DNA between the two forms during hybridisation, as hypothesised by Volobouev et al. (2002). This introgression could explain the incongruity between the molecular (mitochondrial) and the cytogenetical (nuclear) phylogenies, and the later divergence of these species. Hybridisation between *Mastomys* species may occur during the early stage of their diversification, thus explaining the incongruities among the data sets. The chromosomally distinct forms within *M. erythroleucus* also suggest a possible species complex (Volobouev et al. 2002). It will be necessary to test these hypotheses with new data for more systems including nuclear markers, and to add supplementary specimens of the rarer *Mastomys* species.

Conclusion

The various *Mastomys* species are morphologically very similar, and complete discrimination cannot be achieved using only qualitative morphology or classical morphometrics. In all cases, cytogenetic analysis is needed for identification. Sibling species within *Mastomys* are strongly genetically divergent based on both molecular and chromosomal data. Phylogenetic relationships reconstructed using cytogenetic and molecular data are partially incongruent. However, the contrasts between the two data sets have generated new hypotheses on *Mastomys* origins and evolution. The results of this study suggest that, for further progress in *Mastomys* systematics, we will need to explore new fields of investigation, such as geometrical morphometrics or nuclear molecular analyses.

This example demonstrates the importance of the integration of different methods to make correct taxonomic determinations and to accurately infer relationships between species. Incongruence between data sets highlights areas that are testable by other data sets. The combination of these different methods is essential to the development of a precise and reliable method of determination of *Mastomys* species. This is even more important when the species are implicated in applied research, such as in epidemiology or durable interactions.

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SYMPOSIUM 9. RODENT BIOLOGY—CONTRASTING PERSPECTIVES

Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs and Dave M. Spratt, 2003. Rats, mice and people: rodent biology and management. ACIAR Monograph No. 96, 564p.

ISBN 1 86320 357 5 [electronic version]
ISSN 1447-090X [electronic version]

Technical editing and production by Clarus Design, Canberra

Market study of meat from field rats in the Mekong Delta

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Abstract. Rats are caught in the field and sold as dressed meat or as live rats for human consumption in the Mekong River Delta region of Vietnam. This study describes six different components of the rat market and the results of surveys of people involved in different parts of the distribution chain. These surveys were focused in six provinces where the rat market is concentrated: Ca Mau, Bac Lieu, Soc Trang, Can Tho, An Giang and Dong Thap. The annual production of rat meat for human consumption was 3300–3600 t of live rats, with a market value of about Vietnamese dong (VND) 25–30 billion (US$2 million). This market provides an important avenue of income for many poor farmers, who are the primary rat catchers. Supply of rats is highest during February to April and lowest in September. Movements in the price of rats showed a pattern similar to the quantity of rats available.

The survey also considered health risks. No person—from rat catcher to processor—was aware of health risks related to the handling of live rats. Analysis for presence of three types of zoonotic bacteria in water samples collected at processing points and in nearby waterways indicated the presence of *Clostridium perfringens* and *Enterococcus faecalis*. Of concern is that the highest concentrations of *C. perfringens* were found in the waterways. More research is required on the health risks to people involved in this trade and to others living near processing plants.

Introduction

Rodents are one of the most important pests of rice and many other crops in the Mekong River Delta. They feed not only on standing crops but also on grain in storage. In rice cropping systems, rats are most prevalent where cropping is more intensive, particularly where two or three crops are grown a year (Sang 1998). Where two rice crops are grown, rats have a greater impact on summer crops. Farmers attempt to control field rats by several means, including use of chemicals, trapping, digging of burrows, electrocution, or a combination of these methods (Singleton et al. 1999).

A peculiar aspect of field rat control in the Mekong Delta is the existence of markets for rat meat for human consumption. In the province of Bac Lieu alone, there are estimated to be as many as 2000 full-time rat catchers, and in all the provinces in the Mekong River Delta there are about 50 specialist rat distributors. Rat meat is popular in this region, not only because farmers have few sources of protein, but also because it is regarded as ‘good meat’. In addition, catching rats is an important source of income for some poor farmers. Notwithstanding profit motives or health benefits of consuming rat meat, there are health risks associated with the handling and processing of rats (see Gratz 1994). There have been no studies on the marketing of rat meat in the Mekong Delta or on the health problems related to the handling of live rats. This paper reports on a survey aimed at gathering information on the operation and scale of rat catching and processing as meat for human consumption in the region. The specific objectives of this survey were to:

1. describe the marketing channels of rats caught and marketed as meat from catchers to assemblers or traders to consumers;
2. estimate the volume of rats caught and consumed as meat or as feed; and
3. describe the agents involved in the marketing of rat meat, their operations, their income from rat trading, and their awareness of health risks related to rat processing.

Materials and methods

Rats are caught, assembled and processed at several locations in the provinces of the Mekong River Delta. These assembling places are located near town centres and along the sides of roads or along canals that are used for the transport of goods. An initial survey was conducted to gather general information on the distribution of rat processing and collection. The information was gathered through interviews with personnel from provincial and district plant protection services, with people they identified as key informants on the rat meat market, and with participants in rat catching and processing in the provinces of Ca Mau, Bac Lieu, Soc Trang, Can Tho, An Giang and Dong Thap. We then surveyed rat dealers and processors to gain detailed descriptions and estimations of marketing channels for rats. From the assemblers and catchers, we traced backwards for information on smaller rat assemblers and rat catchers, and traced forward along the marketing routes for information on rat-meat dealers and end users.

A further survey was conducted from a random sample of rat processors and rat catchers on the rat business system, including methods of capture, price of rats at different stages in the supply chain, labour linked to their part of the rat trade, awareness of health risks, and history of illness that respondents thought might be associated with handling rats.

Estimation of the quantity of rats traded on the market was obtained based on the amount of rats sold as dressed meat or as live rats by the processors and retailers at principal markets.

Disease assessment

The Pasteur Institute in Ho Chi Minh City tested 1 L samples of water collected from either within the area where rats were processed or near the terminal drainage points of canals and streams where the effluent was discharged from processing households. The samples of water (three from households and six from waterways) were collected in Soc Trang and Can Tho. The water samples were cultured to screen for *Clostridium perfringens, Yersinia cheopis* and *Enterococcus faecalis*.

Results and discussion

Market agents and their operations

The markets for dressed meat and live rats in the provinces of the Mekong River Delta have well-established routes, with up to five levels of handling before the meat is sold at market (Figure 1).

Rat catchers and trappers

Most rat catchers are poor and landless farmers. Farmers use several methods to catch rats. The most popular are digging them from burrows, driving them into nets, and trapping using wire cages. The methods used vary with season, condition of terrain and vegetation of the area. Only live rats are sold to agents. A premium is paid for rats that look healthy if they are to be kept alive and transported long distances to processors or retailers.

All the rat catchers interviewed use steel traps. These are cheap devices costing less than VND2000 (US$0.15) apiece. Many rat dealers and processors invest in steel traps then lend them to rat catchers or advance them to rat catchers as credit. In return, these people catch rats exclusively for the dealer or processor, ensuring a stable supply of rats.

A professional rat catcher usually owns a boat and operates with about 100 traps. When rat numbers are high, a catcher harvests an average of 15 kg of live rats per day, valued at US$7.

Small-scale rat assemblers

These rat dealers usually operate within a local area, 8–10 km from their home. They buy rats from other farmers and re-sell to dealers. They own a small boat or bicycle, collecting live rats from other catchers, then selling them either to rat dealers in a local area (depot) or to mobile rat collectors.

Rat assemblers

Rat assemblers own a motorcycle or boat and operate within 30 km of their home, collecting rats from small assemblers. Many of these rat assemblers are friends or relatives of rat dealers in the province. They usually receive a cash advance from dealers to buy rats from other assemblers or catchers. The amount of live rats collected per trip is 80–100 kg if using a motorcycle or 200–240 kg if using a boat.

