Rats, mice and people:
rodent biology and management

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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
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References

Macdonald, D. 2001. The new encyclopedia of mammals, 2nd edition. Oxford, UK, Andromeda, 961 p.

Singleton, G.R., Hinds, L.A, Leirs, H. and Zhang, Z. (ed.) 1999. Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 494 p.

SYMPOSIUM 1: DISEASE

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 aviru-

lent 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.

References

Barton, L.L. and Hyndman, N.J. 2000. Lymphocytic choriomeningitis virus: reemerging central nervous system pathogen. Pediatrics, 105, E351–E352.

Begon, M., Feore, S., Bown, K., Chantrey, J., Jones, T. and Bennett, M. 1998. The population dynamics of cowpox virus infection in bank voles: testing fundamental assumptions. Ecology Letters, 1, 82–86.

Begon, M., Hazel, S.M., Baxby, D., Bown, K., Cavanagh, R., Chantrey, J., Jones, T. and Bennett, M. 1999. Transmission dynamics of a zoonotic pathogen within and between wildlife host species. Proceedings of the Royal Society Of London Series B, 266, 1–7.

Cavanagh, R., Begon, M., Bennett, M., Ergon, T., Graham, I.M., de Haas, P.E.W., Hart, C.A., Koedam, M., Kremer, K., Lambin, X., Roholl, P. and van Soolingen, D. 2002. *Mycobacterium microti* infection (vole tuberculosis) in wild rodent populations. Journal of Clinical Microbiology (in press).

Chantrey, J., Meyer, H., Baxby, D., Begon, M., Bown, K., Feore, S., Jones, T., Montgomery, W.I. and Bennett, M. 1999. Cowpox: reservoir hosts and geographic range. Epidemiology and Infection, 122, 455–460.

Chitty, D. 1954. Tuberculosis among wild voles: with a discussion of other pathological conditions among certain mammals and birds. Ecology, 35, 227–237.

Elton, C.S. 1942. Voles, mice and lemmings: problems in population dynamics. Oxford, Clarendon Press.

Feore, S.M., Bennett, M., Chantrey, J., Jones, T., Baxby, D. and Begon, M. 1997. The effect of cowpox virus infection on fecundity in bank voles and wood mice. Proceedings of the Royal Society of London Series B, 264, 1457–1461.

Keeling, M.J. and Gilligan, C.A. 2000. Bubonic plague: a metapopulation model of a zoonosis. Proceedings of the Royal Society of London Series B, 267, 2219–2230.

Mills, J.N. and Childs, J.E. 1998. Ecologic studies of rodent reservoirs: their relevance for human health. Emerging Infectious Diseases, 4, 529–537.

Niklasson, B., Hörnfeldt, B. and Lundman, B. 1998. Could myocarditis, insulin-dependent diabetes mellitus, and Guillain-Barré syndrome be caused by one or more infectious agents carried by rodents? Emerging Infectious Diseases, 4, 187–193.

Stenseth, N.C. and Ims, R.A. 1993. The biology of lemmings. London, Academic Press.

Singleton, G.R., Smith, A.L. and Krebs, C.J. 2000. The prevalence of viral antibodies during large fluctuations of house mouse populations in Australia. Epidemiology and Infection, 125, 719–727.

Telfer, S., Bennett, M., Bown, K., Cavanagh, R., Crespin, L., Hazel, S., Jones, T and Begon, M. 2002. The effects of cowpox virus on survival in natural rodent populations: increases and decreases. Journal of Animal Ecology, 71, 558–568.

Wells, A.Q. 1937. Tuberculosis in wild voles. Lancet, 232, 1221.

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 transmis-

sion of the disease in Lushoto District is not well under-stood. 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*.
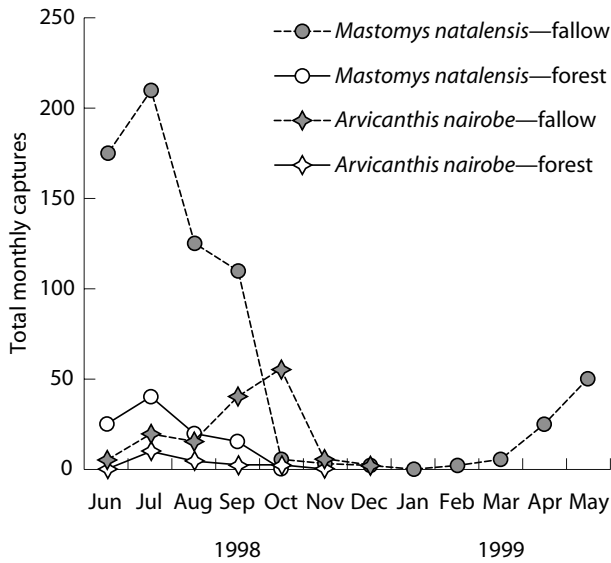
Figure 1. Abundance of *Mastomys natalensis* and *Arvicanthis nairobe* in fallow and forest habitats in Shume Ward, Lushoto District, Tanzania in 1998–1999.
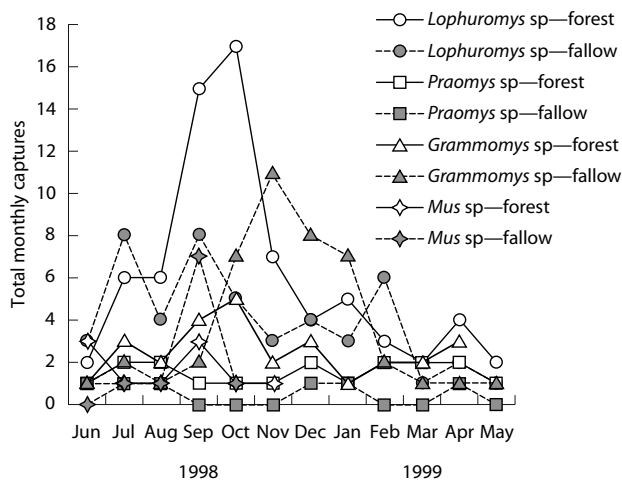
Figure 2. Abundance of non-savanna species of rodents in fallow and forest habitats in Shume Ward, Lushoto District, Tanzania, in 1998–1999.

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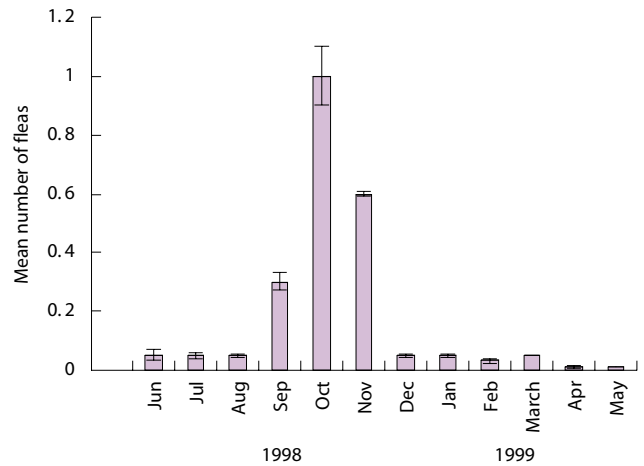
Figure 3. Changes in abundance of fleas on rodent hosts in Shume Ward, Lushoto District, Tanzania.

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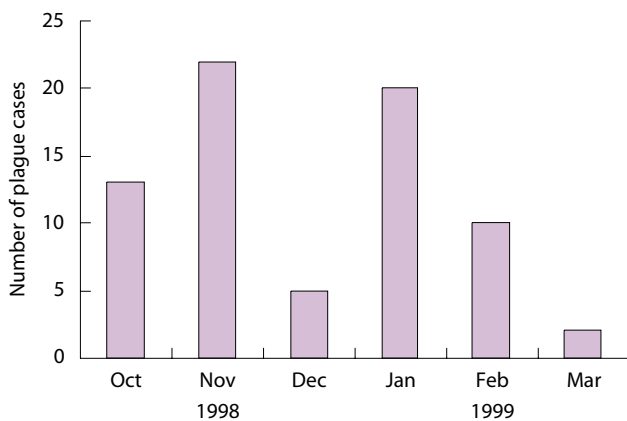
Figure 4. Human plague cases during the 1998–99 outbreak in Shume Ward, Lushoto District, Tanzania.

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).

References

Christensen, J.T. 1996. Home range and abundance of *Mastomys natalensis* (Smith, 1934) in habitats affected by cultivation. African Journal of Ecology, 34, 298–311.

Chu, M.C. 2000. Laboratory manual of plague diagnostic tests. Rome, World Health Organization, Centres for Disease Control and Prevention (CDC), 129 p.

Karimi Y. and Farhang-Azad, A. 1974. On *Pulex irritans*, human flea in the plague focus at Lake General Mobutu (former Lake Albert): epidemiological inference. Bulletin of the World Health Organization, 50, 564.

Kilonzo, B.S., Makundi, R.H. and Mbise, T.J. 1992. A decade of plague epidemiology and control in the western Usambara Mountains, northeast Tanzania. Acta Tropica, 50, 323–329.

Kilonzo, B.S. and Mhina, J.I.K. 1982. The first outbreak of human plague in Lushoto District, north-east Tanzania. Transactions of the Royal Society of Tropical Medicine and Hygiene, 76, 172–177.

Kilonzo, B.S. and Mhina J.I.K. 1983. Observations on the current status of plague endemicity in the western Usambara Mountains, north-east Tanzania. Acta Tropica, 40, 365–372.

Kilonzo, B.S and Msangi, A.S. 1991. Plague. In: Mwaluko, G.M., Kilama, W.L., Mandara, M.P., Murru, M. and Macpherson, C.N.L., ed., Health and diseases in Tanzania. London, Harper Collins Academic, 99–116.

Kilonzo, B.S., Mvena, Z.S.K., Machangu, R.S. and Mbise, T.J. 1997. Preliminary observations on factors responsible for long persistence and continued outbreaks of plague in Lushoto District, Tanzania. Acta Tropica, 68, 215–227.

Leirs, H. 1992. Population ecology of *Mastomys natalensis* (Smith,1834) multimammate rats: possible implications for rodent control in Africa. PhD thesis. Belgium, University of Antwerp, 263 p.

Leirs, H., Verhagen, R., Sabuni, C.A., Mwanjabe, P. and Verheyen, W.N. 1997. Spatial dynamics of *Mastomys natalensis* in a field-fallow mosaic in Tanzania. Belgian Journal of Zoology, 127, 29–39.

Leirs, H., Verhagen, R., Verheyen, W.N., Mwanjabe, P.S. and Mbise, T. 1996. Forecasting rodent outbreaks in Africa. An ecological basis for *Mastomys* control in Tanzania. Journal of Applied Ecology, 33, 937–943.

Mwanjabe, P.S. and Leirs, H. 1997. An early warning system for IPM-based rodent control in small holder farming systems in Tanzania. Belgian Journal of Zoology, 127, 49–58.

Makundi, R.H. 1995. Annual changes of reproduction in rodents in the western Usambara Mountains, north-east Tanzania. Journal of African Zoology, 109, 15–21.

Makundi, R.H. and Kilonzo, B.S. 1994. Seasonal dynamics of rodent fleas and its implication on control strategies in Lushoto District, Tanzania. Journal of Applied Entomology, 118, 165–171.

Njunwa, K.J., Mwaiko, G.L., Kilonzo, B.S. and Mhina, J.I.K. 1989. Seasonal patterns of rodents, fleas and plague status in the western Usambara Mountains, Tanzania. Medical and Veterinary Entomology, 3, 17–22.

Roberts, J.T. 1935. The endemicity of plague in East Africa. East African Medical Journal, 12, 200–219.

Twigg, G.I. 1978. The role of rodents in plague dissemination: a worldwide review. Mammal Review, 8(3), 77–110.

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, menin-

gitis, 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 two-fold: (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 reser-

voirs 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 interme-diate 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 epide-miology. 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

References

Baird, R.W., Stenos, J., Stewart, R., Hudson, B., Lloyd, M., Aiuto, S. and Dwyer, B. 1996. Genetic variation in Australian spotted fever group rickettsiae. Journal of Clinical Microbiology, 34, 1526–1530.

Curzon, P. and McCracken, K. 1993. Plague in Sydney. The anatomy of an epidemic. Kensington, New South Wales University Press.

Dwyer, B.W., Graves, S.R., McDonald, M.I., Yung, A.P., Doherty, R.R. and McDonald, J.K. 1991. Spotted fever in East Gippsland: a previously unrecognised focus of rickettsial infection. Medical Journal of Australia, 154, 121–125.

Faine, S., Adler, B., Bolin, C. and Perolat, P. 1999. *Leptospira* and leptospirosis, 2nd edition. Melbourne, Medical Science, 272 p.

