SYMPOSIUM 7: MANAGEMENT—URBAN RODENTS AND RODENTICIDE RESISTANCE

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Ecological perspectives on the management of commensal rodents

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Abstract. The need to control Norway rats in the United Kingdom has led to heavy reliance on rodenticides, particularly because alternative methods do not reduce rat numbers as quickly or as efficiently. However, such reliance has led to concerns that repeated use of rodenticides poses unacceptable risks to other animals as well as encouraging resistance in the target species. In agricultural areas, frequent use of poison baits is unavoidable when control is concentrated on individual, resource-rich patches, such as farm buildings, because even if total elimination is achieved, reinvasion is inevitable. Population density is highest around buildings during winter when food supplies are most abundant and locations for baits most restricted. Control can be improved by, for example, changing the location of food sources within buildings, so that the environment is less predictable to rats. Rats with the smallest home ranges are most likely to succumb to rodenticide treatment, but those with the largest ranges who nevertheless consume poison bait may pose the greatest risk to predators. Populations reduced to very few animals may take two years or more to recover to their previous levels if there are no nearby reservoir colonies. Not surprisingly, recovery can be severely impeded by limiting the food supply, but in practice the resources of food and harbourage can rarely be controlled to a significant degree on a working farm. Consequently, reducing cover to expose rats to increased predation risks is practicable, but the most successful control strategy necessitates breaking links between populations in resource-rich patches. This may be achieved by treating several patches simultaneously, as well as removing rats in transit between them. Although the initial control may be carried out with rodenticides, the need for subsequent treatments using poison baits should be greatly reduced.

Introduction

The need to control commensal rodents is rarely controversial, as the public has always associated rats, in particular, with lethal, disease-causing organisms, such as bubonic plague. While plague has long been absent from some countries, including the United Kingdom (UK), the potential health threat from commensal rodents is now focused on other zoonotic diseases, such as leptospirosis (Weil's disease) and salmonellosis. While pressure to control problem populations continues, the means of doing so are coming under closer scrutiny, particularly regarding issues of humaneness and environmental impact, in addition to cost-effectiveness. Nevertheless, control tactics need to reduce rapidly the number of potentially disease-carrying rodents and non-lethal management methods are generally unable to achieve this. For example, repellents at best keep rodents at a distance and at worst push the problem elsewhere, while fertility control might only reduce problems over too long a period. Moreover, for many, the only acceptable level of control that mitigates disease risks is total elimination of the rodent population, an objective that, while ideal, is difficult to prove, let alone achieve. Hence, populations invariably recover, largely because the underlying reasons for the problem population developing in the first place are seldom addressed. As the recovery progresses, at some point re-treatment becomes inevitable, but experience has shown that the same level of control is not guaranteed on subsequent occasions. The dynamics of each new population, including the behaviour and physiology of individuals, are subject to change, not only because of the selection pressure imposed by intensively applied control measures, but also because resources vary in distribution and abundance. In this paper, we use the Norway rat (*Rattus norvegicus*) in rural habitats in the UK as a model to illustrate how these ecological processes influence the effectiveness and safety of commensal rodent management strategies.

The Norway rat first arrived in the British Isles nearly 300 years ago, then spread rapidly and largely displaced the ship rat (*Rattus rattus*) that had been present since Roman times. Today, the Norway rat in rural areas is seen predominantly as a storage pest that exploits supplies of harvested cereals, root crops and livestock feeds to be

found in farm buildings. It also lives along field margins but rarely digs burrows in the fields. Changes in the agricultural landscape that came with increasing mechanisation resulted in loss of harbourage for rats as field boundaries were ploughed up to make larger fields. Consequently, the significant damage that the rats reportedly caused to standing crops is now negligible. Despite being a relatively recent arrival and its association with human activities, the species can survive independently in the UK, but large (damaging) populations seem to occur only on working farmsteads with abundant resources. While much of their food may be found indoors, rats prefer to nest in burrows dug in undisturbed ground between buildings or along adjacent hedgerows and ditches. Control measures seem to be particularly successful if they intercept rats before the animals reach their food source and the most extreme form of interception is to dispense poison bait directly into the burrow (Quy et al. 1996). However, active burrows are not always easy to find and rats are also highly mobile (Taylor and Quy 1978), such that some burrows may be 1 km or more away from food sources.

Controlling Norway rats presents similar challenges to achieving successful control of other commensal rodents. The most practicable technique on farmsteads is to use rodenticide bait, but the animals live in a complex, three-dimensional habitat where attractive food is, for weeks at a time, virtually unlimited and where places to put the bait may be restricted. Under such circumstances, bait may be totally ignored while damage and contamination continue unabated. However, the food supplies can also 'disappear' suddenly and there may be little time to intensify baiting before the rats disperse. Harbourage is always available, although it often varies in quantity, quality and distance from food sources. Control measures are usually instigated on farms when the population reaches some arbitrary nuisance or damage threshold, but it is only when such measures fail that the number of rats which can be supported by farmstead habitats is shown to greatly exceed the numbers previously considered to be too high. As rat population density increases, it sometimes becomes impossible to lay the required amounts of bait and efficacy is reduced or treatments prolonged. In this paper, we will consider the ecological factors that affect the efficacy of rodenticide use, in particular those that determine population size, ranging behaviour and the rate of recovery. Placing the operation of control measures in an ecological context should, at the very least, prevent much wasted effort and at best achieve maximal control with minimal risk to other species.

Materials and methods

Data sets

Data on the size of rat populations living in and around farm buildings were collected during all seasons from a total of 102 farms in three counties of the UK: Sussex (n = 24), Hampshire (n = 24) and North Yorkshire (n = 54) between 1990 and 2000. The predominant activity on the Hampshire farms was cereal growing (67%), livestock rearing on those in North Yorkshire (61%), and 42% livestock/42% arable on the Sussex farms. Farming activity on one site in Hampshire, four in Sussex and eight in North Yorkshire was classified as mixed. The location and type of stored food accessible to rats on each farm was recorded. Rats in Hampshire were typically warfarin-resistant with some resistant to difenacoum and bromadiolone also, while rats in Sussex were mostly anticoagulant-susceptible (Cowan et al. 1995); resistance to anticoagulants has also been found in North Yorkshire rats. Population size was estimated immediately before a rodenticide treatment using a calibrated tracking plate technique (Quy et al. 1993). Briefly, tracking plates were evenly spread across each site at a nominal density of 400/ha. The area of each plate covered with rat footprints was given a score and summing the scores gave an index of total rat activity. A mean of 3–4 consecutive daily total scores was then converted via a calibration curve to give an estimate of rat population size.

The ranging behaviour of rats was recorded between 1994 and 1996 on two farms in the county of Warwickshire as part of a study investigating the role these rodents play as vectors of cryptosporidiosis (Quy et al. 1999). Adult rats of >300 g living in and around cattle sheds and those living along field margins on an arable farm 5 km away were fitted with radio-transmitters that also contained mortality sensors. Each tagged rat was tracked intensively for a week approximately every 4 weeks until the animal died, was lost, or the tag came off. Fixes were obtained every 6 hours and a home range was calculated by the minimum convex polygon method for each rat with >10 fixes. Every effort was made to recover animals that had apparently died in order to determine the cause of death. Anticoagulant treatments were carried out periodically on the livestock farm by the farm staff, but no control was carried out along the field margins on the other farm.

The rate of recovery of 20 rat populations in the county of Surrey in south-eastern England was monitored at 2-monthly intervals for approximately one year between 1976 and 1979. Each population was reduced by an acute rodenticide and, where necessary, an anticoagulant to eliminate as far as possible every rat. Hence, reinfestation should have arisen largely by reinvasion rather than by surviving residents reproducing. All treatments were conducted against rats living in and around farm buildings and the degree of control was assessed independently by tracking plates laid before and after treatment. The plates were set out as described above, but rat footprints were recorded as present or absent only and thus gave an index of numbers. Recovery rates were calculated as a percentage of the pre-treatment track score. The same tracking plate positions were used each time a recovering rat population was monitored. The distribution of stored food on each farm was recorded during each monitoring period, along with any major structural alterations that might have affected the ability of rats to recolonise the farm.

Methods of management

The application of rodenticide baits, especially anticoagulant formulations, has become the first, last and only means of controlling rats for many in the UK. Products containing the second-generation anticoagulants difenacoum and bromadiolone now dominate the market, with use of the less potent, first-generation compounds declining. Despite their advantage in controlling warfarin-resistant rats, the more potent anticoagulant baits did not markedly reduce treatment length, leading to speculation about social factors delaying approaches to bait stations. Although resistance has developed to second-generation compounds, it has not, with some notable exceptions, fully explained the poor efficacy that sometimes occurs. Population size differences and the presence of alternative food have been more convincing explanations (Quy et al. 1992a,b). To control rats highly resistant to anticoagulants, zinc phosphide and calciferol formulations are available. Other control methods, such as trapping, fumigation of burrows and contact formulations are suitable only in specific circumstances or to eradicate small numbers of rats. Proofing of buildings to prevent rodent entry is rarely considered cost-effective and physical barriers often seem incompatible with modern methods of bulk-handling grain and other commodities.

Results and discussion

Ecological determinates of population size

Rat population changes are closely tied to the agricultural cycle; in a northern-hemisphere temperate climate this consists of harvesting cereals, such as wheat and barley, in July–August. Fields are ploughed in September–November and then re-sown with winter cereal varieties; spring cereals are sown in February. Harvested grain is transferred from the fields to purpose-built or makeshift silos/clamps/grain bins to be dried and where it may remain throughout September to March, until it is sold. Usually, all of the previous year's harvest is removed by early spring (April/May) and the grain storage areas are cleaned out ready for the next harvest. Rat activity in standing crops increases noticeably during late May–June as the cereals begin to ripen. The average size of rat populations around farm buildings did not vary across the seasons, although the density did (Table 1). Density increased sharply after harvest in late summer and early autumn, perhaps as animals followed the food from the fields to the buildings. In summer, field populations of rats were likely to be at their highest. It was also likely that reproductive rates of rats around buildings increased to take advantage of the concentrated resources. The greatest density of rats coincided with the smallest infested area and probably reflected the reduced cover to be found outside buildings, as vegetation was either killed by frosts or stopped growing. The lowest density occurred in late winter/early spring, as deaths presumably exceeded births at this time. Huson and Rennison (1981) also recorded a similar pattern of activity after examining changes in infestation rates on agricultural premises.

In contrast to arable farms, stored food is often permanently available where livestock are kept, particularly dairy cattle and pigs reared indoors. Beef and dairy cattle are often kept indoors over winter, but are released into the fields in spring. The pens where these animals have been kept are then cleaned out, displacing any rats in the process. Mixed farms, which perhaps offered the greatest range and abundance of food throughout the year, had a higher average rat population density than the other two farm types (Table 2).

Regional differences were also apparent between southern (Hampshire/Sussex) and northern (North Yorkshire) England, with smaller populations in the northern county (Table 3). However, the average infested area was significantly smaller in the Yorkshire sample, resulting in higher densities than in the southern counties. The reason for the difference is uncertain, but might have been related to the larger proportion of pig rearing farms in the Yorkshire sample. Such farms offered greater scope for rat numbers to grow, as the buildings were often constructed with hollow walls and false ceilings, in contrast to the relatively open-plan nature of those holding cattle. Population density is of particular importance for the dynamics of zoonotic diseases where maintenance of infection is dependent on contact rates between animals.

Table 1. Comparison between rat populations in and around farm buildings with respect to season in terms of area infested, population size and population density. Data are means ± sd. The infested area was calculated by the number of tracking plates laid at the predetermined density of 400/ha (ANOVA = analysis of variance, NS = not significant).

Season	*n*	Area infested (ha)	Population size	Population density (*n*/ha)
February–April	32	0.223 ± 0.103	82.5 ± 63.1	373.8 ± 211.0
May–July	19	0.141 ± 0.060	57.3 ± 41.3	400.7 ± 203.2
August–October	38	0.204 ± 0.122	109.3 ± 99.6	513.0 ± 256.6
November–January	13	0.114 ± 0.041	76.2 ± 48.8	635.4 ± 237.4
One way ANOVA	df 3,101	F 5.4, $P = 0.002$	F 2.24, NS	F 5.05, $P = 0.003$

Table 2. Comparison between rat populations in and around farm buildings according to farm type in terms of area infested, population size and population density. Data are means ± sd (ANOVA = analysis of variance, NS = not significant).

	Arable	Livestock	Mixed	One way ANOVA
n	39	50	13	
Area infested (ha)	0.215 ± 0.125	0.164 ± 0.082	0.187 ± 0.11	F 2.67 df 2,101 NS
Population size	92.5 ± 68.8	74.1 ± 63.1	119.8 ± 125.4	F 2.06 df 2,101 NS
Population density (*n*/ha)	445.1 ± 214.0	438.4 ± 230.6	619.3 ± 334.0	F 3.14 df 2,101 *P* = 0.048

Table 3. Comparison between rat populations living in and around farm buildings in Yorkshire and those living similarly in Hampshire/Surrey in terms of area infested, population size and population density. Data were collected during all seasons between 1990 and 2000. Data are means ± standard deviation (ANOVA = analysis of variance).

n	Yorkshire	Hampshire/Sussex	One way ANOVA
	54	48	
Area infested (ha)	0.119 ± 0.050	0.263 ± 0.100	F 87.12 df 1,101 *P* < 0.001
Population size	66.2 ± 53.7	110.4 ± 90.5	F 9.219 df 1,101 *P* = 0.003
Population density (*n*/ha)	523.0 ± 249.0	397.7 ± 224.1	F 70.69 df 1,101 *P* = 0.009

Ecological determinants of management effectiveness

It seems obvious that total removal of the food supply would control rats without recourse to rodenticide use, but in reality supplies can rarely, if ever, be so restricted on a working farm that rats are denied any access. Thus, rodenticide baits will invariably be competing with other foods for the rats' attention and in one study of anticoagulant effectiveness, 12 populations were reduced within 7 weeks by a mean of only 24% when stored cereals were present, but by 75% (n = 19) when such cereals were absent (Quy et al. 1992a). However, a change in the distribution of stored cereals, not involving their complete removal, led to greater control (mean 62%, n = 8). Such change often meant little more than relocation of grain within a building, thus suggesting that predictability of supply was more important than its abundance or continuity and that creating controlled habitat disturbances would encourage rats to approach baits. In this respect, rats are more likely to consume bait on livestock farms, because the movement of farm animals and high turnover of feed gives a degree of inherent habitat instability (Quy et al. 1994).