Dealers

There are usually one to three dealers per province buying rats from catchers or other assemblers. These dealers have fixed business premises. They also buy and

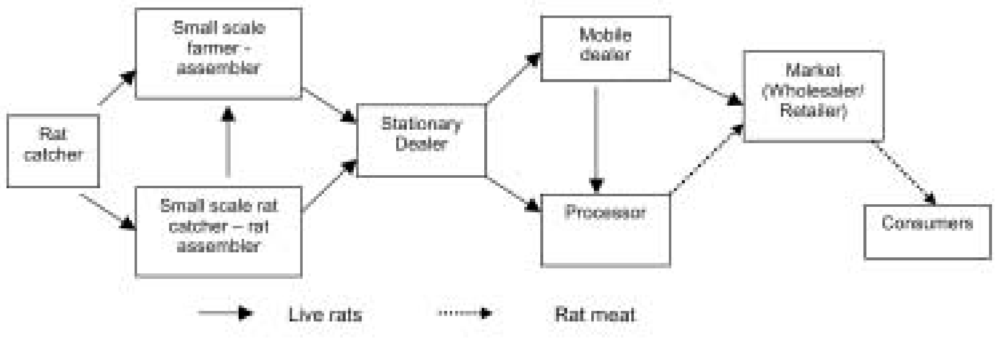

Figure 1. Main collection and distribution channels of live rats and rat meat for human consumption.

sell other animals caught in the field, such as snakes, birds and tortoises.

Long-distance rat assembler-dealers

These operators buy rats from catchers, other local assemblers or from dealers, and sell to rat processors. They operate a motor tricycle with an average of 700–800 kg of rats per trip. Rats are kept in cages 1.2 × 0.8 × 0.2 m that weigh about 50 kg.

Rat processors

Rat processors tend to concentrate in specific places with several households within one hamlet involved in the business. The highest concentrations are 18 households in Xeo Don hamlet of Phung Hiep district, Can Tho, and 36 households in Binh Chien hamlet in Binh Long village of Chau Phu district, An Giang. These two hamlets process about 70% of rats traded daily in the Mekong Delta with highest production occurring from January to May (Table 1). Several households in these hamlets have been involved in rat processing for more than 10 years. In other provinces, such as Bac Lieu, the rat trade is increasing, with many businesses only 2 years old (Table 2).

A large processor can process up to two tonnes of live rat per day or approximately 25,000 rats. The average amount of rats processed daily per household was highest in February (480 kg) and lowest in September (77 kg) (Table 1). Depending on the quantity of rats needed to be processed, one processor will hire 10 to 20 workers—many of them are young children. Processing usually begins at 1700 h and lasts until late in the evening, because live rats are delivered to the processing place late in the afternoon and the meat needs to be brought to market very early the next morning. Workers usually specialise only in one stage of the process and are paid according to the weight of rats processed.

Rat market channels

Principal rat market channels are described in Figure 1. The following routes are the most important channels of live rat transport:

1. Rats collected in Ca Mau are sold in Bac Lieu and Soc Trang.
2. Rats bought in Bac Lieu and Soc Trang are re-sold in O Mon and Can Tho.
3. Rats bought from rat catchers or collectors along the border with Cambodia are re-sold to depots in An Phu district of An Giang province.

About 60–70% of the total traded volume of rats pass through these three channels. From December to April, most of the rat supply comes from the first two routes. From May to July most rats come from grass fields along the Cambodian border.

Rat assemblers in Ca Mau province specialise in buying live rats from farmers or from small rat collectors in the districts. They operate depots in Ca Mau town then

Table 1. Mean quantity of rats processed daily per processor (kg of live rats/day) and mean monthly price (Vietnamese dong (VND) per kg; VND13,000 ≈ US$1).

Factor	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Quantity (kg/day)	367	480	421	336	342	302	191	144	77	101	145	223
Price (VND/kg)	8361	8414	8548	8671	8397	8355	8319	8000	7178	7344	7626	7790

Table 2. Number of living rats (kg) bought monthly at 11 rat businesses (from December 2001 to June 2002) in three provinces (Can Tho, Soc Trang and Bac Lieu) of the Mekong Delta, southern Vietnam.

Province	Shop no.	Years in business	Dec 2001 (kg)	Jan 2002 (kg)	Feb 2002 (kg)	Mar 2002 (kg)	Apr 2002 (kg)	May 2002 (kg)	Jun 2002 (kg)
Bac Lieu	1	4	170,514	170,500	154,120	77,542	56,557	5787	no data
	2	2	8618	12,152	42,165	90,621	48,832	5309	1140
Soc Trang	3	10	3317	2400	29,800	30,000	25,100	23,900	1840
	4	6	7750	8370	6215	16,417	21,655	10,780	2740
	5	8	no data	10,983	21,391	30,452	19,440	9880	570
	6	8	7756	8685	8400	7750	7180	7862	1820
Can Tho	7	12	25,171	24,617	23,400	18,000	21,000	11,500	4500
	8	10	no data	4154	8680	12,400	12,301	10,151	2831
	9	12	4650	4650	11,205	21,724	32,296	22,601	4175
	10	14	9325	15,500	22,436	6226	11,180	19,400	645
	11	3	10,540	13,330	17,645	9345	9178	2851	no data
Total			247,641	275,341	345,457	320,477	264,719	130,021	20,261

sell to traders from Bac Lieu, Soc Trang, Dong Thap, An Giang and Can Tho. In general, rat traders in Ca Mau and Bac Lieu are not involved in rat-meat processing, but sell live rats to traders. These are then processed in Soc Trang, Can Tho (Phung Hiep district) and An Giang (Chau Phu district). Traders in Soc Trang and Bac Lieu buy live rats from assemblers in Ca Mau, Bac Lieu and Soc Trang, and transport them to depots in O Mon, selling them to traders from Cai Dau (An Giang) for processing. Processors in Phung Hiep (Can Tho) buy live rats from assemblers in Bac Lieu and Ca Mau, and then sell meat to dealers in Can Tho.

Rat meat is used for direct human consumption. The survey did not find any other uses of rat meat as in processed food. By-products from processing—heads, skin, tail—are used as feed for fish.

Protection measures and health problems

No labourers who worked at the 69 processing and rat trading units wore protective clothing. Only five processors provided labourers with hand cream to protect skin from long working hours in water, and disinfectant to be applied to rat bites. Workers who participated in rat processing were not aware of health problems related to rat handling. Only 11 of 69 surveyed processors reported that their hired workers had acquired infections from rat bites.

Wastewater from rat processing was discharged directly into canals ($n = 6$), rivers ($n = 8$), enclosed ponds ($n = 6$), or onto the soil surface ($n = 5$). Local government did not allow rat processors to discharge wastewater into waterways, except in Binh Long village in An Giang.

Doctors at local hospitals and Red Cross units were sent a questionnaire enquiring about reported human diseases transmitted by rodents. Few questionnaires were completed because the doctors were not familiar with the range of rodent-borne diseases and so had nothing to report. This is surprising given that leptospirosis is relatively common in Thailand and approximately 25% of rodents sampled in a cross-sectional study of rats collected from processors and dealers in Soc Trang were seropositive for leptospirosis (Singleton, Smythe et al., this volume).

The sampling of wastewater from within and outside the processing households returned positive cultures for both *C. perfringens* and *E. faecalis* (Table 3). Both of these bacteria can be transmitted from rats to humans. No samples were positive for *Yersinia cheopis*. The high levels of *C. perfringens* in the waterways are of particular concern. This bacterium is typically associated with decaying animal carcasses. However, this was a pilot study with small sample sizes and with no comparative measures of these bacterial levels in waterways remote from rat processing plants. Further studies are warranted.

Quantity of rats caught and marketed as meat

We covered all the major rat processors and dealers in the selected provinces, with estimates based on the amount of rats sold as meat or as live rats by the processors and retailers at principal markets. This estimation is conservative.