Gratz, N.G. 1994. Rodents as carriers of diseases. In: Buckle, A.P. and Smith, R.H., ed., Rodent pests and their control. Wallingford, UK, CAB International, 85–108.

Graves, S.R., Dwyer, B.W., McColl, D. and McDade, E. 1991. Flinders Island spotted fever: a newly recognised endemic focus of tick typhus in Bass Strait. Part 2. Serological investigations. Medical Journal of Australia, 154, 99–104.

Graves, S.R., Stewart, L., Stenos, J., Stewart, R.S., Schmidt, E., Hudson, S., Banks, J., Huang, Z. and Dwyer, B. 1993. Spotted fever group rickettsial infection in south-eastern Australia: isolation of rickettsiae. Comparative Immunology and Microbiology of Infectious Diseases, 16, 223–233.

Mills, J.M. 1999. The role of rodents in emerging human disease: examples from the hantaviruses and the arenaviruses. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 134–160.

Morgan, U.M, Sturdee, A.P., Singleton, G., Gomez, M.S., Gracenea, M., Torres, J., Hamilton, S.G., Woodside, D.P. and Thompson, R.C.A. 1999. The *Cryptosporidium* 'Mouse' genotype is conserved across geographic areas. Journal of Clinical Microbiology, 37, 1302–1305.

Nitatapattana, N., Henrich, T., Palabodeewat, S., Tangkanakul, W., Poonsuksombat, D., Chauvancy, G., Barbazan, P., Yoksan, S. and Gonzalez, J.P. 2002. Hantaan virus antibody prevalence in rodent populations of several provinces of northeastern Thailand. Tropical Medicine and International Health, 7, 1–6.

Prociv, P., Spratt, D.M. and Carlisle, M.S. 2000. Neuro-angiostrongyliasis: unresolved issues. International Journal for Parasitology, 30, 1295–1303.

Queensland Health 2002. WHO/FAO/OIE collaborating centre for references and research on leptospirosis, Australia and western Pacific region. Queensland Health Pathology and Scientific Service. Queensland Government, Queensland Health Electronic Publishing Service. On the Internet: <http://www.health.qld.gov.au/qhpss/qhss/lepto_home.htm>.

Rountree, P.M. and Rohan, M. 1941. A fatal human infection with *Streptobacillus moniliformis*. Medical Journal of Australia, 1, 359–361.

Singleton, G.R. 2001. Rodent impacts on rice production in Asia. Consultancy report for the International Rice Research Institute, Los Baños, Philippines, November 2001, 65 p.

Singleton, G.R., Smith, A.L., Shellam, G.R., Fitzgerald, N. and Müller, W.J. 1993. Prevalence of viral antibodies and helminths in field populations of house mice (*Mus domesticus*) in southeastern Australia. Epidemiology and Infection, 110, 399–417.

Smith, A.L., Singleton, G.R., Hansen, G.M. and Shellam, G. 1993. A serologic survey for viruses and *Mycoplasma pulmonis* among wild house mice (*Mus domesticus*) in southeastern Australia. Journal of Wildlife Diseases, 29, 219–229.

Stewart R.S. 1991. Flinders Island spotted fever: a newly recognised endemic focus of tick typhus in Bass Strait. Part 1. Clinical and epidemiological features. Medical Journal of Australia 154, 94–99.

Tangkanakul, W., Tharmaphornpilas, P., Plikaylis, B.D., Bragg, S., Phulsuksombati, D., Choomkasien, P., Kingnate, D. and Ashford, D.A. 1998. Risk factors associated with leptospirosis in northeastern Thailand. American Journal of Tropical Medicine and Hygiene 63, 204–208.

Taylor, J.D., Stephens, C.P., Duncan, R.D., and Singleton, G.R. 1994. Polyarthritis in field mice (*Mus musculus*) caused by *Streptobacillus moniliformis*. Australian Veterinary Journal 71, 143–145.

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 bio-marker (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

References

Caughley, J., Monamy, V. and Heiden, K. 1994. Impact of the 1993 mouse plague. GRDC Occasional Paper Series No. 7. Canberra, Grains Research and Development Corporation.

Chambers, L., Lawson, M. and Hinds, L.A. 1999a. Biological control of rodents—the case for fertility control using immunocontraception. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based rodent management. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 215–242.

Chambers, L.K., Singleton, G.R. and Hinds, L.A. 1999b. Fertility control of wild mouse populations: the effects of hormonal competence and an imposed level of sterility. Wildlife Research, 26, 579–591.

Chambers, L.K., Singleton, G.R. and Hood, G.M. 1997. Immunocontraception as a potential control method of wild rodent populations. Belgian Journal of Zoology, 128, 145–156.

Dalum, I., Jensen, M.R., Gregorius, K., Thomasen, C.M., Elsner, J.I. and Mouritsen, S. 1997. Induction of cross-reactive antibodies against a self protein by immunization with a modified self protein containing a foreign T helper epitope. Molecular Immunology, 34, 1113–1120.

Farroway, L.N., Singleton, G.R., Lawson, M.A. and Jones, D.A. 2002. The impact of murine cytomegalovirus (MCMV) on enclosure populations of house mice (Mus domesticus). Wildlife Research, 29, 11–17.

Fitzgerald, G., Wilkinson, R. and Saunders, L. 2000. Public perceptions and issues in possum control. In: Montague, T.L., ed., The brushtail possum: biology, impact and management of an introduced marsupial. Lincoln, New Zealand, Manaaki Whenua Press, 187–197.

Guynn, D.C. Jr 1997. Contraception in wildlife management: reality or illusion? In: Kreeger, T.J., ed., Contraception in wildlife management. Technical Bulletin No. 1853, United States Department of Agriculture, Animal and Plant Health Inspection Service, 241–246.

Harris, J.D., Hibler, D.W., Fontenot, G.K., Hsu, K.T., Yurewicz, E.C. and Sacco, A.G. 1994. Cloning and characterization of zona pellucida genes and cDNAs from a variety of mammalian species: the ZPA, ZPB and ZPC gene families. DNA Sequence, 4, 361–393.

Hardy, C.M., ten Have, J.F.M., Mobbs, K.J. and Hinds, L.A. 2002a. Assessment of the immunocontraceptive effect of a zona pellucida 3 peptide antigen in wild mice. Reproduction, Fertility and Development, 14, 151–155.

Hardy, C.M., Pekin, J. and ten Have, J. 2002b. Mouse-specific immunocontraceptive polyepitope vaccines. Reproduction, Supplement, 60, 19–30.

Jackson, R.J., Maguire, D.J., Hinds, L.A. and Ramshaw, I.A. 1998. Infertility in mice induced by a recombinant ectromelia virus expressing mouse zona pellucida glycoprotein 3. Biology of Reproduction, 58, 152–159.

Jacob, J., Jones, D.A. and Singleton, G.R. 2002. Retention of the biomarker rhodamine B in wild house mice. Wildlife Research, 29, 159–165.

Jacob, J., Ylönen, H., Runcie, M.J., Jones, D.A. and Singleton, G.R. 2002. What affects bait uptake by house mice in Australian grain fields? Journal of Wildlife Management (in press).

Kerr, P.J., Jackson, R.J., Robinson, A.J., Swan, J., Silvers, L., French, N., Clarke, H., Hall, D.F. and Holland, M.K. 1999. Infertility in female rabbits (Oryctolagus cuniculus) alloimmunized with the rabbit zona pellucida protein ZPB either as a purified recombinant protein or expressed by recombinant myxoma virus. Biology of Reproduction, 61, 606–613.

Lou, Y.-H., Bagavant, H., Ang, J., McElveen, M.F., Thai, H. and Tung, K.S.K. 1996. Influence of autoimmune disease on ZP3 contraceptive design. Journal of Reproduction and Fertility, Supplement, 50, 159–163.

Millar, S.E., Chamow, S.M., Baur, A.W., Oliver, C., Robey, F. and Dean, J. 1989. Vaccination with a synthetic zona pellucida peptide produces long-term contraception in female mice. Science, 246, 935–938.

Moro, D., Lloyd, M., Smith, A., Shellam, G. and Lawson, M. 1999. Murine viruses in an island population of introduced house mice and endemic short-tailed mice in Western Australia. Journal of Wildlife Diseases, 35, 301–310.

Nettles, V.F. 1997. Potential consequences and problems with wildlife contraceptives. Reproduction, Fertility and Development, 9, 137–143.

Oogjes, G. 1997. Ethical aspects and dilemmas of fertility control of unwanted wildlife: an animal welfarist's perspective. Reproduction, Fertility and Development, 9, 163–167.

Pech, R.P., Hood, G.M., Singleton, G.R. Salmon, E., Forrester, R.I. and Brown, P.R. 1999. Models for predicting plagues of house mice (Mus domesticus) in Australia. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based rodent management. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 81–112.

Ramsay, A.J. and Ramshaw, I.A. 1997. Cytokine enhancement of immune responses important for immunocontraception. Reproduction, Fertility and Development, 9, 91–7.

Seamark, R.F. 2001. Biotech prospects for the control of introduced mammals in Australia. Reproduction, Fertility and Development, 13, 705–711.

Shellam, G.R. 1994. The potential of murine cytomegalovirus as a viral vector for immunocontraception. Reproduction, Fertility and Development, 6, 401–409.

Singer, P. 1997. Neither human nor natural: ethics and feral animals. Reproduction, Fertility and Development, 9, 157–162.

Singleton, G.R. 1989. Population dynamics of an outbreak of house mice (Mus domesticus) in the mallee wheatlands of Australia—hypothesis of plague formation. Journal of Zoology (London), 219, 495–515.

Singleton, G.R. and Brown, P.R. 1999. Management of mouse plagues in Australia: integration of population ecology, biocontrol and best farm practice. In: Cowan, D.P. and Feare, C.J., ed., Advances in vertebrate pest management. Fürth, Filander-Verlag, 189–203.

Singleton, G.R., Hinds, L.A., Lawson, M.A. and Pech, R.P. 2001. Strategies for management of rodents: prospects for fertility control using immunocontraceptive vaccines. In: Cowan D.P. and Feare, C.J., ed., Advances in vertebrate pest management II. Fürth, Filander-Verlag, 301–318.

Singleton, G.R. and Petch, D.A. 1994. A review of the biology and management of rodent pests in Southeast Asia. ACIAR Technical Report No. 30. Canberra, Australian Centre for International Agricultural Research, 65 p.

Singleton, G.R. and Redhead, T.D. 1990. Structure and biology of house mouse populations that plague irregularly; an evolutionary perspective. Biological Journal of the Linnean Society, 41, 285–300.

Singleton, G.R., Smith, A.L. and Krebs, C.J. 2000. The prevalence of viral antibodies during a large population fluctuation of house mice in Australia. Epidemiology and Infection, 125, 719–727.

Stohr, K. and Meslin, F.X. 1997. Zoonoses and fertility control in wildlife—requirements for vaccines. Reproduction, Fertility and Development, 9, 149–155.

Tyndale-Biscoe, C.H. 1994. Virus-vectored immunocontraception of feral mammals. Reproduction, Fertility and Development, 6, 281–287.

Tyndale-Biscoe, C.H. 1995. Vermin and viruses: risks and benefits of viral-vectored immunosterilisation. Search, 26, 239–244.

Williams, C.K. 1997. Development and use of virus-vectored immunocontraception. Reproduction, Fertility and Development, 9, 169–178.

Williams, C.K. 2002. Risk assessment for release of genetically modified organisms: a virus to reduce the fertiity of introduced wild mice, Mus domesticus. Reproduction, Supplement, 60, 81–88.

YCHW (Yann Campbell Hoare Wheeler) 1999. Public attitudes towards biotechnology. Biotechnology Australia research report. On the Internet at: <http://www.biotechnology.gov.au>. Once at this web site, select "Industry & Research", then "Reports".

Zhu, X. and Naz, R.K. 1999. Comparison of ZP3 protein sequence among vertebrate species to obtain a consensus sequence for immunocontraception. Frontiers in Bioscience, 4, D212–D215.

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.

References

Albright, J.W. and Albright, J.F. 1991. Rodent trypanosomes: their conflict with the immune system of the host. Parasitology Today, 7, 137–140.

Anonymous 1941. Trypanosome du rat. Archives de l'Institut Pasteur de Madagascar Extrait du Rapport Annuel pour 1940, 40.

Goodman, S.M. 1995. *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. Conservation Biology, 9, 450–453.

Goodman, S.M. and Carleton, M.D. 1996. The rodents of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. Fieldiana Zoology, 85, 257–283.

Holmes, J.C. 1996. Parasites as threats to biodiversity in shrinking ecosystems. Biodiversity and Conservation, 5, 975–983.