Poison baits intended to control commensal rodents are applied as spot treatments and are never broadcast. When setting up rodenticide treatments, it is therefore simplest to distribute baits according to the density of rat signs rather than the movements of individuals, which cannot easily be determined. Animals that have home ranges larger than the size of the treated area may not encounter bait often enough to maximise treatment efficiency. Equally, as the density of signs decreases, the spacing between baits is likely to increase, reducing the likelihood that such baits will intercept rats with large ranges. From the perspective of the efficacy and safety of rodenticide use, the ranging behaviour can reflect the likely fate of rats. The observed ranges of four rats living in and around farm buildings were remarkably small (<0.1 ha), some moving no more than 20 m from a nest, presumably to and from their food supply; these animals succumbed to an anticoagulant rodenticide, as confirmed by signs of haemorrhage on recovery of their bodies (Table 4). Away from farm buildings, resources are often more widely dispersed and rat signs are therefore less concentrated: 11 rats that survived for up to 3 months between collar attachment and the battery failing had a mean observed range of 0.2 ha. However, rats sometimes move long distances, greater than perhaps necessary to find sufficient resources (Taylor and Quy 1978), involving journeys into probably less-familiar parts of their range. Predators (mostly foxes and dogs) killed six rats with the largest home ranges (mean 1 ha). Despite small sample sizes, the differences between the ranges for the three groups shown in Table 4 were significant (Kruskal–Wallis non-parametric analysis of variance,

$\chi^2 = 8.71$ 2 df, $p = 0.03$). These data suggest that rodenticide efficacy is enhanced if rats have ranges smaller than the treated area and, provided predators seldom venture near farm buildings, the risk of secondary poisoning might be relatively small. In contrast, poisoned rats whose ranges extend outside the treated area may have sufficient time to move into a predator's territory, given the delay between ingesting a lethal dose of anticoagulant and death. An inference that may also be drawn from these data is that manipulating habitat features to modify range size might enhance the effectiveness of particular management techniques.

Table 4. Fate of radio-collared rats in relation to home range size on two farms in the county of Warwickshire, United Kingdom. Individuals were tracked for up to 3 months (the life of the transmitter battery) between 1994 and 1996. Data are means ± sd.

Fate	*n*	Home range size (m^2)
Survived till recapture or transmitter battery failure	11	1954.5 ± 2470.4
Predated	5	9580.0 ± 7761.0
Rodenticide	4	450.3 ± 420.0

Ecological effects on population recovery

While ranging behaviour provides an ecological context for efficacy and risk assessment, it also can explain the recovery of rat populations during and after treatments. The influence of adjacent hedgerow populations on the efficacy of treatments around farm buildings was to extend the period of bait exposure in order to achieve the equivalent level of success on those farms without hedgerow populations (Quy et al. 1992b). It was impractical to treat the adjacent infestations simultaneously with those in the buildings and the prolonged treatments probably reflected continual reinvasion that replaced animals succumbing to the poison. Hedgerow populations of rats are particularly common in the eastern half of the UK, where cereal growing predominates.

Conceptually, the rate of recovery is a function of productivity of any residual population and reinvasion into the target habitat, which should diminish as the distance from reservoir populations increases. These processes were explored when 20 rat populations were reduced/eliminated from farms in south-eastern England in a mixed-farming area of cereal growing and pasture and with relatively insignificant numbers of rats along field margins. On one farm, putative immigrants were trapped and removed every 2 months and on two others data were incomplete. The rate of recovery of 17 farm rat populations showed an approximately linear increase over 12–14 months (Figure 1). (Data were insufficient to examine seasonal effects.) Assuming the trend remained linear, the projected mean time to full recovery (i.e. to the size of the initial population) was 27 months. Given the high intrinsic rate of increase of Norway rat populations, recovery seemed to be surprisingly slow and suggested that in this area, by accident or design, ecological factors constrained growth. To illustrate this, two populations with very different recovery rates were selected from the sample (Figure 2). Both were first treated at approximately the same time of year (summer), but there was very little stored food to support the rats on the arable farm during this pre-harvest period. However, seemingly unlimited supplies of food for dairy cattle supported a much larger population on the livestock farm. Post-treatment, both residual populations were of similar size, but that on the arable farm recovered to its pre-treatment level within 2 months as harvested grain was stored in open-topped bins. In contrast, over an extended monitoring period, rat numbers failed to recover (but did not disappear entirely) on the livestock farm, probably because structural alterations to the buildings made any stored food less accessible. In this case, restricting resources did not stop rats invading the farm, but it did reduce the carrying capacity and hence probably prevented significant recolonisation. Given the unlimited food on the arable farm, it was not surprising that a subsequent poison treatment carried out by the farmer had a minimal effect. While these examples present a simple and perhaps self-evident ecological concept, its significance seems to have been lost for many who now rely exclusively on rodenticide use for Norway rat management.

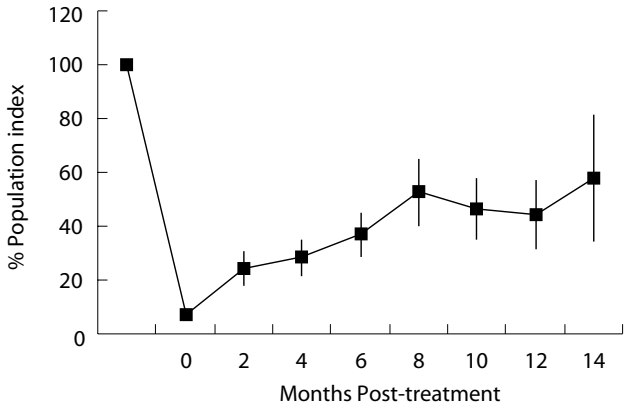

Figure 1. Recovery of rat populations following rodenticide treatment on 17 farms. An index of the post-treatment population size for each farm was derived from tracking plate scores expressed as a percentage of the pre-treatment size (mean ± se).

Ecologically based management strategies

Currently, the economics of rodent control in the UK favour rodenticide use, and to reduce large numbers of rats quickly, its utility is unquestionable. However, repeated use of rodenticides can be avoided if the underlying reasons for population recovery and movements are understood. One approach is to consider rats having a metapopulation structure, whereby they occupy the whole agricultural landscape with population subunits concentrated in resource-rich patches. Transfer between patches takes place along linking corridors, such as hedgerows and ditches. Breaking these links effectively isolates the

patches, although in lowland agricultural areas patches (e.g. farmsteads) can be so close as to fall within the normal home range of many rats. To counteract this problem, the best tactic might be to treat several neighbouring farmsteads simultaneously, thereby removing obvious sources of immigrants. This is contrary to present rodent control practice, which typically focuses on an individual group of farm buildings as this represents (commercially) an easily definable habitat to treat. Such control will inevitably fail long-term because of reinvasion and compensation (density-dependent birth/death rates). To keep rat numbers low in the individual patches post-treatment, it is unlikely, except on rare occasions, that the food supply or harbourage can be controlled. More practicable perhaps is to reduce the cover between the harbourage and food source, thus increasing the risk of predator attack. A recent study by the Central Science Laboratory (unpublished) followed the fate of 13 radio-tagged rats living around farm buildings where the ground cover (e.g. vegetation) was kept permanently short and 18 tagged rats where the cover was untouched. Over a 30-day period, 10 rats in the cleared areas moved away or died with three confirmed predator kills. In the uncleared areas, 10 animals remained *in situ* with only one confirmed predator kill.

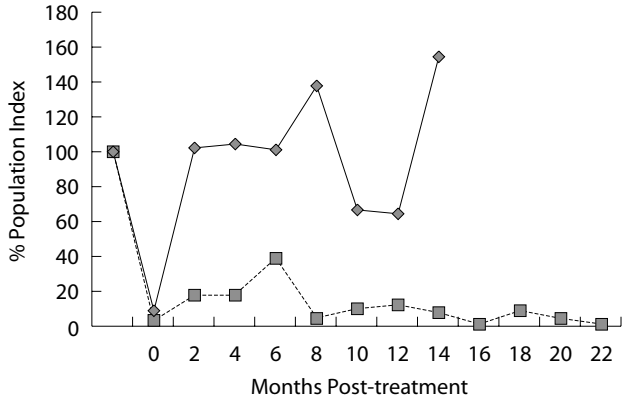

Figure 2. Recovery of rat populations depends on access to food. Numbers recovered rapidly on the arable farm (solid line) after control in June because bulk stores of harvested grain were accessible to rats shortly after the initial treatment and remained so for 12 months. After 8 months, the farmer, concerned about increasing levels of contamination, carried out a treatment, which had a short-lived effect on numbers. In contrast, on the livestock farm (dashed line) after control in August, food was constantly present between 4 and 22 months, but rats were denied easy access to it.

Habitats, such as field margins, which link the patches together support less dense, perhaps ephemeral populations that cannot be controlled cost-effectively and hence are usually ignored. Removing hedgerows and filling ditches might isolate patches, but would conflict with current initiatives to enhance biodiversity by restoring lost hedgerows. The alternative is to intercept animals in transit by creating an artificial resource-rich patch that will attract them, rather than wait for a chance encounter with a trap or bait point. Once there, they can be removed by any humane method. This strategy is similar to the trap–barrier system developed to control rats in the tropics (Singleton et al. 1999). If successful, this strategy would both attract dispersing rats before they settle in farm buildings and also reduce connectance between local populations, perhaps making eradication over large areas feasible. Such an approach would be especially useful in combating anticoagulant resistance and thus needs to be evaluated as a practical management strategy for whole rural rat populations.

Conclusions

New rodenticides are unlikely to be developed in the foreseeable future that will alleviate all public concerns about humaneness and non-target effects. In the meantime, current formulations will continue to be used until either resistance in the target species or restrictions on their use lead to product withdrawal. A more strategic application of rodenticides, along with other measures, has been suggested above that takes account of the potential mobility of rats and the ability of populations to recover when resources are seemingly unlimited. If effective, the strategy should minimise re-application of rodenticides once established populations are brought under control, given that lowland agricultural environments in the UK will always be habitable by Norway rats. This should retain the effectiveness of rodenticides whilst also minimising potential adverse environmental consequences of their use.

References

Cowan, D.P., Dunsford, G., Gill, J.E., Jones, A., Kerins, G.M., MacNicoll, A.D. and Quy, R.J. 1995. The impact of resistance on the use of second-generation anticoagulants against rats on farms in southern England. Pesticide Science, 43, 83–93.

Huson, L.W. and Rennison, B.D. 1981. Seasonal variability of Norway rat (*Rattus norvegicus*) infestation of agricultural premises. Journal of Zoology, 194, 257–260.

Quy, R.J., Cowan, D.P., Haynes, P., Inglis, I.R. and Swinney, T. 1992a. The influence of stored food on the effectiveness of farm rat control. In: Proceedings of the Brighton Crop Protection Conference—Pests and Diseases, Brighton, 23–26 November 1992. Farnham, Surrey, The British Crop Protection Council, 291–300.

Quy, R.J., Cowan, D.P., Haynes, P., Inglis, I.R. and Swinney, T. 1994. Predicting the outcome of rodenticide trials against Norway rats living on farms. In: Halverson, W.S. and Crabb, A.C., ed., Proceedings of the 16th Vertebrate Pest Conference, Santa Clara, 1–3 March 1994. Davis, California, University of California, 133–137.

Quy, R.J., Cowan, D.P., Haynes, P.J., Sturdee, A.P., Chalmers, R.M., Bodley-Tickell, A.T. and Bull, S.A. 1999. The Norway rat as a reservoir host of *Cryptosporidium parvum*. Journal of Wildlife Diseases, 35, 660–670.

Quy, R.J., Cowan, D.P., Morgan, C. and Swinney, T. 1996. Palatability of rodenticide baits in relation to their effectiveness

against farm populations of the Norway rat. In: Timm, R.M. and Crabb, A.C., ed., Proceedings of the 17th Vertebrate Pest Conference, Rohnert Park, 5–7 March 1996. Davis, California, University of California, 133–138.

Quy, R.J., Cowan, D.P. and Swinney, T. 1993. Tracking as an activity index to measure gross changes in Norway rat populations. Wildlife Society Bulletin, 21, 122–127.

Quy R.J., Shepherd, D.S. and Inglis, I.R. 1992b. Bait avoidance and effectiveness of anticoagulant rodenticides against warfarin- and difenacoum-resistant populations of Norway rats (*Rattus norvegicus*). Crop Protection, 11, 14–20.

Singleton, G.R., Sudarmaji, Jumanta, Tran Quang Tan 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 rodent management. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 178–198.

Taylor, K.D. and Quy, R.J. 1978. Long distance movements of a common rat (*Rattus norvegicus*) revealed by radio-tracking. Mammalia, 42, 63–71.

Managing rodent pests in households and food stores through intensive trapping

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Abstract. Field trials involving 1200 rural households from three villages (Pinda, Mutange and Mugaveia) in Mozambique were established to test whether intensive daily trapping inside household-level food stores could effectively reduce rodent pest populations. The species caught inside dwellings where food was stored were *Rattus rattus* [*alexandrinus*] and *Mastomys natalensis*. The proportion of each species caught varied among the three villages and over the 16-month duration of the trial. *R. rattus* was more abundant inside households in Pinda and Mutange; whereas *M. natalensis* was more abundant inside homes in Mugaveia. Pregnant females of both species were caught throughout the year, showing no clear breeding seasonality. Householders that trapped rodents inside their house on a daily basis were able to significantly reduce the level of infestation when compared with householders who did no rodent management. The level of population reduction among households in the same village was similar, but the degree of reduction significantly varied among the three villages. The average weight of *R. rattus* trapped inside households through intensive trapping declined by 40% when compared with those caught in households that did not intensively trap; however, no significant weight difference was noted in populations of *M. natalensis*. The population reduction caused by intensive trapping was maintained over the duration of the trial, and assessments of food stocks indicated that food remained in store up to 3 months longer, with loss assessments indicating savings of 30–40% when compared with households in which rodents were not controlled. The implications of these results are discussed in the context of implementing ecologically based rodent management strategies for poor rural communities in Africa.

Introduction

Ecological studies and the control of rodent pests in rural agricultural settings have largely involved the use of rodenticides (Makundi et al. 1999). However, especially in rural parts of Africa, there are several constraints to their use. Primarily, rodenticides are not affordable for the rural poor who are most affected by rodent pests. Even when rodenticides are widely available, they are often used inappropriately, leading to low efficacy and to health and environmental risks. Recently, there has been an increased effort to apply our understanding of rodent population dynamics to develop more ecologically based methods of rodent management (Singleton et al. 1999).

Most households in Mozambique traditionally store their food inside their dwelling for security and spiritual reasons. However, this storage practice makes it difficult to exclude rodents from the food store, exacerbating food losses and contamination caused by rodents. Rural extension programs have tried to introduce separate food storage structures to the area, but adoption and uptake have been limited. Farmers in Zambezia province have indicated that stored food losses by rodents can be severe and have prioritised rodent pests as one of their most important constraints to improving their livelihoods (Taylor and Phillips 1995). In addition to food losses, recurrent outbreaks of plague (*Yersinia pestis*) occur in parts of Mozambique, and preliminary studies have shown that leptospirosis (*Leptospira icterohaemorrhagiae*) prevalence (IgG) can be as high as 17% (Thompson et al. 2002).