Demand for rat meat appeared to depend on the quality of rat meat and the availability and price of other meat and fish. Rats are more fatty in February to April and very lean in September, coinciding with the highest and lowest quantity of rat processed, respectively. Naturally caught fish are more abundant in September and October. Movement in the price of rats showed a similar pattern as quantity of meat produced (Table 1). These trends for the supply and price of rat meat are unusual since the period of lower supply corresponds with lower prices instead of high prices as in the case of other agricultural commodities. The rats caught and processed annually over the last four years were estimated at around 3300–3600 t (Figure 2).

Conclusion

The rat-meat market in the Mekong Delta of Vietnam provides an important avenue of income for many poor farmers and local businesses. The annual production of rat meat for human consumption (3300–3600 t of live rats) has a market value of VND25–30 billion (US$2 million).

Table 3. Results of analysis of water samples for *Clostridium perfringens* and *Enterococcus faecalis*. Water was sampled from within the households processing rat meat or in the waterways where waste was discharged.

Shop no.	Water sampled at point of rat processing		Water sampled in waterways where waste was discharged	
	C. perfringens (No. bacteria/mL)	*E. faecalis* (No. bacteria/mL)	*C. perfringens* (No. bacteria/mL)	*E. faecalis* (No. bacteria/mL)
1	1	10	1050	10
2	2900	14	2150	10
3	3	10	2250	10
4			2400	10
5			2100	10
6			1800	10

Although there are a number of families that have been involved in the rat trade for up to 20 years, there has been a recent growth in the number of traders, especially in Bac Leiu. It will be interesting to monitor whether this growth of the industry is sustainable.

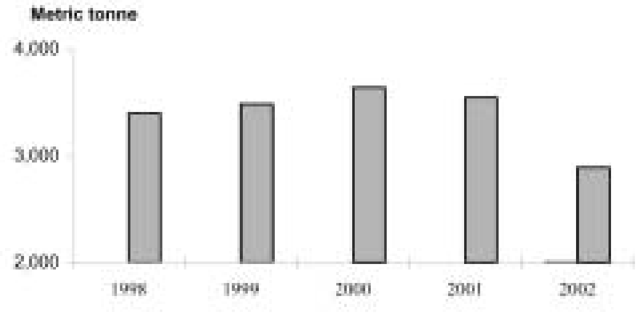

Figure 2. Volume of live rats traded per annum, 1998–2002, in six provinces of the Mekong Delta, Vietnam (data for 2002 only until May).

Despite this level of trade, rats are still the main pre-harvest pest in many provinces in the Mekong Delta. It appears that the rat industry is literally harvesting the rats, with the highest production coinciding with high rat numbers at the end of the main breeding seasons (Brown et al. 1999). Population studies are required to determine the impact of this harvesting operation on rat population dynamics. If a majority of rats are caught at the population peaks, then this may alleviate density-dependent effects on survival, allowing the rat populations to compensate through better survival of remaining rats through to the next breeding season. The impact of the industry on human health also requires urgent attention.

Acknowledgments

The International Rice Research Institute (IRRI), Philippines, through their Rodent Ecology Work Group, funded this study. We thank Dr K.L. Heong (IRRI) and Dr Grant Singleton (CSIRO, Sustainable Ecosystems) for their advice and assistance.

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Seasonal variations in metabolism and thermogenic capacity in greater long-tailed hamsters

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Abstract. The aim of this study was to determine the seasonal changes in metabolic properties and thermogenic capacity in the greater long-tailed hamster (*Cricetulus triton*). During seasonal acclimatisation, there were no significant seasonal changes in basal metabolic rate, however non-shivering thermogenesis and maximum metabolic rate increased significantly in winter compared with summer. We also calculated the shivering thermogenesis by subtracting basal non-shivering thermogenesis (NST) from the maximum metabolic rate. Results suggest that shivering thermogenesis plays an important role in total heat production in summer, and NST plays an important role in winter heat production. In the natural environment, greater long-tailed hamsters mainly depend on an increase in NST to adapt to the cold of winter. These physiological adjustments are closely related to this species' biological characteristics, such as being solitary, nocturnal and non-hibernating, and having a seed-dominant, omnivorous food habit.

Introduction

The greater long-tailed hamster (*Cricetulus triton)* is a very common pest rodent in the farmlands of northern China. It is a predominantly seed-eating, omnivorous species, and nocturnal, burrowing, non-hibernating and of solitary habits. In the natural environment, it faces a large seasonal fluctuation in environmental temperatures and unstable food resources because of agricultural activities. However, this species can use stored food during winter and early spring. Although many aspects, such as population dynamics, chemical communication, and other ecological aspects (Zhang and Wang 1998), have been studied, there is no information available on seasonal patterns of energetics and thermogenesis for this species (Wang and Wang 2002). The primary aim of this research was to determine the seasonal changes in metabolism and thermogenesis of *C. triton* in order to understand its physiological survival strategies.

Methods and materials

Animals

Adult greater long-tailed hamsters (males and non-pregnant, non-lactating females) were live-trapped in the farmlands of Hebei province in spring, summer, autumn, and winter. Animals were kept individually in cages under natural photoperiod and temperature conditions, and fed commercial laboratory rat chow pellets plus cabbages. Food and water were supplied *ad libitum*. All determinations were made within 10 days of capture.

Measurement procedure

Rates of oxygen consumption were measured using a closed-circuit respirometer. Temperatures inside the animal chambers (size = 3.6 litres) were measured and maintained with a water bath (±1°C). The body mass and body temperature of animals were recorded before and after each experiment. Body temperature was measured by insertion of a digital thermometer (Beijing Normal University Instruments Co.) into the rectum to a depth of 3 cm.

Measurements of metabolic rates were made at temperatures ranging from 5–36°C. Before each experiment, animals were weighed to the nearest 0.1 g and fasted for 3 h to minimise the specific dynamic action of food. Each measurement lasted for 60 min and oxygen consumption was recorded at 5 min intervals. Animals were allowed to adapt to the metabolic chamber for about 1 h before measurements started. Two consecutive minimum readings were taken for metabolic rate calculations. All measurements were made daily between 0830–1900 h. Metabolic rates were expressed as mL O_2/g.h, corrected to standard temperature and pressure (STP).

After resting metabolic rate measurements had been completed, non-shivering thermogenesis (NST) was stimulated by a subcutaneous injection of a mass-dependent dosage of noradrenaline. The maximum response to noradrenaline was regarded as the maximum NST.

Maximum metabolic rate was induced using a He:O$_2$ (80%:20%) mixture and was measured at 0°C and 5°C. When the experiments finished, most of the animals had reduced body temperatures.

Statistics

Data were analysed using the SPSS software package. Differences between temperatures in each season were determined by repeated measure analysis of variance (ANOVA) and seasonal differences were determined by ANOVA, with a statistical significance level of $P < 0.05$.

Results and discussion

Basal metabolic rate (BMR), nonshivering thermogenesis (NST), and maximum metabolic rate (MMR) in greater long-tailed hamsters are shown in Figure 1. The thermal neutral zones for spring, summer, autumn, and winter were 26–32°C, 29–34°C, 26–34°C and 24–34°C, respectively; BMRs (mL O$_2$/g.h) were 1.68 ± 0.33 (sd), 1.23 ± 0.02, 1.54 ± 0.22 and 1.59 ± 0.22, respectively; NST rates (mL O$_2$/g.h) were 3.22 ± 0.56, 2.63 ± 0.63, 4.19 ± 0.43 and 4.54 ± 0.31, respectively; and MMRs were 5.02 ± 0.56 mL O$_2$/g.h in summer and 7.49 ± 0.79 mL O$_2$/g.h in winter (Figure 1).