Kreier, J.P. and Baker, J.R. 1987. Parasitic Protozoa. Boston, Allen and Unwin, Inc.

Laakkonen, J. and Goodman, S. M. 2002. Endoparasites of Malagasy mammals. In: Goodman, S.M. and Benstead, J.P., ed., The Natural History of Madagascar. Chicago, University of Chicago Press (in press).

Lehtonen, J.T., Mustonen, O., Ramiarinjanahary, H., Niemelä, J. and Rita, H. 2001. Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. Biodiversity and Conservation, 10, 1185–1202.

Mackerras, J. 1959. The haematozoa of Australian mammals. Australian Journal of Zoology, 7, 105–135.

Pickering, J. and Norris, C.A. 1996. New evidence concerning the extinction of the endemic murid *Rattus macleari* from Christmas Island, Indian Ocean. Australian Mammalogy, 19, 19–25.

Roberts, M. 1991. Parasitological evidence for the presence of other rodent species on 'kiore only' islands. Journal of the Royal Society of New Zealand, 21, 349–356.

Sakla, A.A. and Monib, M.E.M. 1984. Redescription of the life cycle of *Trypanosoma lewisi* from Upper Egyptian rats. Journal of Egyptian Society of Parasitology, 14, 367–376.

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.

References

Cole, J.R., Sulzer, C.R. and Pursell, A.R. 1973. Improved microtechnique for the leptospiral agglutination test. Applied. Microbiology, 25, 976–980.

Everard, C.O.R. 1992. The epidemiology of leptospirosis. In: Terpstra, W.J. and Korver, H., ed., Leptospirosis on the African continent. Proceedings of CEC/STD 3 Research Meeting, Harare, Zimbabwe, p. 31.

Feresu, S. 1990. Leptospirosis in cattle in Zimbabwe. AMBIO, 19, 394–396.

Forrestier, A.T.T., Kranendonk, O., Turner, L.H., Wolff, J.W. and Bohlander, H.J. 1969. Serological evidence of human leptospirosis in Kenya. East African Medical Journal, 46, 497.

Gravekamp, C. van de Kemp, H., Franzen, M., Carrington, D., Schoone, G.J., Van Eys, G.J.J.M, Everard, C.O.R., Hartskeerl, R.A. and Terpstra, W.J. 1993. Detection of seven species of pathogenic leptospires by PCR using two sets of primers. Journal of General Microbiology, 139, 1691–1700.

Hartskeerl, R.A., Terpstra, W.J., Goris, M., Kemp, H. and Korver, H. 2000. KIT Manual for International Course on Laboratory Methods for the Diagnosis of Leptospirosis. Amsterdam, KIT Biomedical Research.

Johnson, R.C. and Harris, V.G. 1967. Differentiation of pathogenic and saprophytic leptospires I. Growth at low temperature. Journal of Bacteriology, 94, 27–31.

Johnson, R.C. and Rogers, P. 1964. Differentiation of pathogenic and saprophytic leptospires with 8-azaguanine. Journal of Bacteriology, 88, 1618–1622.

Kranendork, O., Wolff, J.W., Bohlander, J.W., Roberts, J.M.D., De Geus, A. and Njenga, R. 1968. Isolation of new *Leptospira* serovars in Kenya. World Health Organization (WHO) Zoonotics, 111, 1–5.

Machang'u, R.S., Mgode, G. and Mpanduji, D. 1997. Leptospirosis in animals and humans in selected areas of Tanzania. Belgian Journal of Zoology, 127. Supplement 1, 97–104.

Merien, P.A., Amouriaux, P.A., Perolat, P., Baranton, G. and Saint Girons, I. 1992. Polymerase chain reaction for detection of *Leptospira* spp. in clinical samples. Journal of Clinical Microbiology, 30, 2219–2224.

Terpstra, W. 1992. Human leptospirosis: constraints in diagnosis and research. In: Terpstra, W.J. and Korver, H., ed., Leptospirosis on the African continent. Proceedings of CEC/STD 3 Research Meeting, Harare, Zimbabwe, p.12.

Terpstra, W.J., Lighart, G.S. and Schoone, G.J. 1985. ELISA for the detection of specific IgM and IgG in human leptospirosis. Journal of General Microbiology, 131, 377–385.

Thierman, A. 1984. Leptospirosis: current development trends. Journal of American Veterinary Medical Association, 184, 722–725.

Wolff, J.W. 1954. The laboratory diagnosis of leptospirosis. USA, Thomas Publishers.

Zuerner, R.L. and Bolin, C.A. 1995. IS 1533-based PCR assay for identification of *Leptospira interrogans* 'sensu lato' serovars. Journal of Clinical Microbiology, 33, 3284–3289.

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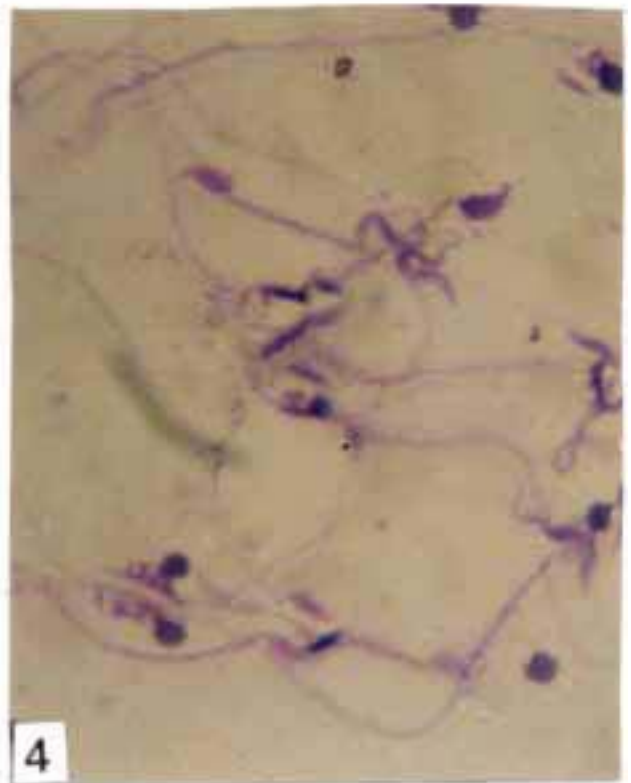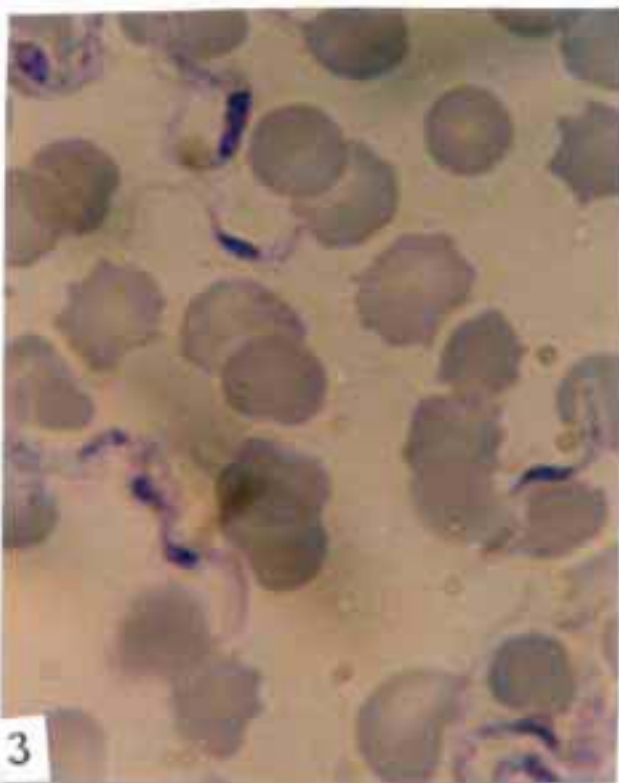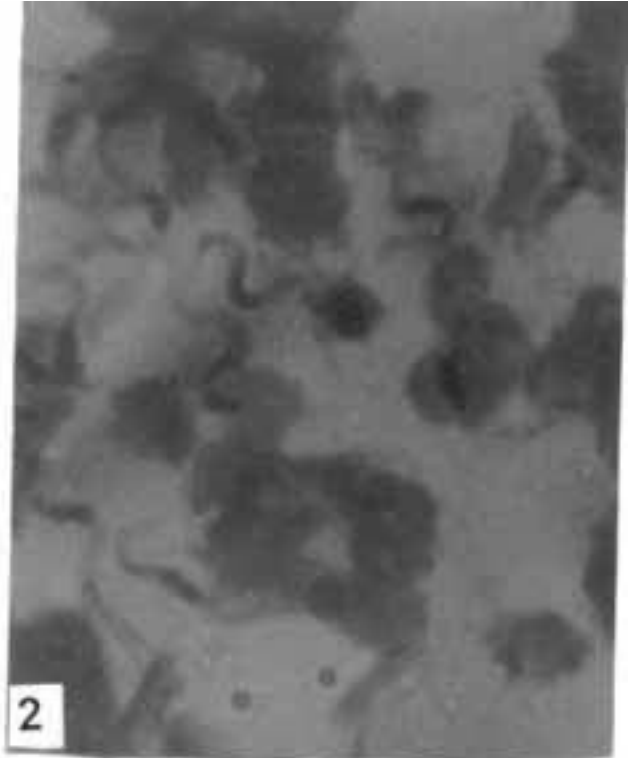
Figure 1. Purified *Trypanosoma evansi* used for inoculation of experimental rats (×200).

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.

References

Gill, B.S. 1991. Trypanosomes and trypanosomiases in Indian Livestock. New Delhi, Indian Council of Agricultural Research, 192 p.

Lanham, S.M. and Godfrey, G.D. 1970. Isolation of salivarian trypanosomes from man and other animals using DEAE cellulose. Experimental Parasitology, 28, 521–534.

Misra, K.K. 1980. Biological control of bandicota rats with *Trypanosoma evansi*. In: Ghosh, A.K., ed., Studies on rodents and their control. Shillong, Meghalaya Science Society, 125–130.

Parshad, V.R. 1999. Rodent control in India. Integrated Pest Management Reviews, 4, 97–126.

Patel, N.M., Avastthi, B.L., Prajapati, K.S., Kathiria, L.G. and Heranjal, D.D. 1982. Histopathological lesions in experimental trypanosomiasis in rats and mice. Indian Journal of Parasitology, 6, 107–109.

Pathak, K.M.L. and Kapoor, M. 1999. Transplacental transmission of *Trypanosoma evansi* in a donkey. Indian Veterinary Journal, 76, 179.

Raisinghani, G., Gupta, M.L., Kumar, D.K. and Manohar, G.S. 1997. Predilection sites of *Trypanosoma evansi* during paroxysmal and non-paroxysmal phases of infection in albino rats. Indian Journal of Animal Sciences, 67, 294–297.

Singla, L.D., Juyal, P.D. and Sandhu, B.S. 2001.Clinico-pathological response in *Trypanosoma evansi* infected and immunosuppressed buffalo-calves. In: Proceedings of 18th International Conference of World Association for the Advancement of Veterinary Parasitology, Stressa, Italy, 26–30 August 2001, p. 39.

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

References

Batzli, G.O. 1992. Dynamics of small mammal populations: a review. In: McCullough, D.R. and Barrett, R.H., ed., Wildlife 2001: population. London, Elsevier Applied Science, 831–850.

Edge, W.D., Carey, R.L., Wolff, J.O., Ganio, L.M. and Manning, T. 1996. Effects of Guthion 2S® on *Microtus canicaudus*: a risk assessment validation. Journal of Applied Ecology, 32, 269–278.

Jellison, W.L., Bell, J.F., Vertrees, J.D., Holmes, M.A., Larson, C.L. and Owen, C.R. 1958. Preliminary observations on disease in the 1957–58 outbreak of *Microtus* in the western United States. Transactions of the North American Wildlife Conference, 23, 137–145.

Jellison, W.L., Owen, C.R., Bell, J.F., Frederick, J. and Kohls, G.M. 1961. *Tularemia* and animal populations: ecology and epizootiology. Wildlife Disease, 17, 1–22.

Kartman, L., Prince, F.M. and Quan, S.F. 1961. Epizootiologic aspects. In: The Oregon meadow mouse irruption of 1957–58. Corvallis, Federal Cooperative Extension Service Oregon State College, 43–54.

Krebs, C.J. 1978. A review of the Chitty hypothesis of population regulation. Canadian Journal of Zoology, 56, 2463–2480.

Krebs, C.J. 1996. Population cycles revisited. Journal of Mammalogy, 77, 8–24.