The development of ecologically based rodent management strategies that are affordable and easily implemented by the rural poor of Africa could substantially improve public health and local economies. The objectives of our research have been to test management strategies that attempt to reduce rodent pest problems in rural areas. Although some researchers have argued that trapping is an ineffective means of population management (Buckle and Smith 1994), previous research has shown that trapping can, under some circumstances, be an effective method of rodent management in field crops (Gebauer et al. 1992; Tobin et al. 1993) and grain markets (Ahmad et al. 1995). In this paper, we test whether trapping can significantly reduce local populations under the high density of rodents found in household-level food stores in Mozambique.

Materials and methods

Three villages in different districts of Zambezia province, Mozambique, were selected for involvement in the trials based on reports from farmers indicating that rodents were a significant pest problem, particularly after harvest when crops are stored within the dwelling. The village of Mutange in Namacurra district lies within a flat lowland rice-growing area, the village of Pinda in Morrumbala district is in a highland plateau maize-growing area and the village of Mugaveia in Gurué district is in a mountainous mixed forest–cropland area. Each village has approximately 400 domestic dwellings which typically consist of a mudded timber-frame rectangle (approx. 4 × 5 m) with a grass or palm-leaf thatched roof. The open-plan interior contains a raised platform where food is stored, a cooking fire and a sleeping area for approximately eight people.

Each village was divided into two portions, one half acting as the treated area and the other as the untreated area (experimental control). The 200 households in the treated area were each given 10 break-back traps (big snap-e-trap™, Kness Manufacturing Ltd, USA), with all 10 traps placed in the dwellings along interior walls and walkways, especially in places where food is usually stored. Farmers were given individual training on the operation of the traps and instructions to set them each evening. Dwellings in the treated area of the three villages were visited each morning, and the number of rodents trapped the night before were recorded daily for the duration of the trial (November 2000 to March 2002). Householders in the untreated area did nothing to manage their rodent problems over this time, and every month a subset of 30 households was randomly selected from this area and the occupiers set traps in the same manner as in the treated dwellings but over three nights only. The number of rodents caught during these three nights from households in treated and untreated areas was recorded, including their sex, weight, species, and whether any females caught were observed to be pregnant. Representative samples of each species were collected for later taxonomic identification. The number of rodents caught among farmers and villages was analysed by analysis of variance (ANOVA) with a post-hoc least significant difference (LSD) test to separate the mean values. Comparisons between treated and untreated areas in the same village were analysed using an independent sample *T*-test evaluating the number of rodents caught and their average weights. The potential interactions between populations of *R. rattus* and *M. natalensis* within each village were evaluated by linear and non-linear regression models using the data obtained on the total number of each species caught in each household during the trial.

A subsample of 10 randomly chosen farmers in each treated and untreated area in Pinda was selected to store 5 kg of their maize cobs in an open-topped basket. The basket of commodity was placed in the same area of food storage as the main household stocks over the usual storage period (May to December 2001), and householders were instructed not to remove any cobs from the basket. The baskets were weighed every 4 weeks from May to December 2001. Maize cobs were assessed for rodent damage by counting the number of missing maize grains on 10 randomly chosen maize cobs from each basket every 4 weeks and calculating the percentage of missing grains per cob. Data from treated and untreated areas were evaluated using the non-parametric Mann–Whitney *U*-test.

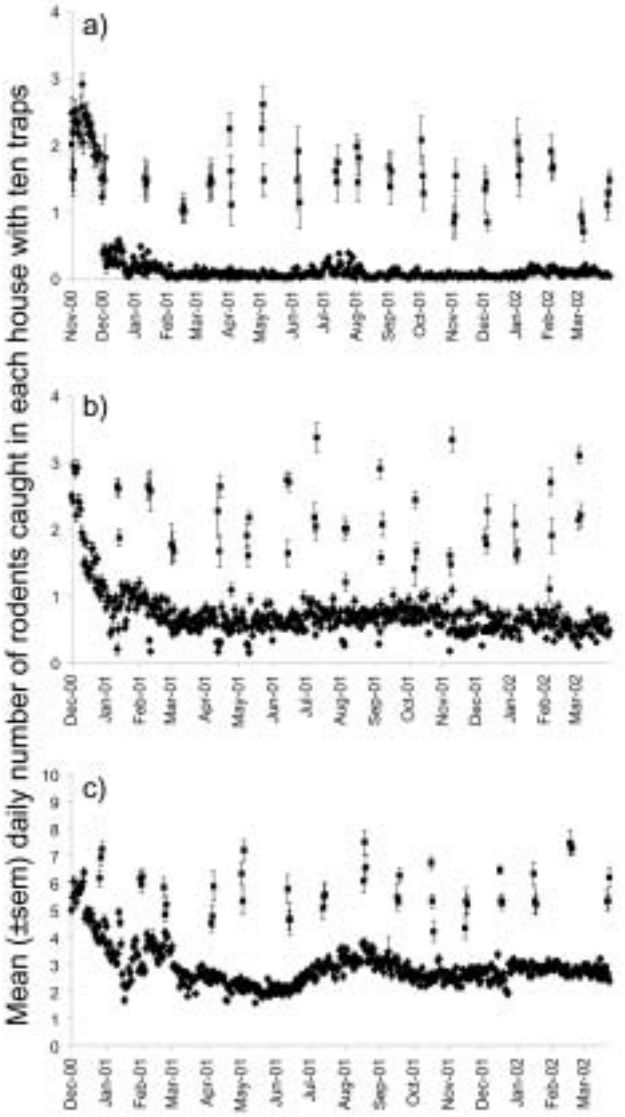

Figure 1. Comparison between the mean number of rodents caught by householders setting ten break-back traps each night (treated = ◆, $n = 200$) and householders that did no rodent management, but where a sample of rodents were trapped over three nights each month from a different sub-set of houses (untreated = ■, $n = 30$) in the villages of a) Pinda, b) Mutange and c) Mugaveia.

Results and discussion

The mean daily catch rate by each householder continuously trapping significantly varied among farmers in the same village (ANOVA with LSD, $P < 0.01$) and among the three villages (ANOVA with LSD, $P < 0.01$).

However, the daily number of rodents caught in households in the same village was relatively similar compared with the numbers caught among the three villages (Figure 1). Higher numbers of rodents were caught during the first month of intensive trapping in all three villages (2.47 ± 0.05, 1.24 ± 0.04, 3.98 ± 0.07 rodents/day/dwelling (mean ± sem) in first 30 days of trapping in Pinda, Mutange and Mugaveia, respectively) when compared with the number of rodents caught in subsequent months (ANOVA with LSD, $P < 0.01$). The decline in the number of rodents caught was most pronounced in Pinda, where relatively few rodents were caught after the first month (0.08 ± 0.002 rodents/day/dwelling over the next 15 months of the trial), followed by Mutange and Mugaveia (0.66 ± 0.006 and 2.78 ± 0.01 rodents/day/dwelling, respectively). The two species, *Rattus rattus* and *Mastomys natalensis*, were present in all three villages and were trapped inside all households (Figure 2). Approximately equal numbers of *R. rattus* and *M. natalensis* were caught in households in Pinda and Mutange, however approximately three times more *M. natalensis* were caught than *R. rattus* in Mugaveia. Linear and non-linear regression analyses showed that the relationship between the number of each species caught within a dwelling was best represented by power regression models for data from Pinda ($F = 215.7$, $r^2 = 0.52$, $P < 0.01$) and Mutange ($F = 176.5$, $r^2 = 0.47$, $P < 0.01$). In these two villages, higher numbers of *R. rattus* were associated with higher numbers of *M. natalensis* (Figure 3). Regression analysis on the data from Mugaveia showed that the relationship between the two species was best represented by a cubic polynomial regression model ($F = 5.15$, $r^2 = 0.42$, $P < 0.01$). The number of each rodent species caught in households in Mugaveia indicated that high numbers of *R. rattus* may regulate the numbers of *M. natalensis* present inside dwellings in this village (Figure 3).

Households within each area of the three villages where continuous trapping did not occur (untreated control) were shown to have greater numbers of rodents inside their houses at each of the 3-day monthly assessments when compared with those where trapping was carried out daily (*T*-test with equal variance not assumed, $P < 0.01$, Figure 1). These households caught approximately twice as many rodents throughout the trial (Figure 1). On average, householders in the untreated area of Pinda caught 1.49 ± 0.26 rodents/day throughout the 16-month trial duration, with 2.11 ± 0.17 and 5.80 ± 0.35 rodents/day caught in Mutange and Mugaveia, respectively. On average, the weight of *R. rattus* caught in untreated dwellings was significantly higher than that of the same species caught in treated dwellings (75.3 ± 1.6 g and 45.9 ± 2.0 g, respectively, *T*-test with equal variance not assumed, $t = 7.46$, df = 30.5, $P < 0.01$). However, there was no significant weight difference between the corresponding samples of *M. natalensis* (untreated = 52.3 ± 3.2 g, treated = 46.5 ± 3.3 g, *T*-test with equal variance not assumed, $t = 1.15$, df = 31.1, $P > 0.05$). No significant differences were noted with respect to changes in the sex ratio of rodents caught between treated and untreated dwellings (Mann–Whitney *U*, $P > 0.05$).

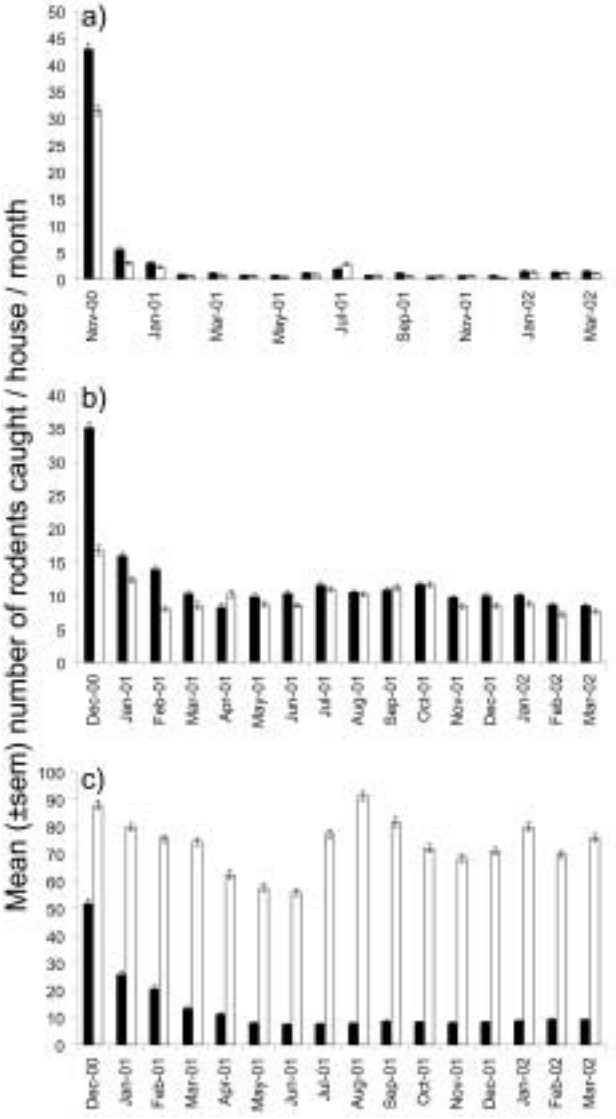

Figure 2. Comparison between the mean number of *Rattus rattus* (■) and *Mastomys natalensis* (❑) caught inside 200 dwellings in traps set by householders each night in the villages of a) Pinda, b) Mutange and c) Mugaveia.

Weight loss of the standard 5 kg baskets of maize was attributed to both rodent and insect damage (Table 1). The main insect pest found in stored maize cobs was the maize weevil, *Sitophilus zeamais*. Damage characteristics to maize caused by insects and rodents are very distinctive, with rodents completely or partially removing grains from the cob, whilst weevils infest grains internally. All missing grains on cobs were attributed to rodent pests. Rodent damage was observed to occur from the outset of the assessment period, whereas weevil damage only became apparent after three or more months of storage. Damage due to rodents was lower in dwellings that intensively trapped compared with dwellings in the untreated areas, while insect damage levels were similar between treated and untreated dwellings. Questionnaires with farmers in

the treated and untreated areas of the village indicated that householders that had been intensively trapping maintained stocks of food for approximately 3 months longer than householders in the untreated area. Farmers that trapped also noted that their food stocks lasted longer when compared with previous years when harvested yields were similar.

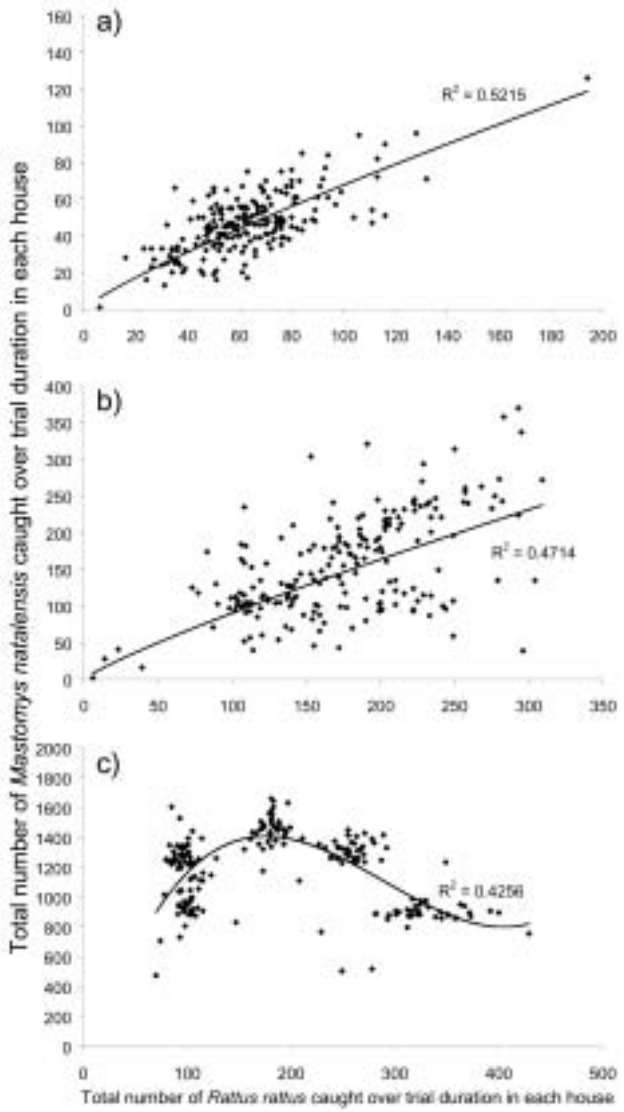

Figure 3. Relationship between the total number of *Rattus rattus* and *Mastomys natalensis* caught inside each dwelling, trapped on a daily basis in a) Pinda, b) Mutange and c) Mugaveia. Regression analysis indicated that data obtained from Pinda and Mutange were best represented by non-linear power models, whereas a cubic polynomial model best represented the data obtained from Mugaveia.