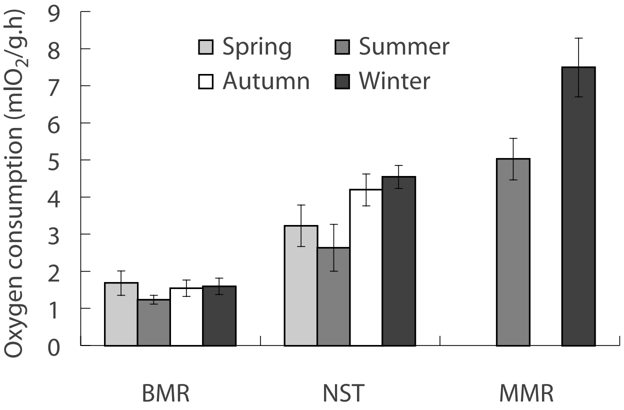

Figure 1. Seasonal variations in basal metabolic rate (BMR), non-shivering thermogenesis (NST) and maximum metabolic rate (MMR) in greater long-tailed hamsters (mean ± standard deviation).

BMR increased by 29% in winter compared with summer, maximum NST increased by 73%, MMR increased by 49%, regulatory NST (maximum NST–BMR) increased by 111%, and shivering thermogenesis (MMR–maximum NST) increased by 23%. In summer, hamsters' BMR contributed 25% of MMR, regulatory NST contributed 28%, shivering thermogenesis contributed 48%, and maximum NST contributed 52%. In winter, hamsters' BMR, regulatory NST, shivering thermogenesis, and maximum NST contributed to MMR by 21%, 39%, 39%, and 61%, respectively. During seasonal acclimatisation, there were no significant seasonal changes in BMR (although it tended to increase in winter), however NST and MMR increased significantly in winter compared with summer.

Many small mammals inhabiting fluctuating and cold environments display enhanced capacity for seasonal changes in NST and MMR, such as the Djungarian hamster (*Phodopus sungorus*) (Heldmaier et al. 1989), short-tailed shrew (*Blarina brevicauda*) (Merritt 1986), red-backed vole (*Clethrionomys rutilus*) (Feist and Rosenmann 1976), plateau pika (*Ochotona curzoniae*) and root vole (*Microtus oeconomus*) (Wang and Wang 1996). However, a fossorial rodent (*Spalacopus cyanus*), which is not faced with cold stress, has a relatively low physiological plasticity which is in accordance with a fossorial mode of life—it has a remarkably high NST, low MMR and, surprisingly, nearly no shivering thermogenic capacity compared to other rodents (Nespolo et al. 2001). Feist and Rosenmann (1976) showed that the arctic–subarctic red-backed vole has a greater capacity for NST than rodents from temperate latitudes, probably because this species is acclimatised to colder seasonal conditions. Holloway and Geiser (2001) showed that BMR and thermal conductance were lower in winter in the sugar glider (*Petaurus breviceps*), a marsupial, but maximum heat production was raised significantly in winter, suggesting that, despite the apparent lack of functional brown adipose tissue, sugar gliders are able to significantly increase heat production in winter.

In conclusion, our present study suggests that shivering thermogenesis plays an important role in total heat production in summer and NST plays an important role in winter heat production for greater long-tailed hamsters. In its natural environment, this species mainly depends on the increase in NST to adapt to the cold winter. These physiological adjustments are closely related to the living habits of this species, such as living singly, being nocturnal and non-hibernating, and having seed-dominant, omnivorous food habits.

Acknowledgments

This study was supported in part by the National Natural Science Foundation of China (No. 39730090), the Chinese Academy of Sciences (CAS) (No. STZ-01-06) and the CAS Innovation Program. This paper was completed while D.-H.W. was as a visiting scholar in the Animal Nutrition Laboratory, Agriculture Faculty, Okayama University, supported by the Japan Society for the Promotion of Science (JSPS). D.-H.W. wishes to thank Professor Ei Sakaguchi for his kindly reception and for providing space for D.-H.W.'s work there.

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Rodent physiological ecology in China

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Abstract. In China, studies of the physiological ecology of rodents began in the 1950s and developed rapidly from the 1980s. Some areas have been well covered for some, but not all, species. Most of the work has focused on thermogenesis, temperature regulation and digestive physiology. Almost 20 small mammal species have been studied and these species are mainly distributed in northern China. Because the majority of these species are rodents, much basic research work must be done before we can test hypotheses and/or make predictions or generalisations. It is essential to continue to develop excellent hypotheses and then undertake experimental manipulations to obtain robust, repeatable and precise results. This paper reviews the status and development of rodent physiological ecology in China, including the history of studies, current trends in research on physiological ecology, and areas for development in the near future.

Introduction

Physiological ecology combines the disciplines of physiology and ecology, and focuses on studies of individuals. Physiological data are used to answer ecological questions, which are related to the animal's survival and reproduction, and to explain their distribution, abundance and richness in the natural environment. Since the 1940s, physiological ecology has become a mature discipline. In this paper, we briefly review the developments in studies of physiological ecology of rodents in China.

History of studies in China

The first systematic studies on the physiological ecology of small mammals appear to be those of Professor Zhao Yibing of Peking University in the 1950s on thermoregulation in hedgehogs. In the late 1950s and early 1960s, Professor Sun Ru-Yong, Beijing Normal University, studied geographical variations in the physiological properties of *Clethrionomys rufocanus* and *Microtus agrestis* at Moscow University in the former Soviet Union (his work was published in the Bulletin of Beijing Normal University). In the 1970s, Sun Ru-Yong measured the metabolism of Chinese white-bellied rats (*Rattus niviventer confucianus*) and Norway rats *(Rattus norvegicus*), two farmland rodent species. He introduced analysis of covariance (ANCOVA) to account for the effect of body mass in studies of metabolism. In the late 1970s, Professor Wang Zu-Wang, Northwest Plateau Institute of Biology (now Institute of Zoology), Chinese Academy of Sciences, and his colleagues measured seasonal changes in metabolic rates and digestibility for two field small mammals (plateau pika, *Ochotona curzoniae*, and plateau zokor, *Myospalax bailyei*) in the Qinghai–Tibet Plateau. This was the first work on seasonal acclimatisation in metabolic rates in China.

Since the 1980s, studies in physiological ecology in China have progressed rapidly. Some new areas and more rodent species have been reported and studied, including: a comparative study on the metabolic rates of three rodent species of the southern Yangtze River; the effects of huddling on the metabolic rates in the lesser rice-field rat (*Rattus losea*); the development of homeothermy in Mongolian gerbils (*Meriones unguiculatus*) and root voles (*Microtus oeconomus*); the relationship between average daily metabolic rates and resting metabolic rates; the metabolic properties and the average daily metabolic rate for root voles in the Qinghai Plateau; the seasonal changes in mass, structure and composition of brown adipose tissue and capacity for non-shivering thermogenesis in plateau pikas and root voles; the metabolism and thermoregulation during hibernation and the non-hibernation period in Daurian ground squirrels (*Spermophilus daurica*) and hedgehogs; and seasonal variations in digestibility in root voles in the Qinghai Plateau.