Vertrees, J.D. 1961. Economic and control aspects. In: The Oregon meadow mouse irruption of 1957–1958. Corvallis, Federal Cooperative Extension Service Oregon State College, 3–13.

Wang, G., Edge, W.D. and Wolff, J.O. 2001. Rainfall and guthion 2S interactions affect gray-tailed vole demography. Ecological Applications, 11, 928–933.

Wolff, J.O., Fox, T., Skillen, R.R. and Wang, G. 1999. The effects of supplemental perch sites on avian predation and demography of vole populations. Canadian Journal of Zoology, 77, 535–541.

Wolff, J.O., Manning, T.A., Meyers, S.M. and Bentley, R. 1996. Population ecology of the gray-tailed vole, *Microtus canicaudus*. Northwest Science, 70, 334–340.

Wolff, J.O., Schauber, E.M. and Edge, W.D. 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. Conservation Biology, 11, 945–956.

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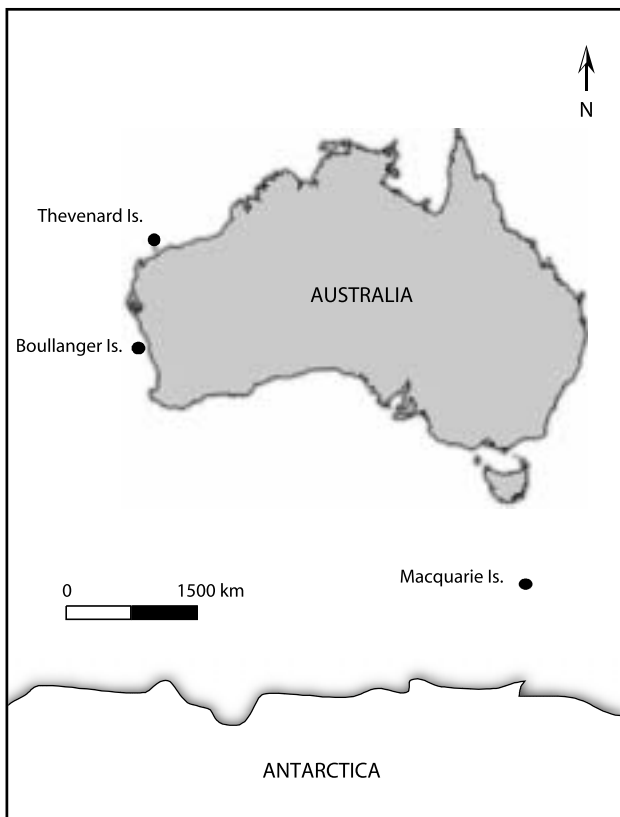
Figure 1. Location map showing sites where house mice were sampled for antiviral antibodies. Island sizes are not to scale.

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 condi-

tion. 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.

References

Berry, R.J. and Peters, J. 1975. Macquarie Island house mice: a genetical isolate on a sub-antarctic island. Journal of Zoology, London, 176, 375–389.

Berry, R.J., Peters, C.J. and van Aarde, R.J. 1978. Subantarctic house mice: colonisation, survival and selection. Journal of Zoology, London, 184, 127–141.

Black, F.L. 1966. Measles endemicity in insular populations: critical community size and its evolutionary implication. Journal of Theoretical Biology, 11, 207–211.

Black, F.L. 1975. Infectious diseases in primitive societies. Science, 187, 515–518.

Canon, R.M. and Roe, R.T. 1982. Livestock disease surveys: a field manual for veterinarians. Canberra, Department of Primary Industry, 35 p.

Chambers, L.K., Singleton, G.R. and Hinds, L.A. 1999. Fertility control of wild mouse populations: the effects of hormonal competence and an imposed level of sterility. Wildlife Research, 26, 579–591.

Copson, G.R. 1986. The diet of the introduced rodents *Mus musculus* L. and *Rattus rattus* L. on subantarctic Macquarie Island. Australian Wildlife Research, 13, 441–445.

Cumpston, J.A. 1968. Macquarie Island. Australian Antarctic Research Expeditions, Scientific Reports, Series A(1), Publication No. 93.

Dobson, A.P. 1988. Restoring island ecosystems: the potential of parasites to control introduced mammals. Conservation Biology, 2, 31–39.

Dobson, A.P. and May, R.M. 1986. Patterns of invasion by pathogens and parasites. In: Mooney, H.A. and Drake, J.A., ed., Ecology of biological invasions of North America and Hawaii. Berlin, Springer-Verlag, 58–76.

Lawlor, T.E. 1986. Comparative biogeography of mammals on islands. Biological Journal of the Linnean Society, 28, 99–125.

Lawson, C.M., Grundy, J.E. and Shellam, G.R. 1988. Antibody responses to murine cytomegalovirus in genetically resistant and susceptible strains of mice. Journal of General Virology, 69, 1987–1998.

McCallum, H., Barlow, N. and Hone, J. 2001. How should pathogen transmission be modelled? Trends in Ecology and Evolution, 16, 295–300.

Moro, D., Lloyd, M., Smith, A., Shellam, G. and Lawson, M. 1999. Murine viruses in an island population of introduced house mice and endemic short-tailed mice in Western Australia. Journal of Wildlife Diseases, 35, 301–310.

Osborn, J.L. 1982. Cytomegalovirus and other herpes viruses. In: Foster, H.L., Small, J.D. and Fox, J.G., ed., The mouse in biomedical research: diseases, volume 2. New York, Academic Press, 267–292.

Pisanu, B., Chapuis, J.L. and Durette-Desset, M.C. 2001. Helminths from introduced small mammals on Kerguelen, Crozet, and Amsterdam Islands (Southern Indian Ocean). Journal of Parasitology, 87, 1205–1208.

Pye, T. 1984. Biology of the house mouse (*Mus musculus*) on Macquarie Island. Tasmanian Naturalist, 79, 6–10.

Saemundsson, B. 1939. Zoology of Iceland: Mammalia, volume 4. Munksgaard, Copenhagen and Reykjavik, 52 p.

Singleton, G.R., Farroway, L.N., Chambers, L.K., Lawson, M.A., Smith, A.L. and Hinds, L.A. 2002. Ecological basis for fertility control in the house mouse (*Mus domesticus)* using immunocontraceptive vaccines. Reproduction, Supplement, 60, 31–39.

Singleton, G.R., Smith, A.L. and Krebs, C.J. 2000. The prevalence of viral antibodies during a large population fluctuation of house mice in Australia. Epidemiology and Infection, 125, 719–727.

Singleton, G.R., Smith, A.L., Shellam, G.R., Fitzgerald, N. and Müller, W.J. 1993. Prevalence of viral antibodies and helminths in field populations of house mice (*Mus domesticus*) in southeastern Australia. Epidemiology and Infection, 110, 399–417.

Smith, A.L., Singleton, G.R., Hansen, G.M. and Shellam, G. 1993. A serologic survey for viruses and *Mycoplasma pulmonis* among wild house mice (*Mus domesticus*) in southeastern Australia. Journal of Wildlife Diseases, 29, 219–229.

Southgate, R. and Masters, P. 1996. Fluctuations of rodent populations in response to rainfall and fire in a central Australian Hummock grassland dominated by *Plectrachne schinzii*. Wildlife Research, 23, 289–303.

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 preharvest 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 reproduc-

tion 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.

References

Anderson R.M. and May, R.M. 1979. Population biology of infectious diseases: part I. Nature, 280, 361–367.

Baker H.J, Lindsey, J.R. and Weisborth, S.H. 1979. The laboratory rat. Biology and disease, Volume I, 313–314.

Cheng, T.C. 1986. General parasitology, 2nd edition. Academic Press College Division Harcourt Brace Javanovich Publisher.

Lam, Y.M. 1988. Rice as a trap crop for the rice field rat in Malaysia. In: Crabb, A.C. and Marsh, R.E., ed., Proceedings of the 13th Vertebrate Pest Conference. Davis, University of California, 123–128.

Scott, M.E. 1987. Regulation of mouse colony abundance by *Heligmosomoides polygyrus*. Parasitology, 95, 111–124.

Singleton, G.R. and Chambers, L.K. 1996. A manipulative field experiment to examine the effect of *Capillaria hepatica* (Nematoda) on wild mouse populations in southern Australia. International Journal for Parasitology, 26, 383–398.

Singleton, G.R. and Petch, D.A. 1994. A review of the biology and management of rodent pests in Southeast Asia. ACIAR Technical Report No. 30. Canberra, Australian Centre for International Agricultural Research, 65 p.

Singleton, G.R. and Spratt, D.M. 1987. Studies on the biology of *Capillaria hepatica* and the effects of *C. hepatica* on productivity and survival of mice: In: Singleton, G.R., ed., *Capillaria hepatica* (Nematoda) as a potential control agent of house mice. Technical Memorandum No. 28. Canberra, CSIRO Division of Wildlife and Rangelands Research, 15–18.

Singleton, G.R., Sudarmaji, Tran Quang Tan, Jumanta and Nguyen Quy Hung 1999. Physical control of rats in developing countries. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 178–198.

Spratt, D.M. and Singleton, G.R. 1986. Studies on the life cycle, infectivity and clinical effects of *Capillaria hepatica* (Bancroft) (Nematoda) in mice, *Mus musculus*. Australian Journal of Zoology, 34, 663–675.

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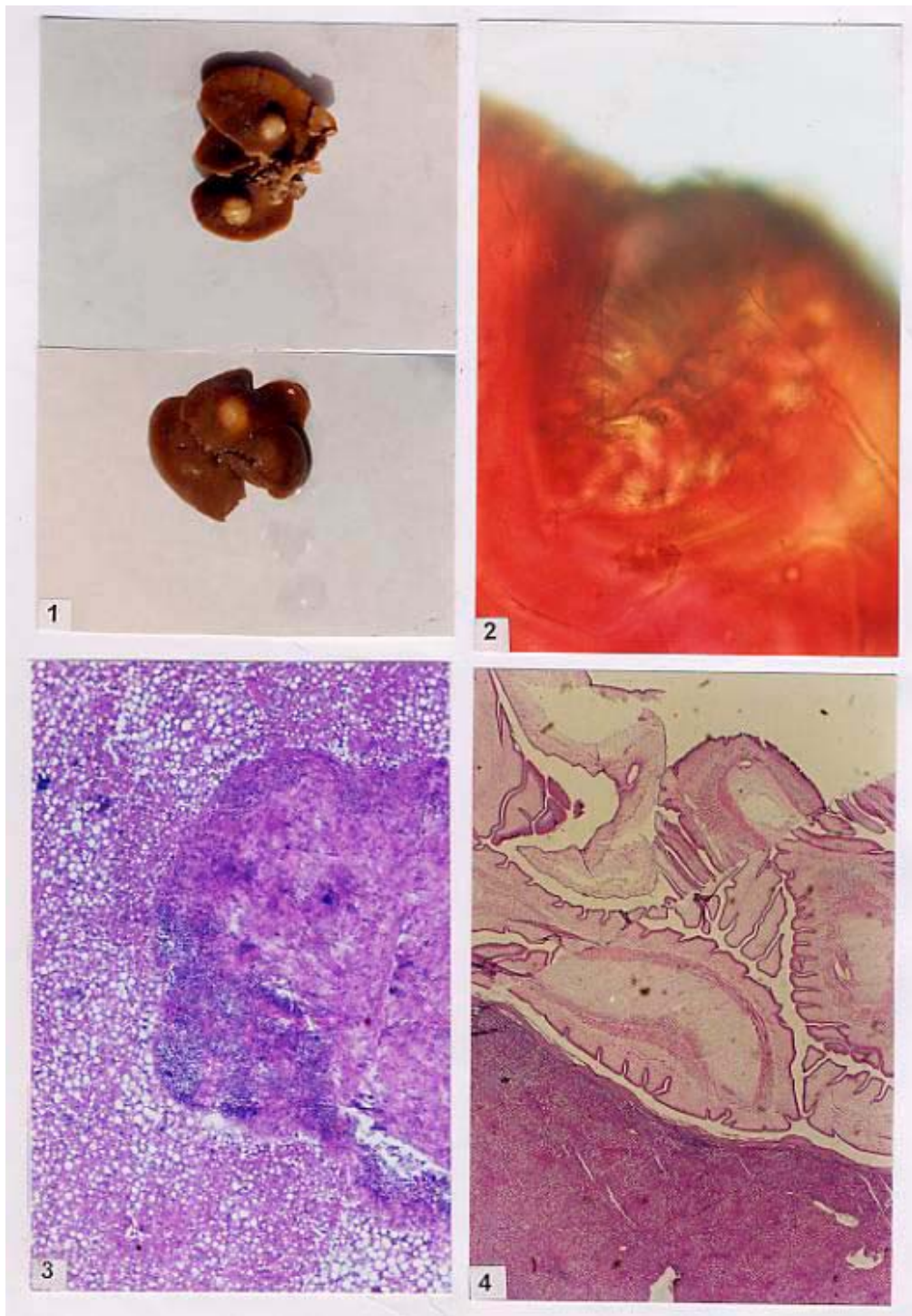
Figure 1. Livers of *Bandicota bengalensis* showing pea-sized or slightly larger, whitish cysts of *Cysticercus fasciolaris***.**

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.