Conclusion

Our study showed that intensive trapping of rodents can effectively reduce their localised population densities within rural African dwellings. Although trapping is labour-intensive, the relatively low cost of inputs and the benefits accrued to the family unit could favour the technique. Household benefits not only included reduced food storage losses as demonstrated in this study, but as rodents are widely eaten by people in Zambezia province, household trapping was seen to provide families with a reliable source of much-needed protein.

At the commencement of the intensive trapping trial, it was not known whether rodent population densities would vary among dwellings or areas. However, it was considered likely that rodent density would be generally dependent upon food availability in the dwelling (Boutin 1990; Krebs 1999). Food stores provide an ideal environment for rodents, offering harbourage and a relatively unlimited food supply. Although building structures and food storage practice were similar in all three villages, there were marked differences in the number of rodents caught among the three villages, the relative abundance of species and in the efficacy of the trapping regime. These differences among the three villages must be related to factors outside the household and to the differing habitats and ecology found in the localities (Ferreira and Aarde 1999). There are two observations that are likely to contribute to these differences. In all three villages, *R. rattus* made nests in the roof thatching of the dwelling, while *M. natalensis* lived in burrows in the fields. Our research on the field trapping of rodents in the area (to be reported elsewhere) indicates that *R. rattus* is very rarely trapped in the bush or in farmers' fields, and the species appears to be predominantly confined to areas of human settlement. Our research would support this difference in nesting behaviour between the two species because *R. rattus* populations appeared to be more susceptible to the trapping program inside dwellings. A second factor likely to be important in explaining the observed differences among the villages is the relative distance between dwellings in the village. Buildings in the village of Pinda were relatively close to each other (50–200 m), whereas buildings in Mugaveia were farther apart (500–1500 m). Our results would suggest that *R. rattus* populations are higher when villages are relatively densely populated, and *M. natalensis* are more prevalent in villages where houses are isolated from each other. In a village such as Pinda, intensive trapping on a community level could have a greater impact because rodent immigration/emigration is reduced and *R. rattus* immigration from the bush will be slow. In a village such as Mugaveia, immigration of *M. natalensis* from the surrounding bush is unaffected by community trapping, and trapping may be relatively less effective in modulating household rodent density. This needs to be tested.

Despite the observed differential efficacy achieved among the three villages, intensive trapping with 10 traps did constrain populations when compared with untreated dwellings in the same area. This was reflected in reduced capture rates and the reduced average rodent weight of *R. rattus* in treated dwellings. A reduced average weight could indicate changes in age structure arising from reduced survival. However, it could be argued that both of these factors are explained by the development of trap-shy animals.

As commonly suggested, long-term development of neophobia could result from an intensive trapping regime

Table 1. Comparison between the cumulative percentage weight loss and percentage damage to 5 kg of maize cobs stored in baskets over 8 months inside dwellings in the village of Pinda where rodents had (treated) or had not (untreated control) been intensively trapped daily (n = 10).

Assessment period (2001)	Weight loss (%) (mean ± sem)		Rodent damage (%) (mean ± sem)		Insect damage (%) (mean ± sem)	
	Treated	Untreated	Treated	Untreated	Treated	Untreated
May	0	0	0	0	0	0
June	2.5 ± 0.04	3.1 ± 0.17	0	1.5 ± 0.03	0	0
July	3.6 ± 0.09	5.1 ± 1.23	0.5 ± 0.01	2.8 ± 0.02	0	0
August	4.1 ± 0.15[a]	12.8 ± 3.07	0.5 ± 0.08[a]	3.4 ± 0.95	0	0.5 ± 0.07
September	8.2 ± 0.96[a]	16.5 ± 3.40	1.4 ± 0.13[a]	6.7 ± 1.26	2.0 ± 0.56	2.8 ± 0.77
October	11.0 ± 1.11[a]	28.3 ± 5.67	3.3 ± 0.77[a]	10.9 ± 3.55	3.1 ± 0.79	3.5 ± 0.92
November	17.0 ± 3.55[a]	46.1 ± 5.45	5.5 ± 0.65[a]	25.0 ± 4.58	9.2 ± 2.32	10.1 ± 2.01
December	18.9 ± 4.15[a]	54.7 ± 5.08	5.8 ± 1.95[a]	28.3 ± 3.83	11.7 ± 2.38	12.3 ± 2.18

[a]Treated value is significantly different from the untreated value (Mann–Whitney U, $P < 0.01$).

(Mathur 1997). As well, smaller size could indicate better survival of young animals with the removal of older animals, or better breeding performance—i.e. the population is compensating.

The two species trapped, *R. rattus* and *M. natalensis*, are known to occur in other parts of eastern and southern Africa (Fiedler 1988). *M. natalensis* is a known carrier of plague (Gratz et al. 1997), and its foraging inside dwellings could increase the risk of human infection. Although much higher numbers of *M. natalensis* were caught in Mugaveia, plague outbreaks are relatively uncommon there, whereas plague cases are recorded nearly every year in Pinda. The degree of interaction between *R. rattus* and *M. natalensis* in these environments is unknown, and the pathways of plague transmission could be complex with infected fleas moving between populations of *M. natalensis* and *R. rattus* in and around human settlements (Mills and Childs 1998). Villagers in all three areas consumed rats as a significant part of their diet. Plague bacilli are known to survive for several days on dead rodents (Liu 1991), and thus the handling and preparation of rodents for food could result in plague transmission. As the trapping program increases the number of dying rodents within dwellings and the handling of dead rodents, it is possible that such a strategy could increase plague incidence within the locality. Using multi-catch live-traps instead of break-back traps may offer a way to reduce plague-infected fleas from remaining inside the dwelling. Further research is planned to determine anthropogenic and interspecific factors that impact upon plague outbreaks. Other rodent-borne zoonoses have been recorded in the area, particularly leptospirosis (Thompson et al. 2002), and research is planned to determine how zoonosis transmission could be affected by intensive trapping inside rural dwellings.

Losses of stored food to rodents were reduced significantly by the intensive trapping. As the baskets of known quantity were placed on top of the household food store, the observed losses in the basket could be an overestimate of the total rodent loss to the overall food store in the dwelling. Some of the observed weight loss is due to a reduced moisture content of the maize as the dry season progresses, particularly in the first 3 months of storage. However, relative comparisons between households in the treated and untreated areas of the village indicate that rodent pressure on the food store was considerably reduced by intensive trapping because relative weight loss and rodent damage was reduced. Questionnaires with farmers indicated that the effects of trapping were noticeable, as the stored food lasted longer than usual, particularly so in the most food-insecure households which normally do not produce enough to meet their household requirements. Other benefits were also noted by farmers, notably a regular supply of rat meat and fewer rat bites to family members.

In conclusion, intensive trapping is likely to be part of any integrated and ecologically based rodent control strategy for rural dwellings in these areas of Mozambique. Further research is required to determine the optimal number of traps needed to effectively modulate rodent populations given particular habitat and population parameters. Studies on the population responses of the two species at a landscape level also are required to understand possible compensatory responses and routes of reinvasion. The cost–benefits of trapping need to be more adequately understood in order to inform and encourage rural communities and agricultural extension programs to adopt trapping as part of an ecologically based rodent management program.

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References

Ahmad, E., Hussain, I. and Brooks, J.E. 1995. Losses of stored foods due to rats at grain markets in Pakistan. International Biodeterioration and Biodegradation, 36, 125–133.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology, 68, 203–220.

Buckle, A.P. and Smith, R.H. 1994. Rodent pests and their control. Wallingford, UK, CAB International, 405 p.

Gebauer, U., Dubbel, V. and Friedrich, E. 1992. Control of small rodent pests with spring traps. Allgemeine Forst Zeitschrift, 47, 408–409.

Gratz, N.G., Leirs, H. and Schockaert, E. 1997. The burden of rodent-borne diseases in Africa south of the Sahara. Belgian Journal of Zoology, 127, 71–84.

Ferreira, S.M. and Aarde, R.J. van 1999. Habitat associations and competition in *Mastomys–Saccostomus–Aethomys* assemblages on coastal dune forests. African Journal of Ecology, 37, 121–136.

Fiedler, L.A. 1988. Rodent problems in Africa. Rodent pest management. In: Prakash, I., ed., Rodent pest management. Boca Raton, Florida, USA, CRC Press, 35–65.

Krebs, C.J. 1999. Current paradigms of rodent population dynamics—what are we missing? 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, 33–48.

Liu, H.W. 1991. Study on the survival of plague bacillus in rodent pelts. Chinese Journal of Vector Biology and Control, 2, 114–117.

Makundi, R.H., Oguge, N.O. and Mwanjabe, P.S. 1999. Rodent pest management in East Africa—an ecological approach. 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, 460–476.

Mathur, R.P. 1997. Effectiveness of various rodent control measures in cereal crops and plantations in India. Belgian Journal of Zoology, 127, 137–144.

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

Singleton, G.R., Leirs, H., Hinds, L.A. and Zhang, Z. 1999. Ecologically-based management of rodent pests—re-evaluating our approach to an old problem. 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, 17–30.

Taylor, D. and Phillips, T. 1995. Household food security status in the Zambezi Valley and Central Mozambique. Report of a United Nations High Commission for Refugees (UNHCR) assessment. Guelph, Ontario, Canada, DTP Studies, 75 p.

Thompson, R., Nala, R., Belmain, S.R. and Meyer, A.N. 2002. Prevalence of leptospirosis (*Leptospira* spp.) and toxoplasmosis (*Toxoplasma gondii*) in Morrumbala, Mozambique. Revista Médica de Moçambique (in press).

Tobin, M.E., Koehler, A.E., Sugihara, R.T., Ueunten, G.R. and Yamaguchi, A.M. 1993. Effects of trapping on rat populations and subsequent damage and yields of macadamia nuts. Crop Protection, 12, 243–248.

Urban commensal rodent control: fact or fiction?

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Abstract. United Nations' predictions on urban development over the coming 30 years indicate that some 2.1 billion extra people will be living in urban areas by 2030. The increase will be most significant in less developed regions.

Any explosion in urban development will favour commensal rodents. The increase will be most significant in those areas least able to cope with the consequences of urban explosion, where refuse, sewage and low housing quality will particularly favour their development. Such increases in rodent populations will bring with them increases in the risks of disease transmission, rat bites and structural damage and contamination of the human environment.

The efficacy of effectively applied proactive rodent control programs has been clearly demonstrated. Yet, resources for such proactive work are being withdrawn in favour of less effective and poorly targeted reactive strategies. This trend must be reversed. The collection of sound data on the costs (financial and social) of rodent infestation, rather than the efficacy of proactive rodent control (which has been clearly demonstrated) must assume a priority. The cost–benefits of proactive rodent control must be clearly demonstrated.

Introduction

Commensal rodents live in particularly close association with people, by all accepted definitions—they 'live off man's table'. In fact, the name suggests a happy and almost symbiotic relationship, an image that is very far from the truth. Their relationship with humans would perhaps better be termed 'cleptoparasitic'. In their wild state, rodents effectively 'steal' from humans and the adverse effects of their presence are significantly detrimental, with people rarely benefiting. The commensal rodents that we find in urban areas make a very good case for being parasitic on people!

With some 2000 rodent species found worldwide, there are in fact very few true commensals. Lund (1994) restricted his list to: the Norway rat (*Rattus norvegicus*), the ship rat (*Rattus rattus*) and the house mouse (*Mus* spp.), all distributed worldwide; the multimammate rat (*Mastomys natalensis*), in Africa; the lesser bandicoot rat (*Bandicota bengalensis*), in central Asia; and the Polynesian rat or the Burmese house rat (*Rattus exulans*), in the Pacific and Asia. There may be a case for including other locally abundant species in this list, but the numbers of species remains relatively small.

None of these species, of course, evolved within urban environments—the development of urban environments suits their ecological requirements and they are very good at exploiting the urban opportunity! They have thrived as urbanisation has thrived and there is no reason for us to suppose that anything will change in the future. Thus any consideration of the future of commensal rodent control must start with a review of the future of urban areas. Are we likely to be creating more of the habitats within which these species will thrive?

The answer is well documented within the *World Urbanization Prospects: The 2001 Revision*, prepared by the United Nations Population Division (UNDP 2001). The conclusions for urbanisation include:

- The world's urban population reached 2.9 billion in 2000 and is expected to rise to 5 billion by 2030. Whereas 30% of the world population lived in urban areas in 1950, the proportion of urban dwellers rose to 47% by 2000 and is projected to attain 60% by 2030. At current rates of change the number of urban dwellers will equal the number of rural dwellers by 2007!
- Virtually all the population growth expected at the world level during 2000–2030 will be concentrated in urban areas. During that period the urban population is expected to increase by 2.1 billion people.
- Almost all the population growth expected at the world level during 2000–2030 will be absorbed within the urban areas of the less developed regions whose populations will likely rise from approximately 2 billion in 2000 to just under 4 billion in 2030.
- The process of urbanisation is already very advanced in the more developed regions, where 75% of the population lived in urban areas in 2000. Nevertheless, the concentration of population in cities is expected to increase further so that, by 2030, 83% of the inhabitants of the more developed countries will be urban dwellers.

- The level of urbanisation is considerably lower in the less developed regions, where 40% of the population lived in urban areas in 2000. This proportion is considerably higher than it was in 1950 (18%) and is expected to rise substantially to reach 56% by 2030.

If you are a commensal rodent, your future is assured. More importantly, for those involved in rodent control, are we able to control them?

What can we learn from history?

The levels of infestation that will be reached will depend upon the conditions in the specific conurbations—the poorer the conditions, the higher the levels of infestation.

Ideal conditions for the development of commensal rodent populations are provided by the increasing availability of food and water sources and, of course, harbourage within which the rodents can live. Thus, exploding human populations can provide increasing availability of these resources because the city and town amenities and the town planning authorities are unable to cope. Rubbish and waste is not efficiently removed, water and sewage facilities are not developed and maintained, and housing quality is poor and develops without the benefits of planning.

All these characteristics are likely to lead to ideal conditions for the rodents and significant rodent populations. There is clear evidence that levels of commensal rodent infestation are determined by the quality of the environment (Meyer 1978). Surveys undertaken in Amman in Jordan, showed that 79% of the variation in Norway rat infestation levels between the different housing types could be accounted for by differences in the levels of hygiene.

Perhaps Europe is the best guide to what may happen elsewhere in the world over coming decades. Table 1 shows how European urban populations have stabilised ahead of most other areas of the world. Indeed, over 50% of Europeans were living in urban areas by 1950.

The history of Europe demonstrates that during the periods of rapid urban growth, particularly when this was associated with poor urban areas with little or no urban facility management, rodent populations thrived. They did this to the extent that some 50% of the European human population died from rodent-borne diseases in the Middle Ages, specifically the plague and rat typhus. The human populations were living in very close contact with the rats that inhabited their dwellings, much as many developing urban populations do today and are likely to increasingly do so in the future.