In the 1990s, Li Qing-Fen, Beijing Normal University, and her group studied the molecular thermogenic mechanisms for Brandt's voles (*Microtus brandti*) and Mongolian gerbils in the laboratory (Liu et al. 1998; Li et al. 2001). Wang De-Hua (1993) examined the effects of photoperiod and temperature on thermogenesis in plateau pikas and root voles after acclimation in the laboratory. Wang Zheng-Kun (1996) studied the thermogenic capacities of tropical and subtropical small mammal species. Wang Yu-Shan (1997) determined energetic constraints on survival, reproduction and growth and development for alpine small mammals. Liu Xiao-Tuan (1998) first studied the molecular adaptive thermogenic mechanisms in Mongolian gerbils and Daurian ground squirrels. Bao (1999) compared the characteristics of ecophysiology and water metabolism in four rodent species from the Ordos Plateau of Inner Mongolia. Wang De-Hua and his colleagues determined the seasonal changes in thermogenesis and thermoregulation in Brandt's voles, Mongolian gerbils, and greater long-tailed hamsters (e.g. Wang De-Hua et al., this volume). Pei (2000) measured the effects of food quality on digestibility and retention time of digesta in Brandt's voles and Mongolian gerbils. Liu He (2002) was the first to systematically determine the reproductive energetics of Brandt's voles and Mongolian gerbils. Nearly 20 rodent species have been studied for their ecophysiology. These species are distributed in the alpine meadows of the Qinghai–Tibet Plateau; across regions of farmland and grassland, the Ordos Plateau of Inner Mongolia; the farmlands of the Northern China Plain; the tropical and subtropical area in Yunnan province of southern China; and some agricultural areas of the southern Yangtze River.

Current trends in research in China on physiological ecology

Today, there are some important trends in our studies of physiological ecology. With the globalisation of research, we are able to test theories in energetics, especially in comparative physiology. We are also able to contribute our ideas on the effects of evolution in the area of evolutionary physiology. Functional ecology and functional morphology and the search for mechanisms that regulate physiological processes using modern molecular biology techniques and instruments are considered very important. It is essential to continue to develop excellent hypotheses and then undertake experimental manipulations to obtain robust, repeatable and precise results. Multi-disciplinary research combines many approaches and techniques (e.g. telemetry to measure the body temperature, metabolic rates and food intake and/or activity of the individual). Individual differences and the relationship between different physiological parameters, structure and function are also important, as is the evolutionary significance of geographical differences in physiological parameters.

Areas for development in the near future in China

The following topics of rodent physiological ecology should be developed strongly in China for the majority of our native rodents. For the testing of hypotheses and/or making predictions or generalisations, much more work must be done in the areas of (1) water balance, especially for desert rodent species; (2) hibernation (torpor) and ecophysiology; (3) individual differences and genetic differences in physiological parameters; (4) relationships between characteristics of physiological ecology and population biology; (5) digestive tract morphology and digestive strategies; (6) reproductive energetics; (7) physiological limitation and its evolutionary significance; and (8) body weight maintenance, regulation and energy balance (leptin and its role in body weight regulation). More rodent species need to be studied for their ecophysiology. We should also expand our knowledge on those species for which we have some information, such as small mammals in the alpine meadows and Inner Mongolian grasslands.

Acknowledgments

This study was supported in part by the National Natural Science Foundation of China (No. 39730090 and No. 39970128), the Chinese Academy of Sciences (CAS) (No. KSCX2-1-03 and No. STZ-01-06), the CAS Innovation Program, and the Ministry of Science and Technology of China (No. FS2000-009). This paper was completed while D.-H.W. was a visiting scholar in the Animal Nutrition Lab, Agriculture Faculty, Okayama University, supported by Japan Society for the Promotion of Science. D.-H.W. wishes to thank Professor Ei Sakaguchi for his kindly reception and providing space for D.-H.W.'s work there.

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Myth, dogma and rodent management: good stories ruined by data?

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Abstract. Many beliefs exist on what influences the population dynamics of rodent pests. In some instances, these beliefs get mentioned so often that they become dogma and in too many instances national policies on rodent management are based on dogma. We review five dogmas that have varying degrees of influence on policies for rodent management in Australia and Southeast Asia. Three are associated with regional or local movement patterns of rodents, one with the efficacy of predators as biological control agents, and one with the influence of farming systems on rodent dynamics. We provide results of experimental studies conducted to test the three dogmas associated with movement patterns. Two of these dogmas were rejected and one accepted. We conclude that rodent management requires a scientific approach, and the science of rodent management requires managers to conduct experiments.

Introduction

In a cogent review of the science and practice of wildlife management, Sinclair (1991) succinctly stated: “A scientific statement is one which can be tested and disproved. If it cannot potentially be disproved than (sic) that statement falls into the realm of religious belief. Such beliefs have no place in a scientific decision-making process for management, because they involve value judgements, subjectivity, bias and dogma.” In rodent management, both in developed and developing countries, there are many beliefs surrounding what leads to outbreaks of rodent populations or to their chronic nature. Mention that you work on rodent pests when visiting a local bar or coffee shop, chatting with farmers or attending a scientific workshop, and you will be soon inundated with unsolicited (but well meaning) advice on why these rodents are pests and on how to control them (see Singleton et al. 1999 for discussion of the range of techniques used in Southeast Asia). In some regions, these beliefs have been around so long or been repeated so often that they become dogma. Yet when one examines the rationale for these dogmas, the scientific data cupboard is usually bare.

The paradigms for scientific studies for wildlife management may be based on the density-dependent school of thought focusing on regulation (see Sinclair 1989) or a more empirical approach focusing on limitation (see Krebs 1995). Regardless of which paradigm one adopts, the proponents of the differing paradigms agree that the way ahead is to adopt an experimental approach with clear alternative hypotheses (McNab 1983; Sinclair 1991; Krebs 2002). In the case of rodent management, we are not arguing that this experimental approach be adopted simply to provide scientific rigour to our art. In too many instances, national policies on rodent management or the beliefs of farmers are based on these dogmas, and therefore it is important that these beliefs are addressed scientifically to assess their worth. If this is not done, then governments and farmers will not be receptive to other, possibly more effective, management regimes.

We review five dogmas of rodent pest management prevalent in Australia and Southeast Asia. We have applied the experimental approach to three of these dogmas and report on our findings. We also briefly review the scientific basis for the other two.

Materials and methods

We describe experimental field studies we conducted to test alternative hypotheses for the first three dogmas. The last two dogmas will be described and reviewed in the Results and Discussion section.

Dogma 1

In Australia, mouse populations undergo aperiodic outbreaks resulting in densities of >1000 mice per ha (Singleton and Redhead 1989). Many farmers attest that mouse populations build up in the south-west (South Australian wheatfields or in areas of natural woodland) and move *en masse* to the north-east to invade the grain fields in Victoria and New South Wales (NSW), devouring crops in their path. Stories of fish (Murray cod) caught in the Murray River, which defines the southern boundary of NSW, with mice in their stomach supposedly provides positive evidence that mice swim across the Murray River to invade NSW.

A 6-year replicated study was designed to distinguish between the following hypotheses:

- Hypothesis A: Mouse populations build up in areas of natural woodland (*Eucalypt* or *Callitris* dominated woodland) and then invade the adjoining cereal-cropping regions. (Accept dogma 1.)
- Hypothesis B: Mouse populations build up in both natural woodlands and cereal-cropping habitats. (Neither accept nor reject dogma 1.)
- Hypothesis C: Mouse populations build up in cereal-cropping regions and then invade the natural woodlands (Reject dogma 1.)

The study site was the central mallee region of Victoria centred around Walpeup (35°08'S, 142°02'E), which is characterised by an extensive strip of cereal-cropping land with woodland to the north and the south (Figure 1). From March 1983 to March 1988, a grid of 7 × 5 Longworth live-capture traps was set on average every 7 weeks in eucalypt woodland (three replicates), *Callitris* woodland (three replicates) and in crops (six replicates) (Figure 1). A line of 35 traps was set also along the margin of the crop (three replicates). This was a capture–mark–release study with trapping conducted for three consecutive nights, or for two consecutive nights per trapping session when greater than 75% of traps were occupied. Each mouse was sexed, breeding condition noted (see Singleton 1983), marked with a uniquely numbered ear-tag, weighed, head–body length measured, and then released at the site of capture.

Abundance indices for mice were calculated using trap success per 100 trap nights, adjusted for frequency using the method of Caughley (1977, p. 20).