References

Bowman, D.D. 1999. Georgis' parasitology for veterinarians, 6th edition. Philadelphia, W.B. Saunders Company, 414 p.

Cheng, T.C. 1991. General parasitology, 2nd edition. Orlando, Academic Press, 965 p.

Hanes, M.A. 1995. Fibro sarcomas in two rats arising from hepatic cysts of *Cysticercus fasciolaris*. Veterinary Pathology, 32, 441–444.

Janssen Animal Health 2002. *Taenia taeniaeformis*. On the Internet at <http://www.janssenpharmaceutica.be/jah/pages/portraits/p_cat3.htm> (accessed 17 July 2002).

Jithendran, K.P. and Somvanshi, R. 1998. Experimental infection of mice with *Taenia taeniaformis* eggs from cats—course of infection and pathological studies. Indian Journal of Experimental Biology, 36, 523–535.

Kohn, D.F. and Barthold, S.W. 1984. Biology and diseases of rats. In: Fox, J.G., Cohn, B.J. and Loew, F.M., ed., Laboratory animal medicine. Orlando, Florida, Academic Press, 91–122.

Shadduck, J.A. and Pakes. P.S. 1978. Protozoal and metazoal diseases. In: Benirschke, K., Garner, F.M. and Jones, T.C., ed., The pathology of laboratory animals, Volume II. New York, Springer-Verlag, 1640–1641.

Tirina, K. 1953. The significance of cysticercosis in mice used for laboratory experiments. Zeitschrift für Tropenmedizin und Parasitologie, 4, 510.

SYMPOSIUM 2: CONSERVATION

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), *Nesoryzomis 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*), *Papag-*

omys 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.

References

Alcover, J.A., Campillo, X., Marcias, M. and Sans, A. 1998. Mammal species of the world: additional data on insular mammals. American Museum Novitates, 3248, 1–29.

Amori, G. and Gippoliti, S. 2001. Identifying priority ecoregions for rodent conservation at the genus level. Oryx, 35, 158–165.

Atkinson, I.A.E. 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand. In: Dingwall, P.R., Atkinson, I.A.E. and Hay, C.R., ed., The ecology and control of rodents in New Zealand nature reserves. Wellington, Department of Lands and Survey Information Series No. 4, 7–31.

Atkinson, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effect on island avifaunas. In: Moors, P.J., ed., Conservation of island birds. Cambridge, UK, International Council for Bird Preservation, Technical Publication No. 3, 35–81.

Atkinson, I.A.E. and Moller, H. 1990. Kiore. In: King, C.M., ed., The handbook of New Zealand mammals. Auckland, Oxford University Press, 175–192.

Brosset, A. 1963. Statut actuel des mammiferes des Iles Galápagos. Mammalia, 27, 338–340 (in French, with English summary).

Carleton, M.D. and Olson, S.L. 1999. Amerigo Vespucci and the rat of Fernando de Norohna: a new genus and species of Rodentia (Muridae: Sigmodontinae) from a volcanic island off Brazil's continental shelf. American Museum Novitates, 3256, 1–59.

Clark, D.A. 1981. Foraging patterns of black rats across a desert–montane forest gradient in the Galapagos islands. Biotropica, 13, 182–194.

Crook, I.G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society, 20, 115–120.

Dowler, R.C., Carroll, D.S. and Edwards, C.W. 2000. Rediscovery of rodents (Genus *Nesoryzomys*) considered extinct in the Galapagos Islands. Oryx, 34, 109–117.

Goodman, S.M. 1995. *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. Conservation Biology, 9, 450–453.

Hilton-Taylor, C. 2000. IUCN red list of threatened species. Gland, Switzerland and Cambridge, UK, International Union for Conservation of Nature and Natural Resources (IUCN), 61 p.

Innes, J.G. 1990. Ship rat. In: King, C.M., ed., The handbook of New Zealand mammals. Auckland, Oxford University Press, 206–225.

Kepler, C.B. 1967. Polynesian rat predation on nesting Laysan Albatrosses and other Pacific seabirds. Auk, 84, 426–430.

King, W.B. 1985. Island birds: will the future repeat the past? In: Moors, P.J., ed., Conservation of island birds. Cambridge, UK, International Council for Bird Preservation, Technical Publication No. 3, 3–15.

Lehtonen, J.T., Mustonen, O., Ramiarinjanahary, H., Niemelä, J. and Rita, H. 2001. Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. Biodiversity and Conservation, 10, 1185–1202.

Lever, C. 1994. Naturalised animals: the ecology of successfully introduced species. London, Poyser Natural History, 354 p.

MacPhee, R.D.E. and Fleming, C. 1999. Requiem Aeternam. The last five hundred years of mammalian species extinctions. In: MacPhee, R.D.E., ed., Extinctions in near time. New York, Kluwer Academic/Plenum Publisher, 333–371.

Matisoo-Smith, E., Roberts, R.M., Irwin, G.J., Allen, J.S., Penny, D. and Lambert, D.M. 1998. Patterns of prehistoric human mobility in Polynesia indicated by mtDNA from the Pacific rat. Proceedings of the National Academy of Sciences, USA, 95, 15145–15150.

Murphy, E.C. and Pritchard, C.R. 1990. House mouse. In: King, C.M., ed., The handbook of New Zealand mammals. Auckland, Oxford University Press, 225–242.

Musser, G.G. and Heaney, L.R. 1992. Philippine rodents: definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). Bulletin of American Museum Natural History, 211, 1–138.

Newman, D. 1988. Evidence of predation on young tuatara, *Sphenodon punctatus*, by kiore, *Rattus exulans* on Lady Alice Island. New Zealand Journal of Zoology, 15, 443–446.

Nowak, R.M. 1999. Walker's mammals of the world, sixth edition. Baltimore, The John Hopkins University Press, 1936 p.

Palmer M. and Pons G.X. 1996. Diversity in western Mediterranean islets: effects of rat presence on a beetle guild. Acta Oecologica, 17, 297–305.

Sommer, S. and Hommen, U. 2000. Modelling the effects of life history traits and changing ecological conditions on the population dynamics and persistence of the endangered Malagasy giant jumping rat (*Hypogeomys antimena*). Animal Conservation, 3, 333–343.

Steadman, D.W. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. Science, 267, 1123–1131.

Thorsen, M., Shorten, R., Lucking, R. and Lucking, V. 2000. Norway rats (*Rattus norvegicus*) on Fregate Island, Seychelles: the invasion; subsequent eradication attempts and implications for the island's fauna. Biological Conservation, 96, 133–138.

Veitch, C.R. and Clout, M.N. 2002. Turning the tide: the eradication of invasive species. Auckland, Invasive Species Specialist Group of the World Conservation Union (International Union for Conservation of Nature and Natural Resources, IUCN) (in press).

Vigne, J.-D. 1992. Zooarchaelogy and biogeographical history of the mammals of Corsica and Sardinia since the last ice age. Mammal Review, 22, 87–96.

Wilson, D.E. and Reeder, D.M. 1993. Mammal species of the world. A taxonomic and geographic reference, 2nd edition. Washington and London, Smithsonian Institution Press, 1206 p.

Woods, C.A. 1990. The fossil and recent land mammals of the West Indies: an analysis of the origin, evolution, and extinction of an insular fauna. Accademia Nazionale dei Lincei, Atti, 85, 641–680.

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 ($\chi^2_{corr} = 24.8$, $P < 0.001$). 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).
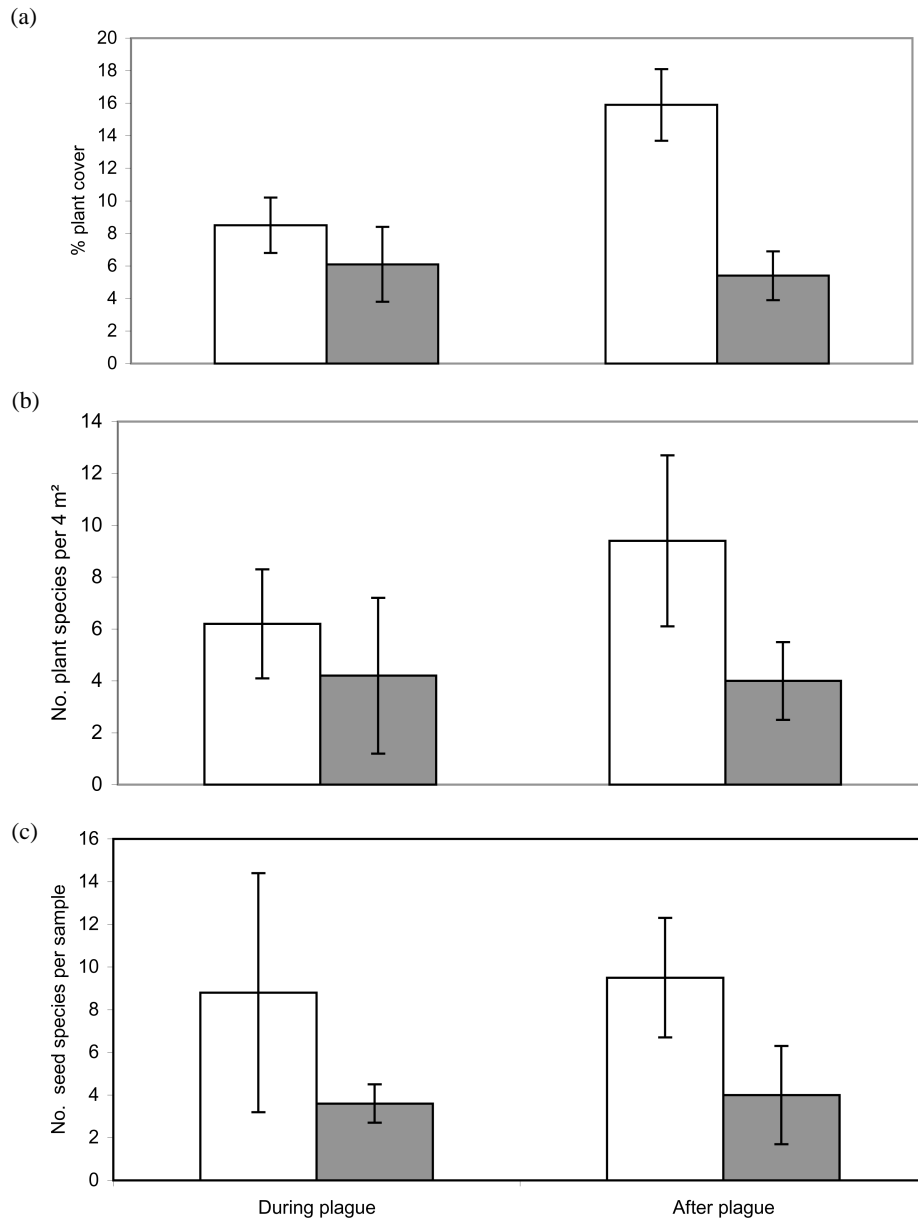
Figure 1. Effects of the long-haired rat, *Rattus villosissimus*, during and after plague conditions on (a) % plant cover, (b) plant species richness, and (c) seed species richness in the Simpson Desert, Queensland. Means are shown ± standard deviations. White bars represent samples taken on burrow complexes, 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 mycor-rhizae, 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.
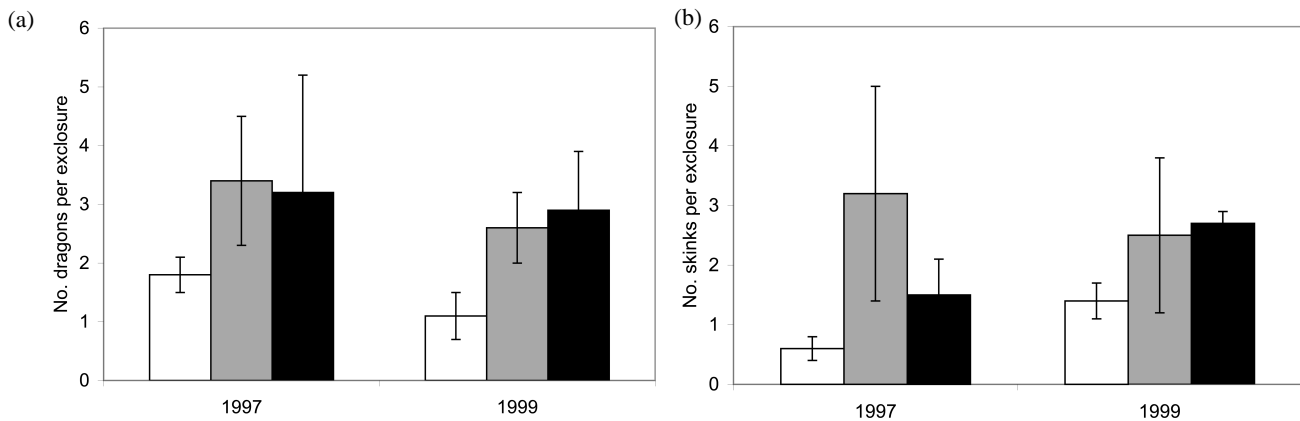
Figure 2. Effects of experimental exclusion of rodents in two years on numbers of (a) military dragons, *Ctenophorus isolepis*, and (b) panther skinks, *Ctenotus pantherinus*, within fenced plots in the Simpson Desert, Queensland. Means are shown ± standard deviations. White bars represent experimental 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.