In these early days, most rodent control would have been by rat catchers working for individual customers. However, there is evidence that city-wide or town-wide attempts were made to control rats. The fable of the *Pied Piper of Hamlyn* in Germany being an example of centralised rodent control! It was probably not until the 19th century, and even more so in the 20th century, that rodent control operations began to be handled on a national basis. In the United Kingdom, for instance, it was not until the Rats and Mice Destruction Order in 1919 that rodent control was to any extent centralised. Even then, the progress was probably very limited, largely due to the absence of any sound scientific information on the ecology of the target commensal rodent species. In addition, the techniques (largely trapping and the use of the acute rodenticides) available at the time were not very efficient and difficult to apply in urban areas.

Urban rodent control is more difficult than in other, less-densely populated rural areas. The higher and denser the human population, the more difficult it is to gain the cooperation of that population and the more difficult it is to gain access to the habitats within which the rodents are living, because the habitat is compartmentalised.

It was not until the middle of the 20th century that science was first effectively applied to commensal rodent control. At this point, the Bureau of Animal Population at the University of Oxford in England was given the specific remit to research effective techniques for control-

Table 1. Percentage (%) of world populations living in urban areas, 1950–2030. (Source: UNDP 2001.)

Region	Year				
	1950	1970	1990	2000	2030
World	29.8	36.8	43.5	47.2	60.2
More developed	54.9	67.7	73.7	75.4	82.6
Less developed	17.8	25.1	35.0	40.4	56.4
Africa	14.7	23.1	31.8	37.2	52.9
Asia	17.4	23.4	26.9	37.5	54.1
Europe	52.4	64.6	72.1	73.4	80.5
Latin America & Caribbean	41.9	57.6	71.1	75.4	84.0
Central America	39.8	53.8	65.7	68.2	77.1
South America	43.6	60.2	74.4	79.6	87.9
North America	63.9	73.8	75.4	77.4	84.5

ling commensal rodents. The Bureau undertook much basic research on rodent control, developing many improved strategies for using the available control techniques. Perhaps their most lasting legacy, however, was to start to identify, for the first time, the key elements relating to the population dynamics of the three main commensal species.

The research indicated that breeding success was a key element in the survival strategies of the rodents. This research was complemented by parallel research in the United States of America (USA) by Davis and colleagues. Knowledge relating to this and to their behaviour patterns helps us set very basic objectives for our control operations today (see Krebs 1999 for review). These studies in the United Kingdom (UK) and the USA highlighted that strategies need to be developed that achieve levels of mortality in excess of 80%. In addition, the target must be to reduce the carrying capacity of the urban areas by developing effective environmental management techniques.

The 50 years following this research not only led to much further research carried out worldwide on the techniques for urban rodent control, but also to the development of strategies designed to use the results of the research as effectively as possible.

Strategy development

There are, practically, three ways of approaching urban rodent control—'**reactive**' control; '**proactive**' control; or a combination of the two. Both strategies have been applied in many parts of Europe and North America over the last 50 years and a brief review of both and their apparent efficacy is appropriate.

Reactive rodent control

Reactive pest control is particularly popular amongst politicians and other policy-makers. This is particularly true when considering those rodent control programs that are funded by local or central government. This is because reactive control essentially means that those with a rodent problem can request that something is done about it. If the work is being undertaken by a governmental organisation, the complainant reports an infestation, the work is done, and the complainant is satisfied that his/her concerns have been met.

A free rodent control service is most likely to reach those with an infestation and the more that payment is involved the lower the level of penetration (control) of the rodent population because people are less likely to respond to infestation. Clearly, the higher the level of the penetration of the problem, the more likely that overall levels of infestation can be reduced. Conversely, the lower the levels of penetration, the less impact that will be achieved.

Accepting that it would be ideal if everyone with a rodent problem did something about it, it would be useful to know what the level of active response is to a rodent infestation. There are few data available worldwide on this issue, although there are data from within the UK.

A survey was undertaken in 1993 (Meyer et al. 1995) involving the inspection of some 11,000 randomly-selected premises in England and Wales for rodent infestation. In domestic premises, about 20% of house mouse and about 30% of Norway rat infestations remained untreated. At this time, a free service for both house mouse and Norway rat infestation was provided by almost all local governments, and about 50% of house mouse infestations were reported to and were treated by local authorities. About 65% of Norway rat infestations were reported to the same local authorities. Owners and occupiers of premises claimed to be treating about 30% of house mouse infestations and about 10% of rat infestations. Contracted servicing companies were rarely used by domestic occupiers.

Thus, even with a free service, only about 50% of mouse infestations and 65% of rat infestations were being treated by professional technicians. There is evidence that as charges are introduced for these services the percentage of infestations that are reported decreases.

Even these figure provide an overly optimistic view of the effective levels of control, because the spatial limits of an 'infestation' will not necessarily coincide with the boundaries of the premises from which the report was received. Work in the London Borough of Lambeth (Meyer and Drummond 1980) on house mice showed that house mouse infestations were not randomly distributed; they were clumped (Table 2). Only 33% of those infested were single premise infestations—the remainder varied between two and six contiguously infested premises. If no proactive control were undertaken and only complaining premises were treated, it is unlikely than more than about 30% of infestations (with a 50% reporting level) would be eliminated by a reactive complaints based strategy. Treated premises within clumps would probably be re-infested from adjoining unreported and therefore untreated infestations, further reducing levels of efficacy.

As a part of the subsequent proactive control program, attempts were made to access all premises. About 39% of the occupied premises could not be surveyed during the normal working week and were surveyed at weekends. The infestation levels of those that were surveyed at weekends (house mouse 52% and Norway rats 7% infested) were higher than for those where weekday access was possible (house mice 29% and Norway rats 2% infested). Thus, in any proactive strategy, both work patterns and occupier activity profiles have to be kept in mind, or disproportionate numbers of infestations may be missed.

The overall conclusions of this work were that numbers of infested premises could be maintained at a level of over 90% lower through the application of proactive control, with only a marginal increase in costs.

It is also likely that reactive strategies may miss the proportion of the population that are most at risk from rodent infestation. If we accept that poor housing and poor

environmental conditions encourage rodent infestation, then it is likely that highest rodent infestation levels will occur in those areas with the poorest housing (Meyer 1978). Those living in these areas will therefore also be at the greatest risk from rodent-borne diseases and rodent damage.

Table 2. Distribution of house mouse infestations within a block of terraced housing (428 premises) in the London Borough of Lambeth, United Kingdom.

Number of contiguously infested premises	Number of clumps	Total infestations (%)
1	45	33
2	23	34
3	4	9
4	4	12
5	1	4
6	2	8

A reactive strategy requires those who are experiencing a rodent problem to complain, in order to initiate a reaction! Those who are most likely to be aware that they can complain and those who are most able to complain—because they have access to a telephone or to transport or indeed to the time to complain—will be those in the higher rather than the lower housing categories. Those in the lower housing categories, who are effectively more at risk, are less likely to complain!

Thus, a complaints-based or reactive strategy is least likely to serve those at greatest risk, and is also unlikely to access sufficient of the infestations to have a significant impact on overall levels of infestation.

Proactive rodent control

The alternative strategy, proactive rodent control, enables resources to be targeted where risk is greatest and in a way that is most likely to achieve effective control. The question is, do proactive strategies work?

Large-scale programs to control rodents in urban areas have been undertaken in many parts of the world, particularly since the discovery of the association between rats and plague. Initially, they usually made use of traps, cyanide and zinc phosphide and usually employed too few resources to make much impact with these relatively inefficient control techniques.

The commercial development of the anticoagulant rodenticides in the early 1950s and their ready availability over the last 50 years provided an ideal catalyst for the application of proactive strategies.

The first attempt seems to have taken place in Lahti in Southern Finland in 1950 and over a period of 3 months some 5000 properties were systematically inspected and the 40–50% found to be infested were made rat-free. The rat problem then remained at an acceptable level by handing out free warfarin bait to householders (Myllymaki 1969). Similar programs were initiated in many towns in Lower Saxony in the 1960s, following pioneer work in Cuxhaven (Steiniger 1956). Unfortunately, although initial levels of infestation are recorded, there were no attempts to monitor progress through random surveys nor resurveys of treated properties.

One of the first attempts to develop an urban rodent control program on any scale—and at the same time to record the progress of the operations in some detail—was probably initiated in the town of Folkestone, on the south coast of England in the early 1960s (Drummond et al. 1977).

In New York State, proactive programs were carried out between 1969 and 1973 in some of the more rat-infested areas (an average of 24% of premises infested) (Brooks 1974). Brooks recorded not only the reduction in infestation levels but also a range of environmental factors and their management, which contributed significantly to the strategy. The work in New York was extended in Boston, USA in the 1990s. Here a comprehensive rat control program was introduced, designed to incorporate all the elements of an effective strategy identified in earlier work (Colvin 1990). The elements of much of this work as well as the concepts of urban rodent control are thoroughly summarised in a later paper (Colvin and Jackson 1999).

Perhaps the most comprehensive and long-term urban rodent control program has been undertaken in Budapest, Hungary. Here, a strategy applied and monitored over some 30 years has incorporated not only effective control strategies but also an analysis of the behaviour and habitat use of urban environments by rats (Bajomi 1983, 1993).

All these programs demonstrate the advantages of proactive rodent control. The later work in particular demonstrates that, when combined with effective environmental management, the strategies can be particularly effective.

If there is a criticism of many of them, it is that whilst they address the efficacy of the control operations, they do not address in the same detail the cost–benefits of such operations when compared with the reactive strategies discussed earlier. This is not only because the costs of the monitored programs are not well documented, but because there is an absence of good data throughout the rodent control literature on the real costs of rodent infestation. There is an abundance of data on the potential problems that rodent infestation can cause, in all its diversity—disease transmission, structural damage, contamination of food… the list is almost endless! But data on the collective costs of rodent infestation are almost totally absent! The question remains: What are the collective costs of heavy rodent infestations in urban areas?

The current situation

In the UK, in spite of all the evidence that proactive control is more effective at reducing rodent infestation than reactive control, the move to reactive control continues. It is cheaper and more politically productive. In the absence of good data on the real economic cost–

benefits of proactive control, to the community as a whole, the trend will continue.

Some years ago, the World Health Organization (WHO) ran a very effective unit advising on the control of rodents in urban areas. That unit no longer operates and there is little input from WHO to commensal rodent control.

In the UK, there is currently no central government department with responsibility for rodent control in urban areas, the Ministry of Agriculture having withdrawn support in the early 1980s. Local authority responses, whereas once very much proactive, are now almost entirely reactive, with resources being withdrawn and indeed increasingly minimal efforts are being made to address the urban rodent problem in any effective strategic sense.

In the USA, "technical support for urban rodent control is very limited. Active research programmes do not exist on the federal, state or university levels. Most States and municipalities have limited knowledge and skill in urban rodent control, resulting in limited effectiveness when programmes are implemented. Most efforts by local authorities are reactive." (Colvin and Jackson 1999)

Conclusion

The almost universal withdrawal of resources for proactive urban rodent control is a product of pressures on financial expenditure. The cost–benefits of applying proactive control are not apparent.

Risk assessments require data on the real costs of rodent infestation in all their infinite diversity. The priority for the future must be to clarify these risks and their associated costs.

The predicted increases in human urban populations provide an opportunity for the commensal rodents such as they have never had before. The technology for the control of these urban rodent populations is available. It is essential that over the coming few years priority be given to identifying the cost–benefits of proactive rodent control. Failure to do so may allow the rodents to demonstrate all too clearly the costs of failure.

References

Bajomi, D. 1983. Examination of the habitats of residual urban Norway rat populations after eradication. Parasit. Hung., 16, 131–135.

Bajomi, D. 1993. Rat free city. Chronology of rat control with lasting success. Public Health, 10, 13–19.

Brooks, J.E. 1974. A review of rodent control programmes in New York State. In: Proceedings of the Sixth Vertebrate Pest Conference. Davis, University of California, 132–141.

Colvin, B.A., Ashton, A.D., McCartney, W.C. and Jackson, W.B. 1990. Planning rodent control for Boston's Central Artery/ Tunnel Project. In: Davis, L.R. and Marsh, R.E., ed., Proceedings of the 14th Vertebrate Pest Conference. Davis, University of California, 65–69.

Colvin, B.A. and Jackson, W.B.1999. Urban rodent control programs for the 21st century. 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, 242–257.

Drummond, D.C., Taylor, E.J. and Bond, M. 1977. Urban rat control: further experimental studies at Folkestone. Environmental Health, 85, 265–267.

Krebs, C.J. 1999. Current paradigms of rodent population dynamics—what are we missing? 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, 33–48.

Lund, M.1994. Commensal rodents. In: Buckle, A.P. and Smith, A.H., ed., Rodent pests and their control. Wallingford, United Kingdom, CAB International, 23–43.

Meyer, A.N. 1978. Planning information for Amman City Rat Control Programme. WHO/VBC/78.702. World Health Organization, 5 p.

Meyer, A.N. and Drummond, D.C. 1980. Improving rodent control strategies in Lambeth. Environmental Health, 88 (4), 77–78 and 80–81.

Meyer, A.N., Shankster, A., Langton, S.D. and Jukes. G. 1995. National commensal rodent survey. Environmental Health. Vol 103/6 June.

Myllymaki, A. 1969. An early approach to a rat free town in Finland. Berlin–Dahlem, SchrReihe Ver. Wass-Boden-Lufthyg, 32, 161–166.

Steiniger, F. 1956. Rattenfreier Hafen und rattenfreies Fischindustiegebiet in Cuxhaven. Desinfektion und Gesundheitswesen, 11, 165–170 (in German).

UNDP (United Nations Development Programme) 2001. World urbanization prospects: the 2001 revision. On the Internet at: <www.un.org/esa/population/publications/wup2001>.

Adapting baiting tactics to match the foraging behaviour of Norway rats: a balance between efficacy and safety

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Abstract. The need to protect rodenticide baits from non-target animals is self-evident, but too much protection can impede control if it stops rodent pests from expressing their natural foraging behaviour, which has evolved to maximise food gain and minimise the risk of attack. One element of foraging is how long individuals are prepared to remain at food sources, which during control operations include rodenticide baits. The duration of visits by wild Norway rats to plain baits placed in burrows and boxes was measured under semi-natural and field conditions. Median visit length in the field to burrows was 12 s (n = 1304 visits) and to a box 17 s (n = 1272), a difference unlikely to be biologically significant. Such short visits are likely to result in bait transfer in which bait particles are removed from secure locations by individual rats and taken anywhere to be eaten or abandoned. However, 80% of visits to the box were ≤145 s and to burrows ≤42 s and under semi-natural conditions rats feeding in groups on whole wheat stayed longer in boxes than those that fed alone. Longer feeding bouts probably minimise the likelihood of bait transfer. To maximise efficacy, containers should therefore be open enough to allow several rats to feed together, a feature not present in some commercial products on grounds of safety. Bait transfer can, however, be used to familiarise rats with a formulation type, such as a wax block, that they have difficulty recognising as edible, especially when it is held securely inside a box to prevent it being removed and eaten by other animals. In the field, the bait that rats are allowed to transfer should not, of course, contain a rodenticide.