Dogma 2

On the Southeast Asian ‘mainland’, rats invade from neighbouring countries, so farmers feel powerless to manage the problem and are only interested in developing palliative (crisis) management rather than tactical management. Since our research on rodent pests began in Southeast Asia in 1995, we have had numerous reports of rats moving across borders from Cambodia to Vietnam, Cambodia to Thailand, Laos to Thailand, Burma to Thailand, and Thailand to Laos.

A 2-year study was designed to distinguish between the following hypotheses:

- Hypothesis A: Rats invade Vietnam from Cambodia. (Accept dogma 2.)
- Hypothesis B: Rats invade Cambodia from Vietnam. (Accept dogma 2.)
- Hypothesis C: Rats show seasonal movements that track the different crop stages with no consideration of national borders. (Reject dogma 2.)

The study was conducted in the Ha Tien district, Kien Giang province (10°23'N, 106°23'E), Vietnam, from 29 September 1996 to 22 March 1997, and from 26 December 1997 to 3 March 1998. These periods were chosen because Vietnamese farmers report migration from Cambodia of rats around the lunar New Year. This is a politically sensitive region and politics influenced the length of the study periods. The region has dry (December to March) and wet (April to November) seasons; 97% of the rainfall occurs during the wet season. The average annual rainfall is 1500 mm.

In Ha Tien (Vietnam), there are two rice crops grown per year, each with a short growing season (90–105 days). In both years, the dry season crop was planted in December and harvested in mid to late March, and the wet season crop was planted in April and harvested in August. In Cambodia, there is one rice crop per year with a 6-month growing season: transplanted in August and harvested in January and February.

Drift fence plus traps

A 1.5 km plastic fence (0.70 m high) was established within 50 m of the Vietnam–Cambodia border. The bottom 50–100 mm of the fence was buried. A live-multiple-capture cage trap made of wire (600 × 300 × 300 mm) was placed every 30 m flush with, and opening to, a hole in the fence. The rats enter a wire cone, squeeze through and are unable to return (see Singleton et al. 1998 for details). Alternate live-capture traps faced either Vietnam or Cambodia. Rats caught only in the central 1 km of the fence (n = 35 traps) were included in the analyses. Rats were necropsied upon capture, identified to species, sexed and females examined for breeding condition (number of embryos, presence of uterine scars).

Dogma 3

Rats invade from neighbouring villages and devour crops. Farmers feel that the rodent problem is beyond their control because it originates from elsewhere. This is in essence the same as dogma 2, except at a more local scale.

A 4-year study was conducted to distinguish between the following hypotheses:

- Hypothesis A: Rats show seasonal movements that track the different crop stages with no consideration for village borders. (Accept dogma 3.)
- Hypothesis B: Rat populations build up only within a village and stay within these bounds. (Reject dogma 3).

The study was conducted in West Java, Indonesia (6°20'S, 107°39'E) from 1995 to 1998. The movements of rats were monitored between two large holdings, a research farm of 400 ha and seed farm of 1400 ha. Share farmers grow the rice on the seed farm and on two-thirds of the research farm with most farmers responsible for 1–5 ha of crop (mean of 2 ha). The two holdings share a common boundary of 3 km that is separated by the national highway. There are two rice crops grown per year, a wet season and a dry season crop The research farm has a short fallow of approximately 1 month between the wet season and dry season crops and a 3-month fallow after the dry season crop. The fallow seasons were more evenly spaced on the seed farm, which led to the crops being planted asynchronously (Figure 2). The main rat access between the two farms was large stormwater drains that ran under the highway. A high flow of traffic on the highway 24 h a day limited the movements of rats across the surface of the road. High rat damage was reported in 1995–97 to the dry season rice crop in May and June. To monitor the level of rat movement to the research farm from late May to mid-June, rat access via the drain was channelled into wire multiple-capture cage traps. These traps were cleared each day and the number of rats recorded.

Results and discussion

Dogma 1: Australia and mouse plagues

The rate and timing of the population increase of mice across the four habitat types shows that populations in woodlands are 2–4 months behind the on-farm habitats

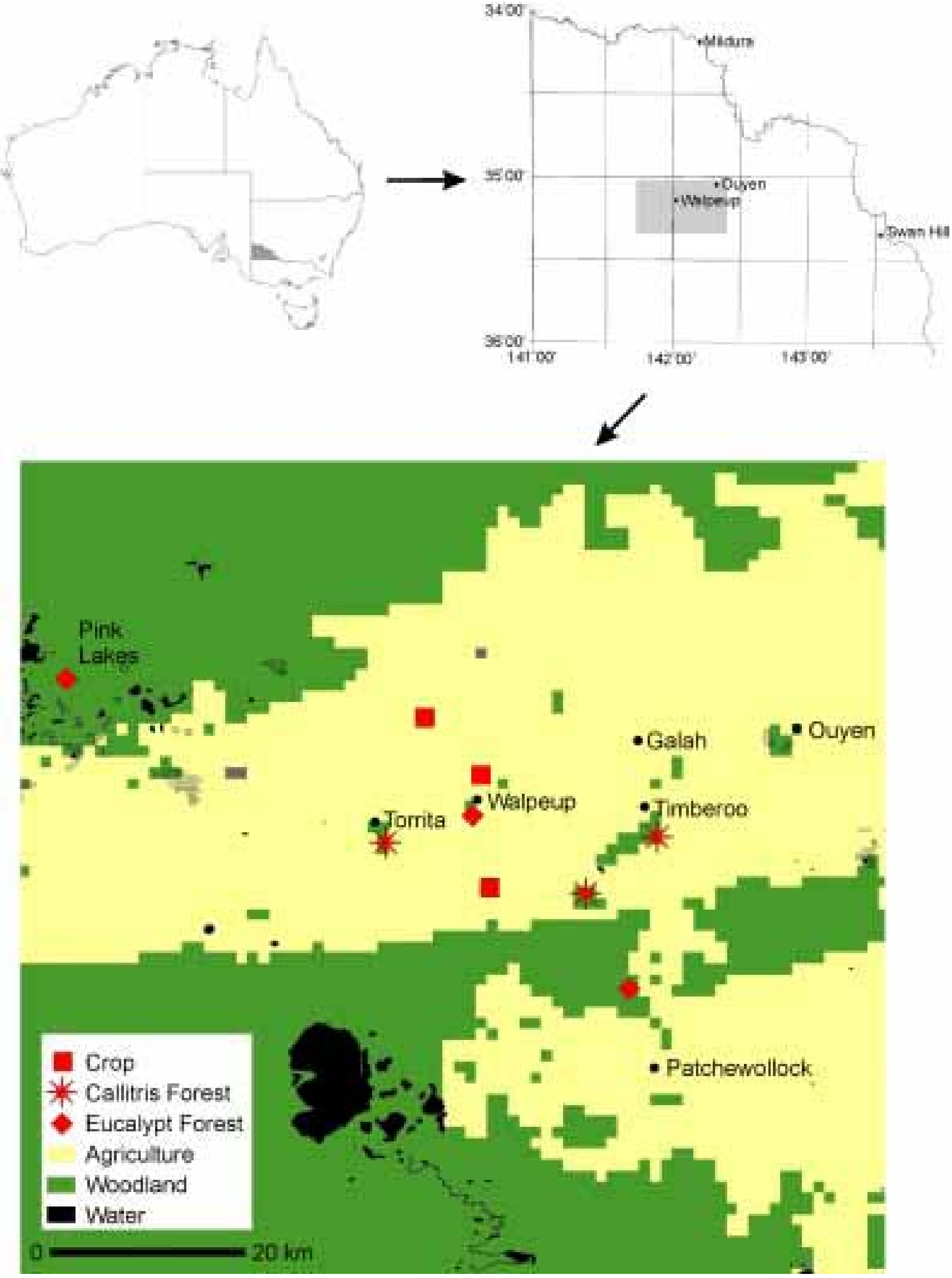

Figure 1. Location of nine study plots in woodland and crop habitats in the central mallee region of Victoria, Australia.