References

Alkon, P.U. 1999. Microhabitat to landscape impacts: crested porcupine digs in the Negev Desert highlands. Journal of Arid Environments, 41,183–202.

Brown, J.H. 1975. Geographical ecology of desert rodents. In: Cody, M.L. and Diamond, J.M., ed., Ecology and evolution of communities. Cambridge, The Belknap Press of Harvard University Press, 315–341.

Dickman, C.R. 1999. Rodent–ecosystem relationships: a review. In: Singleton, G.R., Hinds, L.A., Leirs, H., and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 113–133.

Dickman, C.R., Brunner, H. and Brack, H. 1991. Ecology of the lesser hairy-footed dunnart, *Sminthopsis youngsoni*, in the Simpson Desert. Newsletter of the Australian Mammal Society, Autumn 1991, 22.

Dickman, C.R., Mahon, P.S., Masters, P. and Gibson, D.F. 1999. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. Wildlife Research, 26, 389–403.

Hawkins, L.K. 1996. Burrows of kangaroo rats are hotspots for desert soil fungi. Journal of Arid Environments, 32, 239–249.

Murray, B.R. and Dickman, C.R. 1997. Factors affecting selection of native seeds in two species of Australian desert rodents. Journal of Arid Environments, 35, 517–525.

Pech, R.P., Hood, G.M., Singleton, G.R., Salmon, E., Forrester, R.I. and Brown, P.R. 1999. Models for predicting plagues of house mice (*Mus domesticus*) in Australia. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. Canberra, Australian Centre for International Agricultural Research, 81–112.

Predavec, M. and Dickman, C.R. 1994. Population dynamics and habitat use of the long-haired rat (*Rattus villosissimus*) in south-western Queensland. Wildlife Research, 21, 1–10.

Shenbrot, G.I., Rogovin, K.A. and Heske, E.J. 1994. Comparison of niche-packing and community organisation in desert rodents in Asia and North America. Australian Journal of Zoology, 42, 479–499.

Thompson, D.B., Brown, J.H. and Spencer, W.D. 1991. Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology, 72, 852–863.

Whitford, W.G. and Kay, F.R. 1999. Bioperturbation by mammals in deserts: a review. Journal of Arid Environments, 41, 203–230.

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 cotton-

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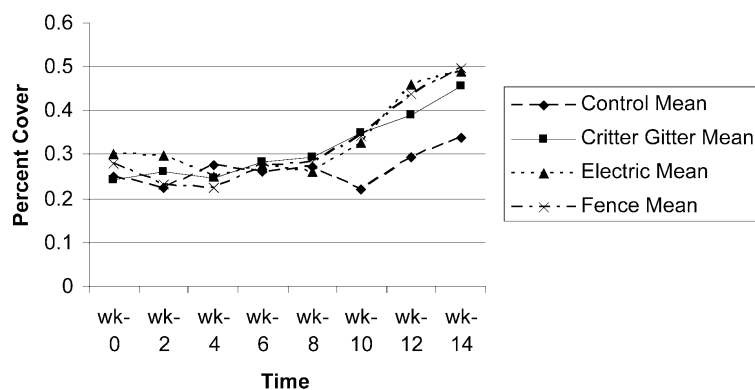
Figure 1. Mean percentage plant cover on plots with fencing, a frightening device, an electro-shocking device, or an untreated control at the start and at 2-week intervals throughout the study.

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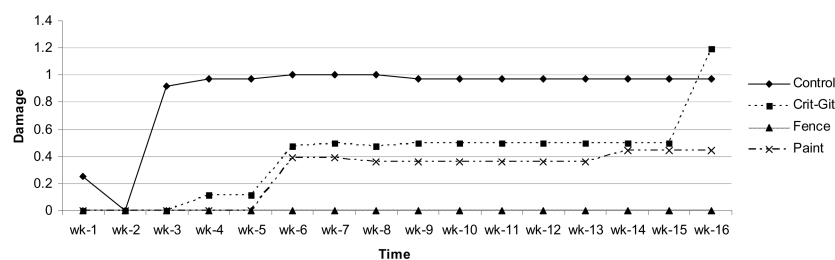
Figure 2. Mean damage scores for plots containing cottonwood stems treated with fencing, a frightening device, a textural repellent, or untreated controls at 1-week intervals throughout the study. A damage score of 0 indicates none of the stems were damaged, while a score of 7 indicates all stems were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

References

Albert, S. and Trimble, T. 2000. Beavers are partners in riparian restoration on the Zuni Indian Reservation. Ecological Restoration, 18, 87–92.

DuBow, T.J. 2000. Reducing beaver damage to habitat restoration sites using less palatable tree species and repellents. Thesis. Logan, Utah State University, 76 p.

Galef, B.G. 1985. Direct and indirect behavioral pathways to the social transmission of food avoidance. In: Braveman, N.S. and Bronstein, P., ed., Experimental assessments and clinical applications of conditioned food aversions. New York, New York Academy of Sciences, 203–215.

Hand, D. 1984. The beaver's tale: out of the woods and into hot water. Smithsonian, 15, 162–171.

Hill, E.P. 1982. Beaver. In: Chapman, J.A. and Feldhamer, G.A., ed., Wildlife mammals of North America. Baltimore, Maryland, The Johns Hopkins University Press, 256–281.

Miller, J.E. and Yarrow, G.K. 1994. Beavers. In: Hygnstrom, S.E., Timm, R.M. and Larsen, G.E., ed., Prevention and control of wildlife damage. Lincoln, Nebraska, University of Nebraska Cooperative Extension, B1–B11.

Koehler, A.E., Marsh, R.E. and Salmon, T.P. 1990. Frightening methods and devices/stimuli to prevent mammal damage—a review. Proceedings of the Vertebrate Pest Conference, 14, 168–173.

Nolte, D.L. 1998. Wildlife considerations when planning plant projects. In: Rose, R. and Haase, D.L., ed., Native plant propagating and planting. Corvallis, Oregon State University, 118–123.

Nolte, D.L. and Mason, J.R. 1998. Bioassays for mammals and birds. In: Millar, J. and Haynes, K., ed., Methods in chemical ecology. London, Chapman and Hall Publishers, 326–395.

Rutherford, W.H. 1955. Wildlife and environmental relationships of beavers in Colorado Forests. Journal of Forestry, 53, 803–806.

Seton, E.Y. 1900. Lives of games animals. Revised 1953 by Charles T. Branford Company, Boston Massachusetts, USA, Volume 4, 441–500.

Wilson. D.E. and Ruff, S. 1999. The Smithsonian book of North American mammals. Washington D.C., Smithsonian Institution Press, 750 p.

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 indica-

tions 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, fence-lines, 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.

References

Achard, F., Eva, H.D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T. and Malingreau, J.-P. 2002. Determination of deforestation rates of the world's humid tropical forests. Science, 297, 999–1002.

Amori, G. and Gippoliti, S. 2000. What do mammalogists want to save? Ten years of mammalian conservation biology. Biodiversity and Conservation, 9, 785–793.

Arbogast, B.S. and Kanagy, G.J. 2001 Comparative phylogeography as an integrative approach to historical biogeography. Journal of Biogeography, 28, 819–825.

Biggins, D.E. and Kosoy, M.Y. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy, 82, 906–916.

Boonsong, P., Hongnark, S., Suasa-ard, K., Khoprasert, Y., Promkerd, P., Hamarit, G., Nookarn, P. and Jäkel, T. 1999. Rodent management in Thailand. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 338–357.

Buckle, A.P. 1999. Rodenticides—their role in rodent pest management in tropical agriculture. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 163–177.

Brocheux, P. 1995. The Mekong Delta: ecology, economy and revolution 1860–1960. Madison, University of Wisconsin Press.

Craig, J.L., Mitchell, N. and Saunders, D.A. (ed.) 2000. Nature conservation 5: conservation in production environments: managing the matrix. Chipping Norton, NSW, Surrey Beatty and Sons, 712 p.

Cully, J.E. Jr and Williams, E.S. 2001. Interspecific comparisons of sylvatic plague in prarie dogs. Journal of Mammalogy, 82, 894–905.

Daszak, P., Cunningham, A.A. and Hyatt, A.D. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. Science, 287, 443-449.

Diamond, J. 1997. Guns, germs and steel: the fates of human societies. New York, W.W. Norton, 480 p.

Dickman, C.R. 1999. Rodent-ecosystem relationships—a review. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No.59. Canberra, Australian Centre for International Agricultural Research, 113–133.

Duckworth, J.W., Timmins, R.J., Khounboline, K., Salter, R.E. and Davidson, P. 1999. Large mammals. In: Duckworth, J.W., Salter, R.E. and Khounboline, K. (compilers), Wildlife in Lao PDR: 1999 status report. Bangkok, Samsaen Printing, 161–220.

Dwyer, P.D. 1975. Observations on the breeding biology of some New Guinea murid rodents. Australian Wildlife Research, 2, 33–45.

Ehrlich, P.R. and Ehrlich, H.A. 1981. Extinction: the causes and consequences of the disappearance of species. New York, Random House, 305 p.

Flannery, T.F. 1995. The mammals of New Guinea, 2nd edition. Chatswood, Reed Books, 568 p.

Fox, B.J. and Pople, A.R. 1984. Experimental confirmation of interspecific competition between native and introduced mice. Australian Journal of Ecology, 9, 323–334.

Francis, C.M. 1999. Order Rodentia, Family Muridae. In: Duckworth, J.W., Salter, R.E. and Khounboline, K. (compilers), Wildlife in Lao PDR: 1999 status report. Bangkok, Samsaen Printing, 237–240.

Glover, I.C. 1986. Archaeology in eastern Timor, 1966–67. Terra Australis 11. Canberra, Department of Prehistory, Research School of Pacific Studies, The Australian National University.

Goodman, S.M. 1995. *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. Conservation Ecology, 9, 450–453.

Hobbs, R.J. and Huenneke, L.F. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology, 6, 324–337.

Hugh-Jones, M.E., Hubbert, W.T. and Hagstad, H.V. 1995. Zoonoses: recognition, control, and prevention. Ames, Iowa State University Press, 369 p.

IUCN (International Union for the Conservation of Nature and Natural Resources) Species Survival Commission 2000. 2000 IUCN red list of threatened species. On the Internet: <http://www.redlist.org/>.

Lehtonen, J.T., Mustonen, O., Ramiarinjanahary, H., Niemela, J. and Rita, H. 2001. Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. Biodiversity and Conservation, 10, 1185–1202.

Marshall, J.T. Jr. 1977. Family Muridae. Rats and mice. In: Lekagul, B. and McNeely, J.A., ed., Mammals of Thailand. Bangkok, Thailand, Association for the Conservation of Wildlife, 397–487.

McDougall, W.A. 1947. An investigation of the rat pest problem in Queensland canefields: 6. Controls and conclusions. Queensland Journal of Agricultural Science, 4, 79–139.

Meehan, A.P. 1984. Rats and mice. Their biology and control. Felcourt, East Grinstead, West Sussex, Rentokil Ltd, 383 p.

Menkhorst, P.W. (ed.) 1995. Mammals of Victoria. Melbourne, Oxford Univeristy Press, 360 p.

Musser, G.G. 1973. Zoogeographical significance of the ricefield rat, *Rattus argentiventer*, on Celebes and New Guinea and the identity of *Rattus pesticulus*. American Museum Novitates, 2511, 1–30.

Musser, G.G. and Brothers, E.M. 1994. Identification of bandicoot rats from Thailand (*Bandicota*, Muridae, Rodentia). American Museum Novitates, 3110, 1–56.