Introduction

Despite widespread concern about the impact on wildlife populations of rodenticide use, no cost-effective alternative means of quickly controlling Norway rats (*Rattus norvegicus*) is currently available in the United Kingdom, and thus rodenticides are likely to remain the means of first choice when an infestation needs to be controlled. However, recognising the potential risk that may arise, the pest control industry has designed bait containers that make it difficult for animals larger than rats to gain access to the bait—described at 'tamper-resistant'—and has developed formulations that are supposedly less likely to be eaten by non-target animals. One such formulation type is the wax block, which is apparently relatively unattractive to birds (Johnson 1988). While such baits are generally thought to be relatively unattractive to rodents also, a degree of unpalatability might be countered with a highly potent rodenticide (Buckle 1994).

In an intensive study of the efficacy of anticoagulant treatments, loose-grain baits were applied for up to 7 weeks in wooden bait boxes. The results showed that the main reason rats survived treatment was that they ate little or no bait (Quy et al. 1992). The number that survived in each case varied from a few individuals to almost the entire population. The presence of alternative food, particularly stored cereals, notably 'prevented' rats consuming lethal quantities of bait. However, applying the same baits directly into rat burrows overcame any apparent reluctance to feed on bait presented in boxes (Quy et al. 1996). Unfortunately, baiting burrows is not always possible as active burrows are sometimes difficult to find and uneaten bait is not easily recoverable. On grounds of safety, therefore, a protected bait container seems desirable but it has long been recognised, and shown experimentally, that any kind of bait container appearing as a novel object to rats is likely to be avoided at first (Inglis et al. 1996). To allow rats time to overcome their initial wariness of new objects, empty containers have been put out several days in advance and then rat activity has been monitored during the treatment to distinguish baits that remain uneaten because they are misplaced from those uneaten because rats are still reluctant to approach the container (Quy et al. 1994). It became apparent during such monitoring that a third category existed, namely, boxes that were entered by rats which then ate little or no bait, regardless of how palatable the bait had seemed to be during laboratory tests. During some treatments, the majority of baits fell into this third category. To

rats, baits are potential food sources and the strategies they use to find, approach and finally eat their usual foods should apply to these also. A more detailed knowledge of these strategies might enable the tactics deployed during rodenticide treatments to be modified to achieve control more quickly without compromising the safety of other animals.

There have been few accounts of the foraging behaviour of free-living rats when new food sources are introduced into their environment. Rats seem prone to transport food and, according to optimal foraging theory, they do so to minimise the risk of predation while maximising food gain. Indeed, the likelihood of bait transfer has provoked manufacturers to mould wax block baits, which weigh about 20–30 g, with a central hole so that they can be secured on a rod inside a bait box and hence cannot be carried away. Rats that transfer bait may subsequently eat it, cache it or abandon it, but do not appear to deliberately give it to another rat. It has been suggested that rather than minimise predation risk, transfer occurs in order to avoid conspecific aggression (Whishaw and Whishaw 1996). Thus, small rats are particularly prone to make frequent brief visits to food sources to collect particles, which may or may not subsequently be stolen by other rats that find the cache.

In this study, we have attempted to answer three questions: (1) because all rats are likely to transport food, how long will individuals be prepared to stay at a food source (i.e. bait point) if they cannot take particles away; (2) is the apparent success of burrow baiting over container baiting due to rats feeling safer when feeding close to where they presumably nest, so making risky foraging trips unnecessary; and (3) under what circumstances would rats be prepared to stay long enough at a distant bait point, so that if rodenticide baits are introduced, relatively little is carried away and the rate of bait uptake is sufficiently high to minimise poison bait exposure periods while ensuring effective control?

Materials and methods

Field trial

Rat activity at baited burrows and a bait box was recorded on a farm in North Yorkshire, United Kingdom (UK), between April and May 1997. The farm buildings were used mainly for storage and the site was therefore relatively undisturbed. Rats were present in and around the buildings and along a ditch that ran parallel about 10 m away. The ditch, which was about 1.5 m deep and 2.4 m wide at the top, had shallow pools of water intermittently along its length. Eight active rat burrows, identified by well-padded soil and lack of debris in the entrances, were found along a 74 m long section. The distance between one burrow and the next one varied from 2–18.7 m. (There were other active burrows along the same section that had too small an entrance or were too close to the ditch bottom and thus liable to be flooded.) A tube, 60 mm long with internal and external diameters 80 mm and 107 mm, respectively, was pushed into each of the 8 burrows until it was flush with the entrance. Care was taken not to damage the walls of the burrow as the inhabitant might then abandon it. The tube was made of a hard resin, which encased a detector designed to energise and receive signals from a passive integrated transponder (PIT tag). A PIT tag lying along the central axis was detectable not more than 50 mm beyond the end of the tube. An armoured cable carried the signal from the detector to a reader unit and then to a four-channel data logger (Francis Scientific Instruments, Cambourne, UK) up to 20 m away. Two loggers were needed to monitor activity at the eight burrows. The bait box was 360 mm (l) × 260 mm (w) × 140 mm (h) and made of marine plywood, but had a metal lid. Entrances at both ends were 70 mm × 70 mm and an internal baffle 25 mm high prevented bait spilling out. Two square-section tunnels (plastic drainpipe), 320 mm × 76 mm × 76 mm, were attached to each side of the box. Each tunnel was fitted with two PIT tag detectors 300 mm apart and was protected by a wooden case designed to be compatible with the bait box. The signals from the four detectors were relayed to a four-channel data logger via cables of 20 m in length. Each data logger channel was time synchronised so that the direction of movement could be determined from the time stamp recorded with the PIT tag identification. Twelve-volt car batteries powered the loggers and detectors.

Nineteen rats (9 males, 10 females) were live-trapped and each animal was lightly anaesthetised with isoflurane before a Sokymat® PIT tag, encased in a biocompatible glass tube 12 mm (l) × 2 mm (d), was injected subcutaneously between the shoulder blades along the line of the spine. Each animal was sexed and weighed and was released at its point of capture when it had fully recovered. Of the 19 rats, 6 were juvenile (<100 g) and the adults weighed 280–620 g. On the first day of the trial, 100–200 g of bait was placed into each of the eight burrows just beyond the end of the detector tube so that it could be easily seen. The bait consisted of pinhead oatmeal (92.5% w/w), caster sugar (5% w/w) and corn oil (2.5% w/w). A chemical bait marker (decachlorobiphenyl) was dissolved in the corn oil to give a final concentration in the bait of 0.01% (w/w). The baits were inspected daily for 10 days, the take at each burrow being recorded as partial or completely eaten and the bait replenished to maintain a surplus until the next inspection—although the amount that could be laid was limited by the capacity of the burrow. The data loggers recorded visits by tagged rats to the burrows every day. On day 10, the bait box was placed on a rat run along the bottom of the ditch. The box was sited at one end of the 74 m section where it was dry: the furthest logged burrow was 58.9 m away and the closest 4.3 m away. The box was baited with initially 500 g of the pinhead oatmeal bait; any uneaten bait remaining in the burrows was removed and replaced with a 1:1 maize meal:barley meal mix (97.5% w/w) and corn oil (2.5% w/w). This bait contained the chemical marker hexachlorobiphenyl (0.01% w/w) dissolved in the oil. (The markers were

present as part of another study which is not reported here.) The bait in the box was inspected daily for the next 12 days, the amount remaining each day recorded and replenished to maintain a surplus until the following day. After 12 days, all uneaten marked bait was removed from the box and burrows and dry whole wheat was placed in the box for a further 2 days. The data logger recorded visits by tagged rats to the box every day for 14 days.

Enclosure trials

Untagged rats may have influenced the responses of the tagged rats at the box in the field. To examine the effect of social interactions more closely, family groups of rats were established in enclosures. For ethical reasons, it was not possible to study relationships between unrelated individuals under such circumstances, but interactions based on size differences could be investigated. The enclosures, which were erected inside a large building, were 12 m long and 2.5 m wide, bounded by sheet-metal walls bolted to a concrete floor. They were naturally lit through windows in the roof and there was no artificial heating, although a cooling fan could be switched on during hot weather. A tunnel connected two adjacent enclosures so that the nest area could be separated from the bait box by up to 15 m. Hay was provided as cover and wooden boxes were supplied for the animals to build nests in. Water was available in both enclosures ad libitum from founts, and a tray containing surplus amounts of a ground laboratory animal diet was placed near the nest area and was present during all experiments. A bait box identical to the one used in the field trial, but with a perspex lid, was placed in the adjacent enclosure. Pittag detector tunnels of similar design and construction to those described above were attached to each side of the box and the signals were relayed to a data logger located outside the enclosure. Additional detectors were placed by the connecting tunnel. Since all rats had to pass through the tunnel that separated the box from the nest area, these detectors served as back-ups, because tagged animals, particularly if they were moving fast, could be missed as they entered or left the bait box.

Three family groups were derived, each from a wild-caught adult male and two wild-caught adult females. The females were allowed to produce 1–2 litters; sufficient to give a colony of 10–20 individuals. Subsequent litters were removed as soon as they were found to prevent over-crowding. After the young were at least 6 weeks old, each family group was trapped and each animal was sexed, weighed, lightly anaesthetised with isoflurane and injected subcutaneously with a PIT tag.

Two series of experiments were conducted once most individuals in each group were regularly visiting the bait box. This was done to avoid any neophobic responses confounding interpretation of the results. Firstly, using whole dry wheat as the bait, the number and length of visits to the box were compared between the adults and members of the litter when the litter was at different stages of development. A further factor was whether each animal was alone or with at least one other rat. The respective mean weights of adults and litter in each of group were: 412 g (n = 3), 107 g (n = 12) immature; 447 g (n = 3), 210 g (n = 17) maturing; and 503 g (n = 2), 470 g (n = 12) fully mature. The responses of each group when presented with surplus amounts of whole wheat in the box were recorded over one night.

In the second experiment, each of two groups was presented with 10 wax blocks (a commercial blank formulation, each block weighing 20 g) threaded onto two wires fixed inside the box. One group was familiar with the formulation after previously being presented with loose blocks until they consistently carried them away and ate them. The other group was naïve. The responses of the ‘trained’ group on their third presentation of the secured blocks were compared with those of the naïve group on their sixth presentation. (By the third and sixth presentations, respectively, it was clear that the responses were not being influenced by other factors such as temperature.)

Data analysis

The data loggers were designed with a time base that incremented every 62.5 ms. If the four detectors attached to the box were numbered as channels 1 to 4 in sequence, then the output would show, in time order, that a rat passing through the box was detected by channels 1, 2, 3, 4 or 4, 3, 2, 1, where 2 and 3 were the internal detectors closest to the box and 1 and 4 at the entrances/exits to the tunnel. The entrance detectors were set into the tunnel so that they did not detect a rat passing by. For a rat entering and leaving by the same tunnel, the sequence would be 1, 2, 2, 1 or 4, 3, 3, 4. The length of a visit was taken to be the time difference between the first and last channel number in a string of 2s and 3s before an entrance/exit channel (1 or 4) was recorded. A string would occur if a rat moved relatively slowly through the detection field. Thus, rats that entered the tunnel and then backed out could be distinguished from those that went into the box. By recording the time that the loggers were started each day, all visits were related to real time. The detectors fixed into burrow entrances were single channel and could not give direction of movement. However, as the detectors could nominally record many events every second, a rat feeding on the bait in the burrow entrance would remain in the detection field and its tag identification (ID) would be logged repeatedly for as long as it stayed there. The number and length of visits recorded for each rat to each burrow therefore depended on the time difference between two consecutive detections that signified the end of one visit and the beginning of another. By convention in this study, two events at a burrow separated by more than the average visit length ≤22 s, derived from a log-transformed distribution of visit lengths) to the box in the field study were taken to indicate separate visits. (In practice, halving or doubling the interval made little difference to the average visit length to burrows.)

The distribution of visit lengths was highly skewed and therefore the median is given as the most appropriate summary statistic. Differences between visit lengths

related to the various factors under study were examined by t-test after first log transforming the data (Inglis et al. 1996). In most cases, the test formula for unequal variances was used. All tests were two-tailed and the level of significance (α) was $p < 0.05$.

Results and discussion

Field trial

Over 10 days, 1623 visits were recorded at the 8 burrows by 12 of the 19 tagged rats. No juveniles were detected. Tagged rats visited seven of eight baited burrows on the first night. Only two rats (males) visited all the baited burrows during the trial. From the total number of visits, 1304 involved multiple detection events within the time reference for a valid visit and were therefore classified as putative feeding visits. The median visit length was 12 s and 80% of visits were ≤42 s (Figure 1). Mean visit length for males (median 16 s, $n = 432$) differed from that of females (median 11 s, $n = 872$) ($t = 2.82$, $p < 0.005$). The average number of feeding visits to each burrow by 5 males over the 10 days was 10.8, and 15.6 by 7 females, although one female made a total of 413 visits to 4 burrows over the period.

No visits were made to the box by tagged rats and no bait was eaten by any rat for the first 2 days. Thereafter, over the next 12 days, 11 tagged rats made 1272 putative feeding visits, the first visit by each tagged rat occurring at different times over the period. The median visit length was 17 s and 80% of visits were ≤145 s (Figure 1). Mean visit length for males (median 21 s, $n = 373$) differed from that of females (median 17 s, $n = 899$) ($t = 2.28$, $p = 0.02$).

The median length of a visit to a baited burrow and that to the box differed by 5 s and is probably of little biological significance. (Equally, the differences between visit lengths for males and females may have little biological meaning.) More significance should perhaps be attached to the differences that can be seen at higher percentiles (Figure 1). At the highest percentiles, not shown in the figure, extremely long visits confound any comparison, as such visits are probably the result of tag IDs being missed, which can happen if rats move too quickly through the detection field. The time synchronisation of events recorded by the logger meant that it was possible to determine how many tagged rats were in the box at the same time and whether the number feeding together had any effect on the time individuals were prepared to remain there. There may be a selective advantage in feeding together, in that 'safety in numbers' can be a defence against predator attack. Such social facilitation might be advantageous when rodenticide baits are laid, as rats may be encouraged to eat more bait at each visit. In contrast, the confines of a burrow necessarily restrict the number of rats that can feed at any one time and while the burrow occupant may feel safe emerging from its nest, passing individuals that feed opportunistically risk attack from behind as they reach for the food. However, the number of rats feeding together in the box or by each burrow remained unknown, because untagged animals might also have been present. This problem was overcome by marking every rat in an enclosed colony.