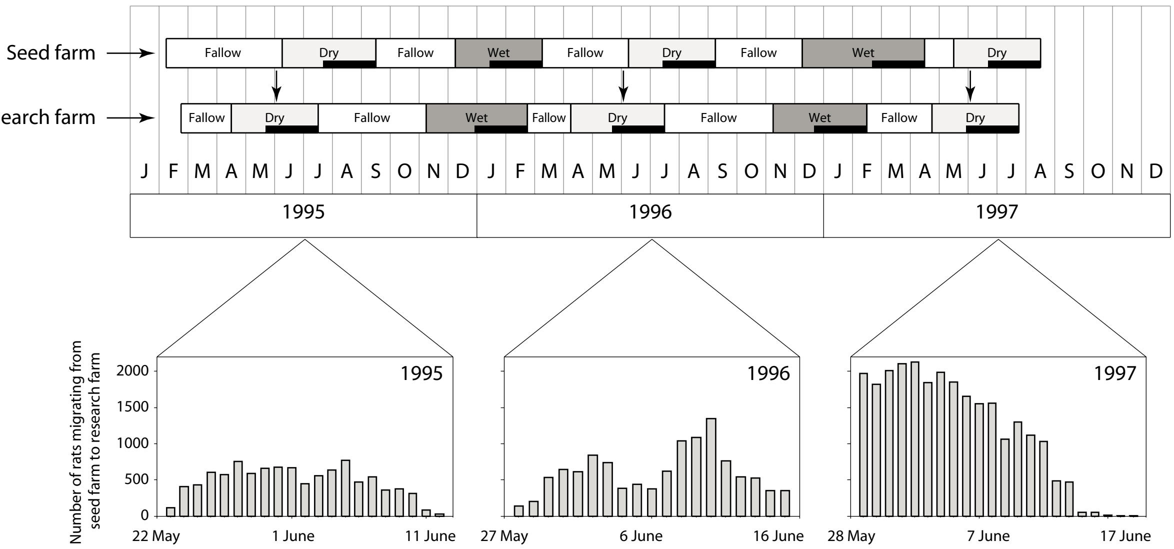

Figure 2. A schematic illustration of the timing of crops on the seed farm and the research farm at West Java, Indonesia, for 1995–97. The histograms show how many rice-field rats moved from the seed farm to the research farm during late May and June of each year. Movement between the farms was highest in 1997 when the time lag was short between harvest of the seed farm wet season crop and planting of the research farm dry season crop. The black bars indicate the period of crop development that is most attractive to rats (Dry = dry season rice crop; Wet = wet season rice crop).

(Figure 3a). Also, the populations in the woodlands increase with few, if any, females in breeding condition (pregnant and/or lactating) in the sample before the increase (Figure 3b). Together these results suggest that crop habitats are source habitats for mice, whereas woodlands are sink habitats.

There have been five detailed studies of changes in the demographic machinery of mice during the formation of a mouse plague in Australia. Three studies were conducted in irrigated crops in NSW (Redhead 1982; Boonstra and Redhead 1994; Twigg and Kay 1994), and two on rain-fed cereal farms: one in South Australia (Newsome 1969) and one in Victoria (Singleton 1989). A further study in South Australia reported changes in mouse abundance, breeding performance and habitat use of mice over a 10-year period (Mutze 1991). The live-trapping components of all of these studies were conducted either in one or two paddocks of a single farm or in a number of habitats but still within the borders of a single farm. Mutze (1991) conducted snap-trapping over large geographic areas, but these studies were restricted to monitoring changes in abundance and breeding of mice for three habitat types: cropped areas, roadsides and grassland/pasture. All of these studies highlighted the importance of seasonal use by mice of different habitats within a cropping landscape. However, the current study is the first to address the issue of whether native woodland is a source or sink habitat for mice. It is clear that mouse populations build up in cereal-cropping regions and then invade the natural woodlands. This leads us to reject dogma 1.

Dogma 2: border region of Vietnam and Cambodia

In 1996/97, rats began moving primarily from Vietnam into Cambodia after the harvest of the wet season crop in Vietnam and at the onset of annual flooding of the Mekong delta (October/November). These movements appeared to be associated with the stage of the crop on either side of the border. Before flooding, 2544 rats were caught migrating from Vietnam and only 49 from Cambodia. After flooding, the trend reversed: 279 rats were caught migrating from Vietnam and 3718 were caught migrating from Cambodia. The movements from Vietnam corresponded to completion of harvest of the rice crop in Vietnam and the flowering/booting stage of Cambodia's rice crop. After waters had subsided in Vietnam (January/February), rats began moving from Cambodia. This coincided with the harvest of Cambodian rice and burning of rice straw. At the same time, the Vietnamese dry season crop was approaching the tillering/booting stage (Table 1).

In the 1997/98 wet season, the fence was erected only in late December so we could monitor the movement patterns of rats only after the floods had receded. As in 1996/97, most rats (2021 of 2367 rats caught in the 6 weeks after 19 January) migrated from Cambodia to Vietnam. However, in 1998, the migration began in mid-January and peaked at the end of January, one month earlier than in 1997. The earlier timing of movements was most likely related to the rainy season ending in late December 1997 with the floods subsiding a month earlier than in 1996/97 and harvesting beginning earlier in Cambodia.

In summary, these seasonal rat migrations appear to track the availability of high-quality food on a local geographical scale (Table 1). National borders did not define a high net flow of rats in one direction, indicating that dogma 2 could be rejected.