Musser, G.G. and Newcomb, C. 1983. Malaysian murids and the giant rat of Sumatra. Bulletin of the American Museum of Natural History, 174, 327–598.

Mutze, G.J. 1991. Mouse plagues in South Australian cereal-growing areas. III. Changes in mouse abundance during plague and non-plague years, and the role of refugia. Wildlife Research, 18, 593–604.

Poland, J.D. and Barnes, A.M. 1979. Plague. In: Steele, A.H., ed., CRC Handbook series in zoonoses. Volume I. Section A: Bacterial, rickettsial and mycotic diseases. Boca Raton, Florida, CRC Press.

Roberts, M. 1991. The parasites of the Polynesian rat: biogeography and origins of the New Zealand parasite fauna. International Journal for Parasitology, 21, 785–793.

Saunders, D.A., Arnold, G.W., Burbidge, A.A. and Hopkins, A.J.M. (ed.) 1987. Nature conservation: the role of remnants of natural vegetation. Chipping Norton, NSW, Surrey Beatty and Sons, 410 p.

Saunders, D.A. and Hobbs, R.J. (ed.) 1991. Nature conservation 2: the role of corridors. Chipping Norton, NSW, Surrey Beatty and Sons, 442 p.

Singleton, G.R., Brown, P.R., Jacob, J., Aplin, K. and Sudarmaji 2002. Unwanted and unintended effects of culling. In: Harris, S. and Lavigne, D., ed., Culling of mammals. Cambridge, Cambridge University Press (in press).

Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z. (ed.) 1999b. Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 494 p.

Singleton, G.R. and Petch, D.A. 1994. A review of the biology and management of rodent pests in Southeast Asia, ACIAR Technical report No. 30. Canberra, Australian Centre for International Agricultural Research, 65 p.

Singleton, G.R. and Redhead, T.D. 1990. Structure and biology of house mouse populations that plague irregularly; an evolutionary perspective. Biological Journal of the Linnean Society, 41, 285–300.

Singleton, G.R., Sudarmaji, Jumanta, Tam, T.Q. and Hung, N.Q. 1999a. Physical control of rats in developing countries. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 179–198.

Soulé, M.E. 1995. An unflinching vision: networks of people defending networks of lands. In: Saunders, D., Craig, J.L. and Mattiske, E.M., ed., Nature conservation 4: the role of networks. Chipping Norton, NSW, Surrey Beatty and Sons, 1–8.

Watts, C.H.S. and Aslin, H.J. 1981. The rodents of Australia. Sydney, Angus and Robertson, 321 p.

White, J., Horskins, K. and Wilson, J. 1998. The control of rodent damage in Australian macadamia orchards by manipulation of adjacent non-crop habitats. Crop Protection, 17, 353–357.

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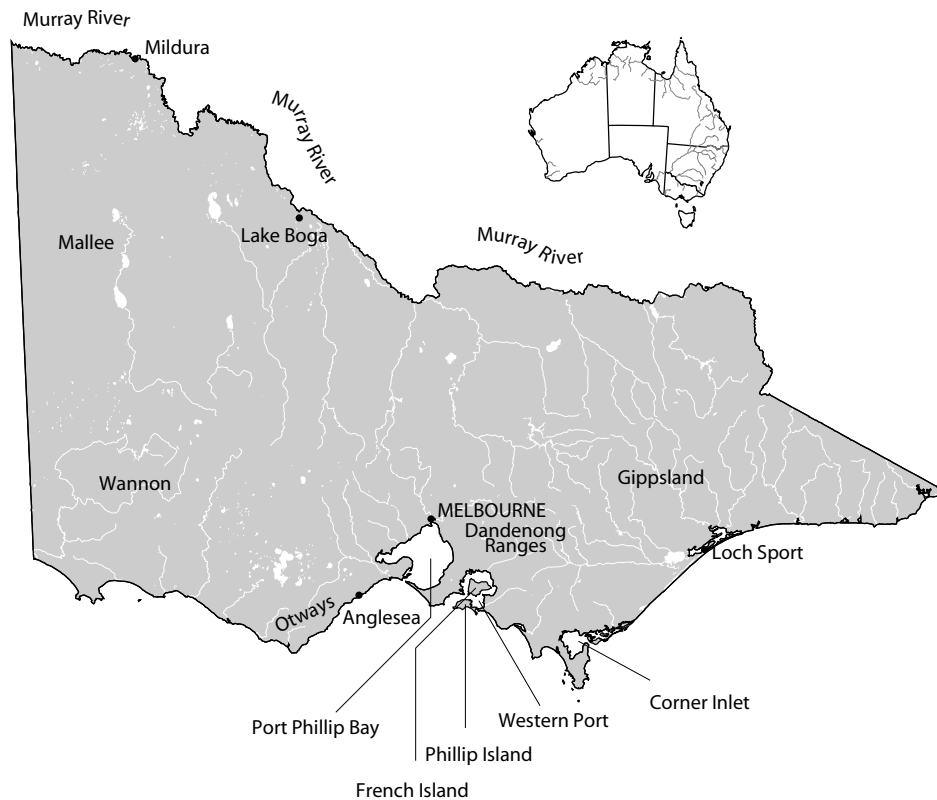
Figure 1. Key locations discussed in the text with regard to rodent species in Victoria, Australia.

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 salt-water 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. Tech-niques 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.

References

Bennett, A.F., Lumsden, L.F. and Menkhorst, P.W. 1989. Mammals of the mallee region of south-eastern Australia. In: Noble, J.C and Bradstock, R.A., ed., Mediterranean landscapes in Australia: mallee ecosystems and their management. Melbourne, CSIRO, 191–220.

Gardenfors, U., Hilton-Taylor, C., Mace, G. and Rodriguez, J.P. 1999. The application of IUCN red list criteria at regional levels. Conservation Biology, 15, 1206–1212.

IUCN (International Union for Conservation of Nature and Natural Resources) 2001. IUCN red list categories and criteria version 3.1. Gland, Switzerland, IUCN.

Krefft, G. 1866. On the vertebrated animals of the lower Murray and Darling. Their habits, economy and geographical distribution. Transactions of the Philosophical Society of New South Wales, 1862–1865, 1–133.

Lee, A.K. 1995. The action plan for Australian rodents. Canberra, Australian Nature Conservation Agency, 62 p.

Menkhorst, P.W. (ed.)1995. Mammals of Victoria: distribution, ecology and conservation. Melbourne, Oxford University Press, 359 p.

O'Callaghan, P. 1999. Conservation ecology of the New Holland mouse *Pseudomys novaehollandiae* (Waterhouse 1843) at Anglesea: a geographic information systems approach. MSc thesis. Armidale, University of New England.

Robertson, P., Bennett, A.F., Lumsden, L.F., Silviera, C.E., Johnson, P.G., Yen, A.L., Milledge, G.A. Lillywhite, P.K. and Pribble, H.J. 1989. Fauna of the mallee study area, north-western Victoria. Arthur Rylah Institute for Environmental Research Technical Report Series No. 87. Victoria, Department of Conservation, Forests and Lands, viii + 91 p.

Seebeck, J. and Menkhorst, P. 2000. Status and conservation of the rodents of Victoria. Wildlife Research, 27, 357–369.

Seebeck, J.H., Menkhorst, P.W., Wilson, B.A. and Lowe, K.W. 1996. New Holland mouse *Pseudomys novaehollandiae*. Flora and Fauna Guarantee Action Statement No. 74. Victoria, Department of Natural Resources and Environment, 8 p.

Watts, C.H.S. and Aslin, H.J. 1981. The rodents of Australia. Sydney, Angus and Robertson, 321 p.

Wilson, B.A. 1991. The ecology of *Pseudomys novaehollandiae* (Waterhouse, 1843) in the eastern Otway Ranges, Victoria. Wildlife Research, 18, 233–247.

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 km² to the total area of only c. 1065 km² 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)

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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).

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.

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												

References

Avenant, N.L. 2000. Small mammal community characteristics as indicators of ecological disturbance in the Willem Pretorius Nature Reserve, Free State, South Africa. South African Journal of Wildlife Research, 30, 26–33.

Avenant, N.L. and Kuyler, P. 2002. Small mammal diversity in the Maguga Dam inundation area, Swaziland. South African Journal of Wildlife Research (in press).

Avenant, N.L. and Watson, J.P. 2002. Mammals recorded in the Sandveld Nature Reserve, Free State province, South Africa. Navorsinge van die Nasionale Museum Bloemfontein (Navors.Nas.Mus.), 18, 1–12.

Cardinale, B.J., Nelson, K. and Palmer, M.A. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. Oikos, 91, 175–183.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. and Diaz, S. 2000. Consequences of changing biodiversity. Nature, 405, 234–242.

Els, L.M. and Kerley, G.I.H. 1996. Biotic and abiotic correlates of small mammal community structure in the Groendal Wilderness Area, Eastern Cape, South Africa. Koedoe, 39, 121–130.

Fonseca, C.R. and Ganade, G. 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology, 89, 118–125.

Hastwell, G.T. and Huston, M.A. 2001. On disturbance and diversity: a reply to Mackey and Currie. Oikos, 92, 367–371.

Johnson, K.H. 2000. Trophic–dynamic considerations in relating species diversity to ecosystem resilience. Biological Review, 75, 347–376.

Joubert, D.F. and Ryan, P.G. 1999. Differences in mammal and bird assemblages between commercial and communal rangelands in the Succulent Karoo, South Africa. Journal of Arid Environments, 43, 287–299.

Kerley, G.I.H. 1992. Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. Journal of Zoology, London, 227, 17–27.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos, 91, 3–17.

Magurran, A.E. 1988. Ecological diversity and its measurement. Cambridge, Cambridge University Press, 179 p.

McCann, K.S. 2000. The diversity–stability debate. Nature, 405, 228–233.

Petchey, O.L. 2000. Species diversity, species extinction, and ecosystem function. The American Naturalist, 155, 698–702.

Smith, B. and Wilson, J.B. 1996. A consumer's guide to evenness indices. Oikos, 76, 70–82.

Valone, T.J. and Kelt, D.A. 1999. Fire and grazing in a shrub-invaded arid grassland community: independent or interactive ecological effects? Journal of Arid Environments, 42, 15–28.

Wootton, J.T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. The American Naturalist, 152, 803–825.

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 ($\chi^2 = 1834$, df = 19, $P = <0.000$), as did rabbit-rats from site 2 ($\chi^2 = 159$, 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

References

Bradley, A.J., Kemper, C.M., Kitchener, D.J., Humphreys, W.F. and How, R.A. 1987. Small mammals of the Mitchell Plateau Region, Kimberley, Western Australia. Australian Wildlife Research, 14, 397–413.

Friend, G., Kemper, C. and Kerle, A. 1992. Rats of the tree tops. Landscape, 8, 10–15.

Frith, H.J. and Calaby, J.H. 1974. Fauna survey of the Port Essington district, Cobourg Peninsula, Northern Territory of Australia. Technical Paper No. 28. Canberra, CSIRO Division of Wildlife Research.

Hooge, P.N. and Eichenlaub, B. 1997. Animal movement extension to Arcview, version 1.1. Anchorage, Alaska Biological Science Center, United States Geological Survey.

Taylor, J.M. and Horner, B.E. 1971. Reproduction in the Australian tree-rat *Conilurus penicillatus* (Rodentia: Muridae). CSIRO Wildlife Research, 16, 1–9.

Woinarski, J.C.W. 2000. The conservation status of rodents in the monsoonal tropics of the Northern Territory. Wildlife Research, 27, 421–435.

Woinarski, J.C.W., Palmer, C., Fisher, A., Southgate, R., Masters, P. and Brennan, K. 1999. Distributional patterning of mammals on the Wessel and English Company Islands, Arnhem Land, Northern Territory, Australia. Australian Journal of Zoology, 47, 87–111.

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.
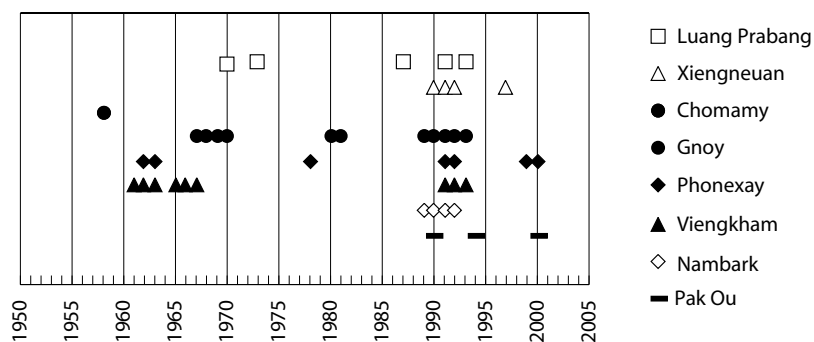

Figure 1. Historical pattern of rodent outbreaks in Luang Prabang province, by district.