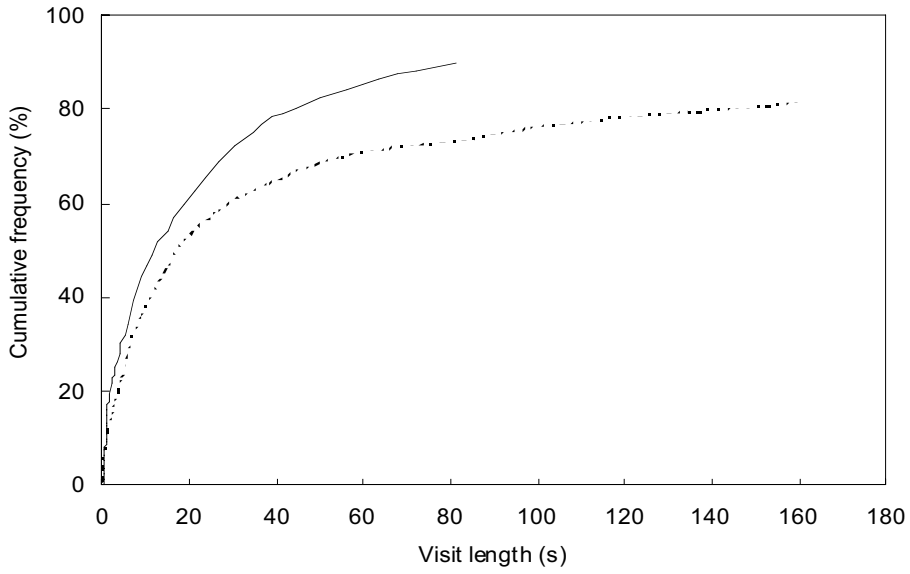

Figure 1. The length of time rats spent over a 10-day period at the entrances of burrows (solid line) located along the sides of a ditch near farm buildings and then inside a box (dashed line) placed on the ditch bottom for a further 14 days. The same loose-grain plain bait that was placed in the burrows was dispensed into the box for the first 12 days. The median and its 95% confidence limits for each curve are: 12 s (10–14 s) for visits to burrows, and 17 s (15–21 s) for visits to the box.

Enclosure trials

Regardless of the age or size of the rat or the type of bait in the box, visits by single rats were short, with a range of median values from 2–15 s (Table 1). With whole wheat laid in the box, visits by an adult, when at least one other rat was present, were longer than those by an immature rat (juvenile) that was also not alone ($t = 2.27$, $p = 0.03$) — a difference that was not found when members of a fully grown litter were the same size as their parents ($t = 0.29$, $p = 0.8$). Despite a difference of 76 s between the median visit lengths for a group with at least one adult and a group with at least one young adult (maturing) rat, the difference was not statistically significant ($t = 1.26$, $p = 0.2$). Nevertheless, these results support the interpretation that the foraging behaviour of rats is dictated more by fear of conspecific aggression than by fear of predation (Whishaw and Whishaw 1996), even when, as in this case, the animals were related. It could not be determined if every visit to the box was to obtain food, but incidental observations revealed that any rat, entering the box alone, often emerged after a few seconds carrying grains of wheat in its mouth and would then move elsewhere in the enclosure to eat them.

In a study in which the apparatus used to monitor rat feeding patterns apparently permitted only one individual at a time to obtain food (Berdoy and Macdonald 1991), the minimum duration of a feeding visit (presumably to take food rather than eat it on the spot) was found to be 0.4 s, while the majority of visits lasted 1–8 s. The implication of such behaviour during a rodenticide treatment is that bait transfer becomes more likely when only one individual at a time can access the bait. The rats in our family groups appeared to prefer eating in the presence of one or more other individuals, provided they were not obviously larger than themselves. By staying longer, bait transfer probably occurs less often. It is noticeable that the design of many commercial bait boxes seems to restrict access to bait with high internal baffles intended to deter non-target animals.

Rats unfamiliar with wax blocks had made no attempt to gnaw the blocks secured on the wires after six consecutive presentations. The median length of 91 visits on the sixth night by 13 out of 14 colony members was 8 s; solitary animals made 65 (71%) visits (Table 1). For rats familiar with the block bait, on the third presentation all the blocks were eaten. The median length of 494 visits by 18 rats was 14 s; solitary animals made 196 (40%) visits. The ratio of solitary:group visits for the naïve colony was different to that for the trained group ($\chi^2 = 30.1$, 1 df, $p < 0.001$), largely because of group visits by the offspring in the trained group. The commercial block used was rather brittle and it was probably easy for rats to break off relatively large pieces with their incisors. Such pieces were then most likely to have been carried outside the box instead of being eaten inside it and may explain why the visit length for the trained group was similar to that of the naïve group. Wild rats seem to have difficulty recognising wax blocks as food items, a characteristic that has long been recognised (Bentley 1960). Moreover, the presentation of blocks on a wire suspended above the floor of a box prevents a rat feeding in its preferred manner—which is to pick up a food particle in its mouth, then sit on its haunches, rotating the particle with the paws as it is eaten (Whishaw and Tomie 1987). Nevertheless, training rats by allowing them to take loose (plain) blocks away and eat them at least allows the animals to become familiar with similar objects and to discover that they are, after all, edible. For practical control purposes, such 'training' may be deemed unworkable, as there would be no means of knowing where blocks were taken and how many rats would be 'informed' in the process. The alternative is that secured poison blocks are left in containers until such time as rats feel able to eat them. In the meantime, other animals, less inhibited than rats, might eat them instead.

Table 1. Median duration (s) of visits (*n* in brackets) by individual rats in different colonies (family groups) to a bait box containing plain whole wheat or plain wax blocks. Visits are divided into those by an individual on its own or with at least one other rat (adult or offspring) present in the box. For the latter category, statistical differences between adult and offspring visit lengths within each family group are shown as * ($p \leq 0.05$) or † (not significant). Each colony had an alternative food source available. The 'training' given to the colony presented with wax blocks threaded onto wires consisted of offering the rats loose blocks until all were regularly removed and eaten. The 1:>1 ratio of total number of visits for the naïve group (65:26) differed from that for the trained group (196:298, $p < 0.001$).

Bait	Number of rats in box	Status of litter					
		Immature		Young adults		Fully mature	
		Adults	Offspring	Adults	Offspring	Adults	Offspring
Whole wheat	1	2 (9)	6 (95)	2 (15)	6 (79)	–	15 (17)
	>1	200 (44)	28*(250)	96 (39)	20†(170)	100 (38)	105†(206)
		Status of colony					
		Naïve		Trained			
		Adults	Offspring	Adults	Offspring		
Wax blocks on wires	1	3 (12)	7 (53)	5 (28)	9 (168)		
	>1	11 (14)	23 (12)	13 (23)	24 (275)		

Conclusion

Because current rodenticides are not species-specific, it is imperative that every effort is made to prevent other animals eating the bait during treatments. Whatever measures are taken should not also discourage rats from eating bait and in practice many operators find it hard to balance efficacy with safety. Some designs of bait boxes and formulations seem to be out of tune with rat foraging behaviour, through which the animals seek easy access and an easy escape from food sources. Such boxes and baits should perhaps not be used if a population needs to be controlled urgently. Baits laid in burrows may be found quickly by rats during nightly excursions across their home range, especially if they follow established runs that will naturally pass close to such burrows. But the restricted access to such baits leads to a series of brief visits that can be interrupted by the presence of other rats. Clearly, to capitalise on such short visits during control operations, a highly potent rodenticide is desirable.

In contrast, baits available in a more open container that allows the possibility of group feeding, need not be quite so toxic, as the rate of bait uptake should be higher. However, the bait chosen to present to rats in such circumstances should not be one that is easily carried away in bulk and also not one that cannot be carried away. This apparent contradiction can be resolved with a loose-grain cereal bait, which rats living on farms clearly have no difficulty in recognising as food. The disadvantage of loose-grain baits is that they are attractive to a wide range of other animals and are easily lost if the container is disturbed. Faced with a damaging infestation, the choice seems to be either a short intensive treatment with high rates of bait uptake and relatively rapid elimination of rats, but with a greater short-term risk to other animals, or a longer treatment with lower rates of bait consumption, slower elimination of rats, but less risk of primary poisoning to animals bigger than rats. While both strategies should be equally effective in reducing damage, albeit at different rates, the latter would seem to offer more chance of selecting resistant individuals, especially when second-generation anticoagulants are used.

A solution to the problem of having safety with efficacy is to test whether rats can be ‘trained’ with unsecured, plain block baits to eat poison blocks ‘on the spot’ inside protected containers. By careful adjustment of the number of plain blocks available for transfer and the location and density of stations with poison blocks, a practicable method for use in the field may be possible.

References

Bentley, E.W. 1960. Control of rats in sewers. London, Her Majesty’s Stationery Office (HMSO). Ministry of Agriculture, Fisheries and Food (MAFF) Technical Bulletin No. 10, 22 p.

Berdoy, M. and Macdonald, D.W. 1991. Factors affecting feeding in wild rats. Acta Oecologica, 12, 261–279.

Buckle, A.P. 1994. Rodent control methods: chemical. In: Buckle, A.P. and Smith, R.H., ed., Rodent pests and their control. Wallingford, CAB International, 127–160.

Inglis, I.R., Shepherd, D.S., Smith, P., Haynes, P., Bull, D.S., Cowan, D.P. and Whitehead, D. 1996. Foraging behaviour of wild rats (*Rattus norvegicus*) towards new foods and bait containers. Applied Animal Behaviour Science, 47, 175–190.

Johnson, R.A. 1988. Performance studies with the new anticoagulant rodenticide, flocoumafen, against *Mus domesticus* and *Rattus norvegicus*. EPPO Bulletin, 18, 481–488.

Quy, R.J., Cowan, D.P., Haynes, P., Inglis, I.R. and Swinney, T. 1992. The influence of stored food on the effectiveness of farm rat control. In: Brighton Crop Protection Conference—Pests and Diseases, Brighton, 23–26 November 1992. Farnham, Surrey, The British Crop Protection Council, 291–300.

Quy, R.J., Cowan, D.P., Haynes, P., Inglis, I.R. and Swinney, T. 1994. Predicting the outcome of rodenticide trials against Norway rats living on farms. In: Halverson, W.S. and Crabb, A.C., ed., Proceedings of the 16th Vertebrate Pest Conference, Santa Clara, 1–3 March 1994. California, University of California, Davis, 133–137.

Quy, R.J., Cowan, D.P., Morgan, C. and Swinney, T. 1996. Palatability of rodenticide baits in relation to their effectiveness against farm populations of the Norway rat. In: Timm, R.M. and Crabb, A.C., ed., Proceedings of the 17th Vertebrate Pest Conference, Rohnert Park, 5–7 March 1996. California, University of California, Davis, 133–138.

Whishaw, I.Q. and Tomie, J.-A. 1987. Food wresting and dodging: strategies used by rats (*Rattus norvegicus*) for obtaining and protecting food from conspecifics. Journal of Comparative Psychology, 101, 202–209.

Whishaw, I.Q. and Whishaw, G.E. 1996. Conspecific aggression influences food carrying: studies on a wild population of *Rattus norvegicus*. Aggressive Behavior, 22, 47–66.

Coumatetralyl residues in rats and hazard to barn owls

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Abstract. The secondary poisoning hazard of coumatetralyl was evaluated through analysis of residues in rats (*Rattus norvegicus*, *R. tiomanicus* and *R. sordidus*) that had eaten coumatetralyl baits in laboratory and field trials, and in a feeding trial with captive barn owls. In *R. norvegicus* fed Racumin® over three nights, approximately 4% of the coumatetralyl eaten was detected as residue in the whole body. In a similar study with *R. tiomanicus*, approximately 3.7% of the coumatetralyl eaten was detected in the whole body. The range of total body coumatetralyl residues per body weight found in three rodent species had similar maximum values, despite interspecies differences in body sizes and bait intake. Three-day laboratory feeding studies with Racumin® produced similar maximum residue concentrations in tissues to those measured in field-poisoned rodents. Captive barn owls fed for 6 days on coumatetralyl-poisoned *R. tiomanicus* did not exhibit any secondary poisoning symptoms during the subsequent 30-day period, consistent with other findings that suggest coumatetralyl presents a relatively low hazard of acute secondary poisoning to predatory birds.

Introduction

Reports of anticoagulant residues in predatory birds (e.g. Newton et al. 2000) and other wildlife (e.g. Eason et al. 2002) appear to have increased over the last decade, heightening worldwide concern regarding non-target effects of rodenticide use. While this increase may be due in part to more sensitive monitoring and analytical techniques, the presence of residues indicates that primary or secondary exposure of non-target wildlife occurs. Non-target risk is a function of both exposure and hazard, and estimates of secondary poisoning hazard to rodent predators may be derived from evaluating residue concentration and distribution in rodent carcasses following lethal, or sublethal, bait intake. Studies have addressed aspects of secondary poisoning risk to owls from first- and second-generation anticoagulants (e.g. Lee 1994), but most have not included the first-generation anticoagulant coumatetralyl (Racumin®). An oral LD_{50} of 5 × 0.3 mg/kg coumatetralyl has been determined for rats (Hermann and Hombrecher 1962). Racumin® products (375 ppm coumatetralyl) are increasingly used on farms and crops, thus there is potential for predators to be exposed to poisoned rodents. To assess hazard, residues of coumatetralyl were determined after poisoning three rat species in laboratory trials, and in rodents collected after Racumin® application in the field. A feeding study investigated the effect of repeated consumption of coumatetralyl-poisoned rats on barn owls.

Materials and methods

Residues in *Rattus norvegicus* following coumatetralyl bait ingestion

Rats (*R. norvegicus* Wistar) were maintained at the Landcare Research Animal Facility, in a controlled-temperature environment (18°C ± 2°C) with water available *ad libitum*. Seventy-eight young adult rats were offered Racumin® wax block bait (375 ppm coumatetralyl: Bayer AG) without alternative food over three consecutive nights. On the fourth day, rats were anaesthetised using CO_2 gas, then killed by cervical dislocation. Six of these rats, chosen at random, were analysed for coumatetralyl concentrations in liver, gut (stomach, intestines and contents), and remainder of carcass (including skin, feet, and tail). The analytical limit of detection was 0.01 µg/g and uncertainty (95% confidence interval; c.i.) was ±11%.

Secondary hazard to barn owls from coumatetralyl-poisoned *Rattus tiomanicus*

Thirty adult wood rats (*R. tiomanicus*) were trapped and maintained at the Malaysian Cocoa Board Research and Development Centre, Hilir Perak. Rats were fed with Racumin® over 3 days *ad libitum* and without alternative

feed. Six rats were euthanased by cervical dislocation on the fourth day. Samples of liver, gut (stomach, intestines and contents) and the remainder of carcass were frozen at –20°C for later analysis. The analytical limit of detection was 0.02 µg/g ± 9% (95% c.i.). The remaining dead, whole rats were utilised in a feeding trial with barn owls (*Tyto alba*). Four owls were wild-caught and allowed one month acclimatisation to individual housing of timber and chicken wire construction, approximately 12 m^2, with a nesting box in one top corner. Owls were offered one unpoisoned rat per day as their normal diet, and during the trial offered one poisoned rat per day for six successive days. Food intake by owls was monitored, and the owls observed for 30 days after being returned to a normal diet.