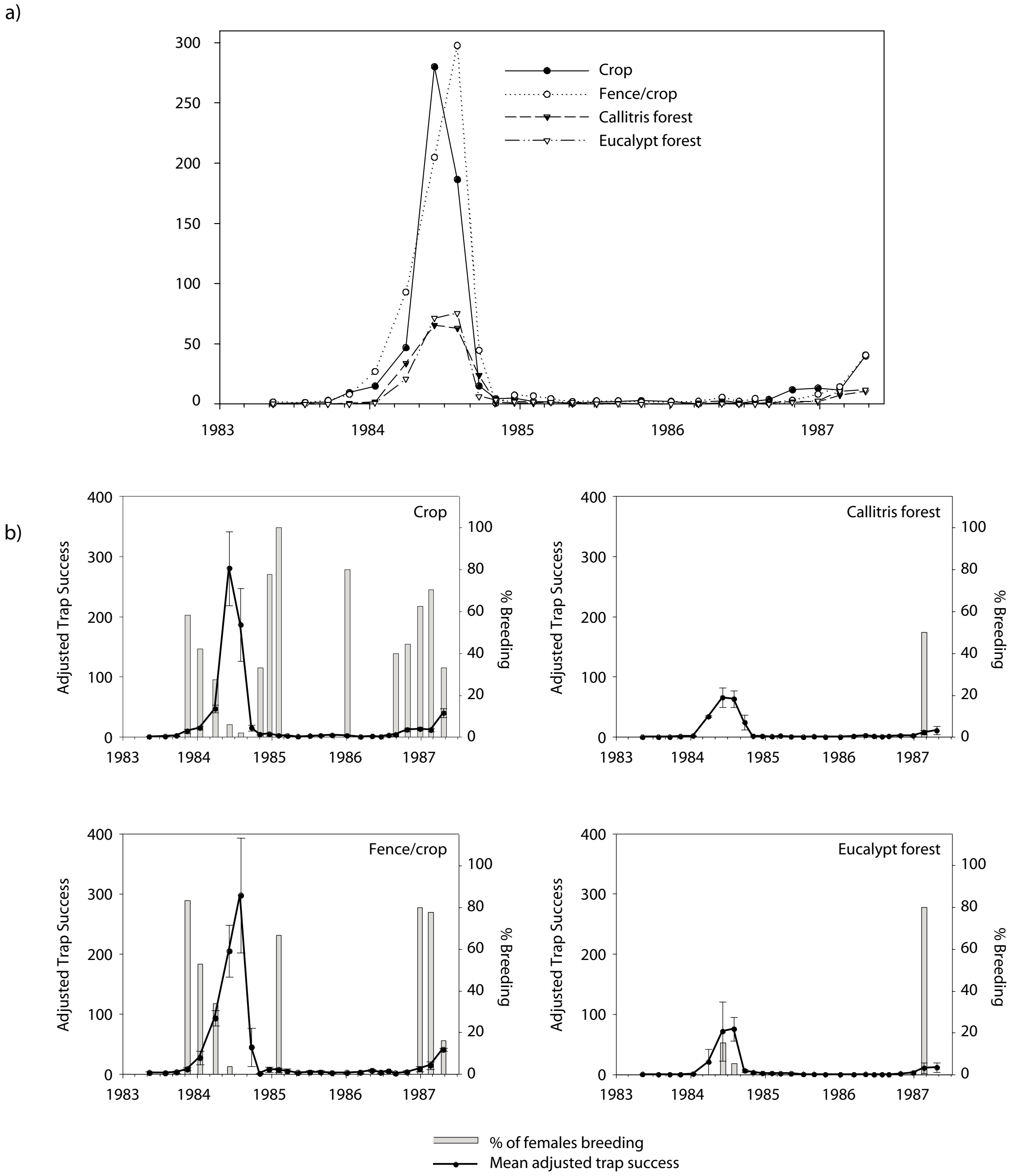

Figure 3. (a) Trap success of house mice in four habitat types in the Walpeup region shown in Figure 1. Population changes in the forest habitats lag behind the agricultural habitats by several months. (b) Percentage of female mice breeding and trap success in each habitat type. Breeding mice were captured in the forest habitats only after the population had increased; indicating the forest habitats are sinks rather than sources.

Dogma 3: local rodent movements in Java

Large numbers of rats were caught within a 3-week period each year from 1995 to 1997. These pulses of movements from the seed farm to the research farm were associated with the harvest of the rice crops and subsequent land preparation on the seed farm. The rats moved to the research farm where the crop was beginning the generative stage of development. The shorter the fallow following the wet season crop on the seed farm, the higher the number of rats caught moving towards the research farm (Figure 2). In 1998 and 1999, the seed farm and the research farm decided to plant both their wet and dry season rice crops synchronously. There were so few rats moving from the seed farm to the research farm in those years that it was decided by the farm managers (with input from scientists who had valuable research plots to protect) that there was no need to set up a barrier plus rat traps.

We accept dogma 3 that rats show seasonal movements that track the different crop stages with no consideration of village borders. Similar *en masse* movements have been reported by Saucy and Schneiter (1997) in juvenile water voles, *Arvicola terrestris*. In this case, it was natal dispersal of a species that spends much of its time as an adult in underground burrows. We know of no other well-documented reports of *en masse* dispersal of rodents.

Dogma 4: predators and rats

Predators, particularly barn owls, have been proposed as a biological method for limiting rodent pest populations in rice agro-ecosystems below levels that cause economic hardship to farmers (Lee and Ho 1999). The reason that barn owls are not able to do so is the lack of nest sites. Provision of nest boxes (one per 6–8 ha) will lead to recruitment of barn owls into an area where they will raise young and the resulting increase in barn owl predation will limit rodent populations (Smal et al. 1990). However, many of these studies were done in conjunction with rodenticides, where they were aiming to poison 90% of the rat population. This high knock-down rate is required because models indicate that owls are unlikely to be able to limit rat populations if there are >60–70 rats/ha (Smal et al. 1990). There is evidence that avian predators are a major cause of density-dependent (see Sinclair et al. 1990) or delayed density-dependent (Lima et al. 2001) mortality of rodents, however too few studies have examined the ability of rodent populations to compensate for predator removal (see discussion by Singleton and Petch 1994).

In the Red River delta of North Vietnam, it is claimed that a reduction in cat numbers (allegedly through trade to China for body parts but also from misuse of poisons) has led to substantial increases in rodent populations. Although there is no scientific evidence to support or refute this allegation, the Vietnamese government is encouraging farmers to raise cats and research is in progress on the breeding performance of different breeds of cats. Promoting predators, particularly cats, was part of a Prime Ministerial Decree on 18 January 1998 (number 09/1998/CT) to encourage farmers to manage rodent pests.

There are insufficient replicated studies, with appropriate controls, to assess the impact of predators on rodent populations. This dogma therefore requires more research.

Dogma 5: farming intensification and rats

Changes in farming systems, especially intensification of rice production in Asia and greater heterogeneity of crops and continuous-rotational cropping in Australia, lead to extension of breeding seasons of rodents and better survival, which in turn is responsible for increased rodent problems in agricultural systems (Singleton and Brown 1999). In Southeast Asian countries, increases in areas of irrigation and changes to their market economies have led to two rice crops per year being grown where there was previously one grown, and three crops where there were previously two. Also, many of the crops are now grown asynchronously within a region.

The Mekong delta in Vietnam is a region that would provide a good test of the effect of farming intensification on rodent populations. Before 1990, rodents were not considered a major pre-harvest pest to rice. In the following decade, rats became a serious pest. In two provinces, Bac Lieu and Soc Trang, the rat situation is so severe that enterprising farmers have taken advantage of the situation by 'harvesting' millions of rats each year and processing them for rat meat. In 2001, we visited two rat-processing businesses and knew of one other. In 2002, the number of businesses had grown to at least eight, with production of dressed rat meat in the vicinity of 1 tonne per day per business from February to April.

Table 1. Summary of patterns of cropping systems on either side of the Vietnam and Cambodia border in Kien Giang province, Vietnam, and the migratory responses of rats from 29 September to 20 March in 1996/97 and 26 December to 2 March in 1997/98.

	Vietnam side	Cambodia side	1996/97	1997/98
Terrain	Low terrain (<5 m above sea level)	Higher terrain, small mountains, 4 km from border		
Cropping system	Irrigated; two crop seasons/year	Rainfed; one crop season/year		
Land preparation	April and November	July		
Rice variety	Improved, dwarf variety of rice; 90–115 days growing season; two crops per year	Local, 'traditional' variety of rice; 180–240 days growing season		
Planting time	15 April – early May 20 November – early December	End of July – early August		
Harvesting time	August 15 March–15 April	Mid to late February in 1997 Mid to late January in 1998		
Fallow	September to October	March to July		
Migration periods			*Migration to:*	
October	Fallow before floods	Vegetative rice	Cambodia	No data
January–February	Vegetative rice	Harvesting and straw burning	Vietnam	Vietnam
March–May	Harvesting and then fallow	Fallow	No migration in March	No data

That farming intensification leads to more rodent problems is an emerging dogma that is vitally important to sustainable agriculture and needs to be examined further. The more we know about the effects of changes in farming systems on rodent population dynamics, the better equipped we will be to not only tackle existing problems but also to anticipate the responses of rat populations to new or proposed agricultural production systems.

Conclusion

This review has considered five beliefs associated with rodent pest biology and management. This is but a subset of the beliefs that have become dogma for rodent managers in both developed and developing countries. This brief review is telling because of the three dogmas for which we had reasonable scientific data, two were rejected. No matter how simple or unrealistic beliefs may appear to a wildlife biologist, it is of paramount importance to make a scientific assessment of those that become dogma. Too often in our experiences in Australia and Southeast Asia, dogmas form the foundation of policies for rodent management adopted by government or agricultural industries. These dogmas are of particular concern because governments often adopt the consequent management approaches to the exclusion of emerging practices or do not invest funds to develop and test alternative management practices because they think they already have the solution.

We end by paraphrasing the concluding statement of Sinclair (1991)—rodent management requires a scientific approach, and the science of rodent management requires managers to conduct experiments.

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