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
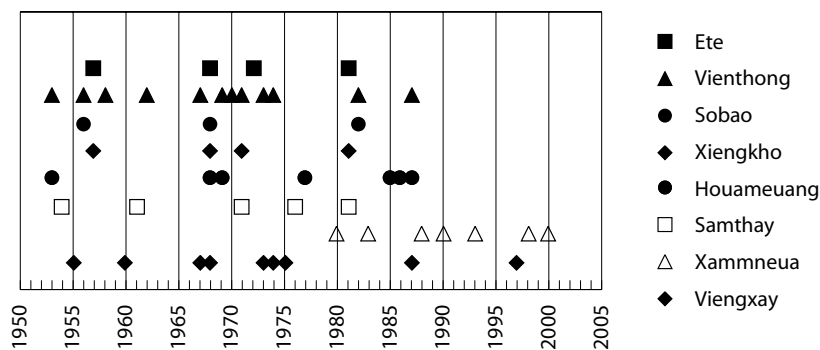

Figure 2. Historical pattern of rodent outbreaks in Houaphanh province, by district.
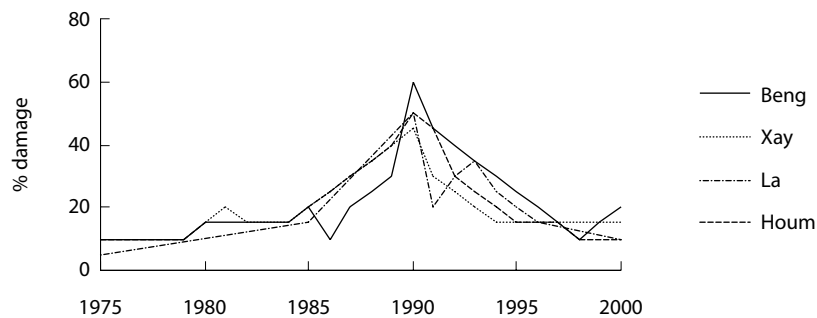

Figure 3. Recent pattern of crop damage attributed to rodent outbreaks in four districts of Oudomxay province.

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
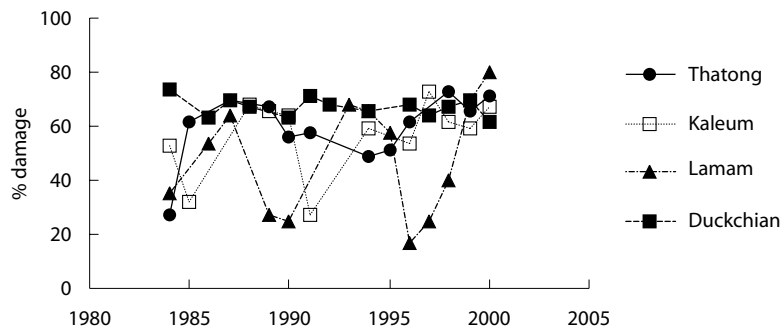

Figure 4. Recent pattern of crop damage attributed to rodent outbreaks in four districts of Sekong province.
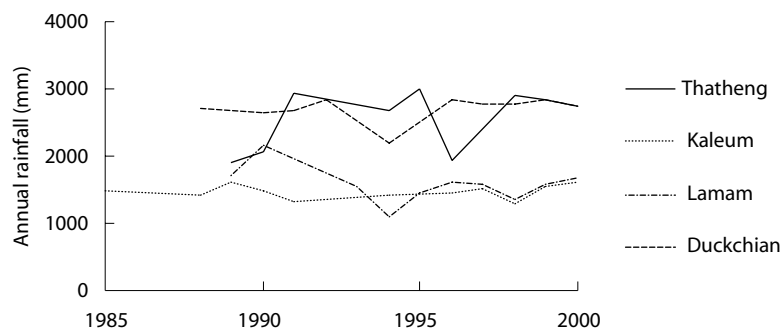

Figure 5. Variation in annual rainfall in four districts of Sekong province.

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 inter-masts 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

References

Chauhan, N.S. and Saxena, R.N. 1985. The phenomenon of bamboo flowering and associated increase in rodent population in Mizoram. Journal of the Bombay Natural History Society, 82, 644–647.

Christanty, L., Mailly, D. and Kimmins, J.P. 1996. Without bamboo, the land dies: biomass, litterfall, and soil organic matter dynamics of a Javanese bamboo talun-kebun system. Forest Ecology and Management, 87, 75–88.

Francis, C.M. 1999. Order Rodentia, Family Muridae. In: Duckworth, J.W., Salter, R.E. and Khounboline, K., compilers, Wildlife in Lao PDR: 1999 status report. Bangkok, Samsaen Printing, 237–240.

Gadgil, M. and Prasad, S.N. 1984. Ecological determinants of life history evolution of two Indian bamboo species. Biotropica, 18, 161–172.

Gressit, J.L. 1970. Biogeography of Laos. Pacific Insects Monograph, 24, 573–626.

Holmgren, M., Scheffer, M., Ezcurra, E., Gutierrez, J.R. and Mohren, G.M.J. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution, 16, 89–94.

Hompangna, K., Phomavongsa, S., Phouvayong, S., and Sounnalath, P. 2000. Effects of El Niño and La Niña on Laos. On the Internet: <http://www.cru.uea.ac.uk/tiempo/floor0/briefing/igcn/igcn2000.htm>.

Jaksic, F.M. and Lima, N. 2002. Myths and facts on "ratadas": bamboo blooms, rainfall peaks and mouse outbreaks. Ecography (in press).

Janzen, D.H. 1976. Why bamboos wait so long to flower. Annual Review of Ecology and Systematics, 7, 347–391.

Kane, R.P. 1999. El Niño timings and rainfall extremes in India, Southeast Asia and China. International Journal of Climatology, 19, 653–672.

Keeley, J.E. and Bond, W.J. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. The American Naturalist, 154, 383–391.

Kelly, D. 1994. The evolutionary ecology of mast-seeding. Trends in Ecology and Evolution, 9, 465–470.

King, C.M. 1983. The relationship between Beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*) in three New Zealand forests. Journal of Animal Ecology, 52, 141–166.

Lima, M., Marquet, P.A. and Jaksic, F.M. 1999. ENSO-driven rainfall variability and delayed density-dependence cause rodent outbreaks in western South America: linking demography and population dynamics. American Naturalist, 153, 476–491.

Lima, M., Julliard, R., Stenseth, N.C. and Jaksic, F.M. 2001. Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic factors. Journal of Animal Ecology, 70, 761–775.

McPhaden, M.J. 1999. Genesis and evolution of the 1997–98 El Niño. Science, 283, 950–954.

McShea, W.J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology, 81, 228–238.

Meserve, P.L., Yunger, J.A., Gutiérrez, J.R., Contreras, L.C., Milstead, W.B., Lang, B.K. and Cramer, K.L. 1995. Heterogeneous responses of small mammals to an El Niño southern oscillation event in north central semiarid Chile and the importance of the ecological cycle. Journal of Mammalogy, 76, 580–595.

Musser, G.G. and Newcomb, C. 1985. Definitions of Indochinese *Rattus losea* and a new species from Vietnam. American Museum Novitates, 2814, 1–32.

Nag, S. 1999. Bamboo, rats and famines: famine relief and perceptions of British paternalism in the Mizo Hills (India). Environment and History, 5, 245–252.

Numata, M. 1970. Conservational implications of bamboo flowering and death in Japan. Biological Conservation, 2, 227–229.

O'Donnell, C.F.J. and Phillipson, S.M. 1996. Predicting the incidence of mohua predation from the seedfall, mouse and predator fluctuations in beech forests. New Zealand Journal of Zoology, 23, 287–293.

Ostfeld, R.S. and Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution, 15, 232–237.

Parry, N.E. 1931. On the flowering of bamboos. Journal of the Bombay Natural History Society, 34, 1099–1101.

Rana, B.D. 1994. Strategies for rodent management in NFH region with special reference to bamboo flowering areas. Rodent Newsletter, 18, 12–15.

Roder, W. (ed.) 2001. Slash-and-burn rice systems in the hills of northern Lao PDR: description, challenges, and opportunities. Los Banos, Philippines, International Rice Research Institute, 201 p.

Roder, W., Phengchanh, S., Keoboualapha, B. and Maniphone, S. 1995. *Chromolaena odorata* in slash-and-burn rice systems of Northern Laos. Agroforestry Systems, 31, 79–92.

Schiller, J.M., Douangboupha, B. and Bounnaphol, O. 1999. Rodents in agriculture in Lao PDR—a problem with an unknown future. In: Singleton, G.R., Hinds, L.A., Leirs, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 372–387.

Singh, Y.P., Kumar, D. and Gangwar, S.K. 1994. Status paper on rodents of North Eastern Hill Region and their management. Rodent Newsletter, 18, 3–11.

Singleton, G.R. and Petch, D.A. 1994. A review of the biology and management of rodent pests in Southeast Asia. ACIAR Technical Report No. 30. Canberra, Australian Centre for International Agricultural Research, 65 p.

Sisophanthong, B. and Taillard, C. 2000. Atlas of Laos. The spatial structures of economic and social development of the Lao People's Democratic Republic. Chiangmai, Thailand, Silkworm Books, 160 p.

Soderstrom, T.R. and Calderón, C.E. 1979. A commentary on the bamboos (Poaceae: Bambusoideae). Biotropica, 11, 161–172.

Wolff, J.O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of Mammalogy 77, 850–856.

Yue, S. 2001. A statistical measure of severity of El Niño events. Stochastic Environmental Research and Risk Assessment, 15, 153–172.

Zubair, L. 2002. El Niño–Southern Oscillation influences on rice production in Sri Lanka. International Journal of Climatology, 22, 249–260.

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).

References

Amori, G. and Gippoliti, S. 2001. Identifying priority ecoregions for rodent conservation at the genus level. Oryx, 35, 158–165.

Carleton, M.D. 1984. Introduction to rodents. In: Anderson, S. and Jones, J.K., ed., Orders and families of recent mammals of the world. New York, John Wiley and Sons, 255–265.

Carleton, M.D. and Musser, G. 1984. Muroid rodents. In: Anderson, S. and Jones, J.K., ed., Orders and families of recent mammals of the world. New York, John Wiley and Sons, 289–379.

Castresana, J. 2001. Cytochrome b phylogeny and the taxonomy of great apes and mammals. Molecular Biology and Evolution, 18, 465–471.

Corti, M. 2001. Rodent taxonomy at the end of the 20th century. Bulletin Institut Royal Sciences Naturelles Belgique, 71 (suppl.), 17–33.

Faith, D.P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation, 61, 1–10.

Graur, D., Hide, W.A. and Li, W.-H. 1991. Is the guinea-pig a rodent? Nature, 351, 649–652.

Groves, C.P. 2001. Primate taxonomy. Washington, Smithsonian Institution Press, 350 p.

Haring, E., Herzig-Straschil, B. and Spitzenberger, F. 2000. Phylogenetic analysis of alpine voles of the *Microtus multiplex* complex using the mitochondrial control region. Journal of Zoological Systematics and Evolutionary Research, 38, 231–238.

Honacki, J.C., Kinman, K.E. and Koeppl, J.W. 1982. Mammal species of the world. A taxonomic and geographic reference. Lawrence, KA, Allen Press and Association of Systematic Collections, 694 p.

Kitchener, D.J., How, R.A. and Maharadatunkamsi 1991. *Paulamys* sp. cf. *P. naso* (Musser, 1981) (Rodentia: Muridae) from Flores Island, Nusa Tenggara, Indonesia—description from a modern specimen and a consideration of its phylogenetic affinities. Records West Australian Museum, 15, 171–189.

Matthee, C.A. and Robinson, T.J. 1997. Molecular phylogeny of the springhare, *Pedetes capensis*, based on mitochondrial DNA sequences. Molecular Biology and Evolution, 14, 20–29.

Michaux, J., Reyes, A. and Catzeflis, F. 2001. Evolutionary history of the most speciose mammals: molecular phylogeny of muroid rodents. Molecular Biology and Evolution, 18, 2017–2031.

Purvis, A. and Hector, A. 2000. Getting the measure of biodiversity. Nature, 405, 212–219.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. and Cosson, J.-F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. Molecular Ecology, 7, 453–464.

Wilson, D. E. and Reeder, D.M. 1993. Mammal species of the world. A taxonomic and geographic reference, second edition. Washington and London, Smithsonian Institution Press, 1206 p.