Residues in *Rattus sordidus* following coumatetralyl bait ingestion

Cane-field rats (*R. sordidus*) were captured from cane fields near Ingham, Queensland, Australia. After 7 days on a sunflower seed diet, the individually caged rodents were offered a fresh Racumin® wax block each day in addition to sunflower seeds. Water was available *ad libitum* and food consumption recorded daily. One group of six rats was euthanased, using CO_2 gas, after 2 days and a second group after 4 days. Analysis for coumatetralyl concentration in the liver, gut (stomach, intestines and contents) and carcass (including skin, feet, tail and remaining internal organs) was carried out by Conmac Laboratories, Bethania, Queensland, according to the method described by Mundy and Machin (1982). The limit of quantification was 0.1 µg/g with average recoveries of 87% (Bureau of Sugar Experiment Stations, unpublished data, 1998).

Field residues in Australian rodents following application of Racumin®

In October 2000, the Australian National Registration Authority approved an emergency use permit for use of Racumin® wax blocks to control *R. sordidus* and the climbing rat (*Melomys burtoni*) in sugarcane crops. Baits were applied once in November 2001 to two field locations in Tully, northern Queensland, at a rate of 3 × 25 g blocks on a 15 × 15 m grid pattern (Bureau of Sugar Experiment Stations, unpublished data, 2002). After baiting, target species were collected from within and just outside the sites by breakback-trapping or carcass searches, and were sampled for liver, gut (including stomach, intestines and contents) and remainder of carcass, and frozen for later analysis. The analytical limit of detection was 0.02 mg/g ± 9% (95% c.i.).

Analysis of tissue samples for coumatetralyl

Except for the analysis of residues of coumatetralyl in *R. sordidus* in the cage trial described above, tissue samples were analysed at the International Accreditation New Zealand (IANZ) accredited Landcare Research Toxicology Laboratory, Lincoln, New Zealand, using methods based on Hunter (1983). The coumatetralyl analysis was shown to be robust with high recoveries (92.5%) and low method uncertainty. Analyses were validated in an inter-laboratory comparison, where the mean coumatetralyl residues from the same (n = 6) rat livers were 0.75 ± 0.08 µg/g and 0.78 ± 0.08 µg/g.

Results and discussion

Residues in *R. norvegicus* following coumatetralyl bait ingestion

The six rats sampled for tissue analysis weighed (mean ± sd) 298.10 ± 84.66 g, and ate a mean of 31.1 ± 3.5 g Racumin® per night for 3 nights, resulting in each rat consuming a total coumatetralyl dose of between 81.94 and 147.80 mg/kg. This was equivalent to approximately seven times the LD_{50} value for this species (WHO 1995). Coumatetralyl concentrations by weight of tissues were: liver (13.35 ± 10.45 mg/g), carcass (5.03 ± 2.59 mg/g) and gut (2.74 ± 5.81 mg/g). These concentrations, and the weight of the respective tissues sampled, were used to calculate total mean amounts of coumatetralyl (mg) in rat tissues (Table 1). The considerable variability in concentrations detected in gut was probably attributable to the presence of visible bait fragments in some samples. Total residues in a rat were 5.21 ± 2.55 mg/kg, so that approximately 4% of the coumatetralyl eaten as bait over 3 nights was found as residues in the whole body on the fourth day.

Table 1. Coumatetralyl residues in *Rattus norvegicus* (Rn) and *R. tiomanicus* (Rt) after 3 days' feeding with Racumin® (375 ppm coumatetralyl). Amounts of coumatetralyl shown are based on concentrations of coumatetralyl measured in samples (µg/g) and the weight of tissue sampled, with the mean calculated from values for individual rats (BW = body weight, n = number in sample, sd = standard deviation).

Species (n)	Mean BW (± 1 sd) (g)	Mean total coumatetralyl eaten (± 1 sd) (mg/kg BW)	Mean (± 1 sd) total amount of coumatetralyl in tissues (µg)		
			Gut	Liver	Carcass
Rn (6)	298.10 (84.66)	123.34 (27.65)	49.56 (104.91)	135.85 (140.05)	1235.08 (602.73)
Rt (6)	103.67 (20.68)	109.15 (22.57)	119.54 (83.25)	22.91 (20.66)	264.02 (118.00)

Secondary hazard to barn owls from coumatetralyl-poisoned *R. tiomanicus*

The six rats sampled for tissue analysis weighed (mean ± sd) 103.67 ± 20.68 g and consumed a total of 30.33 ± 8.91 g Racumin® over 3 nights, resulting in a total coumatetralyl dose of 109.15 ± 22.57 mg/kg. Coumatetralyl concentrations by weight of tissue were: liver 13.37 ± 14.94 mg/g, gut 11.22 ± 6.95 mg/g and carcass 2.88 ± 0.93 mg/g. Total mean amounts of coumatetralyl in rat tissues were calculated as above (Table 1). The total residues in *R. tiomanicus* were 3.86 ± 1.36 mg/kg, so approximately 3.7% of the coumatetralyl eaten as bait over 3 nights was found as residues in the whole body on the fourth day.

Each owl consumed one entire rat on each of 6 days, eating a mean total of 661.50 ± 7.12 g of rat. Based on the total mean residue concentration estimated in *R. tiomanicus* feeding on Racumin® (described above) and the body weight of individual owls (467.50 ± 25.86 g), it was estimated that owls had each secondarily consumed a 6-day total of up to 5.89 ± 2.07 mg/kg coumatetralyl, or approximately 1 mg/kg per day. This is a substantially lower dose than an 8-day LD_{50} for coumatetralyl in hens, given as >50 mg/kg daily consumption (Worthing and Hance 1991, p. 188). No visible effects on owls were observed and all four were alive and appeared healthy 30 days after feeding on the rats. This result is consistent with survival in a steppe buzzard (*Buteo buteo*) and a spotted eagle owl (*Bubo africanus*) fed coumatetralyl-killed sparrows (Heÿl 1986). In addition, a lack of obvious ill effects on weka (*Gallirallus australis*), a scavenging New Zealand bird that ate coumatetralyl-poisoned rats over 3 days, has been reported (O'Connor et al. 2002).

Residues in *R. sordidus* following coumatetralyl bait ingestion

The six *R. sordidus* sampled for tissue analysis after 2 days feeding on Racumin® weighed (mean ± sd) 148.0 ± 34.1 g and consumed a 2-day total of 11.48 ± 9.72 g, resulting in a coumatetralyl dose of 27.23 ± 18.91 mg/kg. The six *R. sordidus* sampled for tissue analysis after 4 days feeding weighed 131.7 ± 36.7 g and consumed a 4-day total of 10.05 ± 5.84 g Racumin®, resulting in a total coumatetralyl dose of 27.77 ± 11.27 mg/kg. In comparison to the *R. norvegicus* and *R. tiomanicus* trials, where no alternative food was offered, the availability of alternative food may have partly explained the relatively smaller coumatetralyl intake in this trial by *R. sordidus*. Generally reduced feeding could also be expected 2–3 days after the first ingestion of bait due to the onset of symptoms. The group sampled on the fourth day generally had lower daily intakes of bait than the group sampled on the second day, which may explain why residues were higher in *R. sordidus* feeding for 2 days than those feeding for 4 days (Table 2). Considerable variability of coumatetralyl concentrations in gut samples after 2 days' feeding suggested the presence of undigested bait.

Field residues in Australian rodents following application of Racumin®

Coumatetralyl was detected in six *R. sordidus* recovered between 1 and 6 days after bait application. Residue

Table 2. Coumatetralyl residues in tissues of *Rattus sordidus* after laboratory feeding or field application of Racumin® (*n* = number in sample, sd = standard deviation).

Trial (*n*)	Days after baiting	Mean total bait (g/rat)	Mean (± 1 sd) coumatetralyl residues (mg/g)		
			Gut	Liver	Carcass
Laboratory (6)	2 days	11.48	20.61 (34.33)	8.02 (5.05)	2.40 (1.48)
Laboratory (6)	4 days	10.05	1.01 (2.24)	2.11 (2.32)	0.46 (0.64)
Field (6)	1–6 days	not known	8.90 (9.65)	6.16 (7.11)	1.68 (2.15)

Table 3. Coumatetralyl residues (total all tissues) found in *Rattus sordidus* (Rs) and *Melomys burtoni* (Mb) according to days after Racumin® bait treatment in sugarcane fields, and residues in *Rattus norvegicus* (Rn) and *Rattus tiomanicus* (Rt) fed Racumin® in the laboratory (BW = body weight, *n* = number in sample, sd = standard deviation).

Treatment (days)	Species	*n*	Coumatetralyl residues (mg/kg BW)		
			Mean	sd	Range
1 (field)	Rs	4	1.57	3.19	0.02–6.44
5 (field)	Rs	1	6.51	–	–
6 (field)	Rs	1	3.02	–	–
11 (field)	Mb	1	0.15	–	–
3 (lab)	Rn	6	5.21	2.55	0.51–7.98
3 (lab)	Rt	6	4.36	1.84	2.26–6.89

profiles in these rats were similar to those in the same species offered Racumin® in the laboratory for 4 days, and much less than those feeding for 2 days (Table 2). Consistent with observations in the laboratory trials with other rat species, the variable residue concentrations detected in some field-collected *R. sordidus* gut samples (mean 8.90 ± 9.65 µg/g of tissue) suggests that undigested bait may have been present in some instances. Table 3 summarises the total coumatetralyl residues detected in rodents from three laboratory and one field trial with Racumin®. The data are limited by small sample sizes and not statistically comparable, but show that the range of total coumatetralyl residues found in three rat species had similar maximum values on a body weight basis (mg/kg), despite interspecies differences in body sizes and bait intake. On this basis, laboratory studies over 3 days seemed to provide a reasonable simulation of maximum field residues of coumatetralyl found in a limited sample of rodents.

Conclusions

There were similar concentrations of coumatetralyl (approximately 4% coumatetralyl eaten as Racumin® over 3 nights) detected in tissues of *R. norvegicus* and *R. tiomanicus*. The major route of elimination after oral administration of anticoagulants in rats is through the faeces (WHO 1995), however residues are probably highest if there is undigested bait in the gut within a few days of bait application. In field scenarios, such target animals would present the greatest hazard of secondary poisoning. Rodents in the laboratory trials were expected to have consumed in excess of a lethal dose of coumatetralyl, with the corresponding residue concentrations in the whole body close to a worst-case scenario in terms of secondary hazard to predators or scavengers. Comparison of the total body residues of coumatetralyl in different species of rodents after Racumin® intakes showed that laboratory feeding trials produced similar residue concentrations in tissues to those measured in target rodents after a field application of Racumin®. These results, alongside limited data regarding the toxicity of coumatetralyl to birds, suggest that there is a low acute hazard to barn owls feeding on rats containing relatively high concentrations of coumatetralyl residues.

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References

Eason, C.T., Murphy, E., Wright, G.R. and Spurr, E.B. 2002. Assessment of risks of brodifacoum to non-target birds and mammals in New Zealand. Ecotoxicology, 11, 35–48.

Hermann, G. and Hombrecher, S. 1962. Ratten- und Maeusebekaempfung mit Racumin® 57-Praeparaten. Pflanzenschutznachrichten Bayer, 15, 93–112.

Heÿl, C.W. 1986. Cumatetralyl as an avicide against the Cape sparrow. South African Journal for Enology and Viticulture, 7, 71–75.

Hunter, K. 1983. Determination of coumarin anticoagulant rodenticide residues in animal tissue by high-performance liquid chromatography: I. Fluorescence detection using post-column techniques. Journal of Chromatography, 270, 267–276.

Lee, C.H. 1994. Secondary toxicity of some rodenticides to barn owls. In: Proceedings of the 4th International Conference Plant Protect. Trop., Kuala Lumpur, Malaysia, 161–163.

Mundy, D.E. and Machin, A.F. 1982. The multi-residue determination of coumarin-based anticoagulant rodenticides in animal materials by high performance liquid chromatography. Journal of Chromatography, 234, 427–435.

Newton, I., Shore R.F., Wyllie, I. and Birks, J.D.S. 2000. Empirical evidence of side-effects of rodenticides on some predatory birds and mammals. In: Cowan, D.P. and Feare, C.J., ed., Advances in vertebrate pest management. Furth, Filander Verlag, 347–367.

O'Connor, C.E., Eason, C.T. and Endepols, S. 2002. Evaluation of secondary poisoning hazards to ferrets and weka from the rodenticide coumatetralyl. Wildlife Research (in press).

WHO (World Health Organization) 1995. Anticoagulant rodenticides. Environmental Health Criteria 175. Geneva, World Health Organization, 121 p.

Worthing, C.R. and Hance, R.J. 1991. The pesticide manual, 9th edition. Surrey, Great Britain, British Crop Protection Council, 1411 p.

Bromadiolone resistance does not respond to absence of anticoagulants in experimental population of Norway rats

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Abstract. Resistance to anticoagulant rodenticides in Norway rats (*Rattus norvegicus*) is documented to be associated with pleiotropic effects, notably with an increased dietary vitamin K requirement. The aim of this study was to quantify these effects in small populations of Norway rat in Denmark and to see how bromadiolone-resistant phenotypes are manifested when bromadiolone selection is absent. Experimental populations were established under semi-natural conditions with wild rats trapped at two Danish farms. The individuals caught on each of the two farms were divided into two experimental groups. One group was regularly exposed to bromadiolone whereas the other group was untreated. The level of bromadiolone resistance in the experimental populations was followed for two years. The results presented here are those results obtained in the absence of bromadiolone selection.

The pleiotropic selection against resistance in the two non-treatment populations was found to be insignificant. Thus, absence of anticoagulant, under the environmental conditions provided, did not lead to a selection favouring anticoagulant-sensitive rats. However, we found some evidence of selection against presumed homozygous resistant rats under non-anticoagulant conditions. Haemorrhagic symptoms are not only observed in sensitive rats exposed to anticoagulants, but are also a symptom for severe vitamin K deficiency in resistant rats. This suggests that bromadiolone resistance leads to loss of fitness, albeit that the cost is not strong enough to reduce the phenotypic resistance level or minimise the effect of random genetic drift.

Introduction

The documented pleiotropic effect of anticoagulant rodenticide resistance in rats is an increase in the dietary requirement for vitamin K in order to maintain reasonable production of blood clotting factors (Hermodson et al. 1969). Resistant rats that become vitamin K deficient will eventually suffer from haemorrhage, leading to death of the animal (Partridge 1980).

It is generally assumed that resistance to anticoagulants is selected against when anticoagulants are absent from the environment (Partridge 1979; Smith et al. 1991). The apparent selective disadvantage of anticoagulant resistance caused by the increased vitamin K requirement may be beneficial in rodent control. It could be hypothesised that by limiting the access to vitamin K, a common additive to animal feedstuffs, selection against resistant rats may be enforced.

However, the outcome of such initiatives will depend on a number of factors such as environmental conditions, the type of resistance (defined by the vitamin K requirement) and genotype frequencies. It is obvious that fitness, and thus selection against phenotypically resistant rats, must vary in correspondence with the requirement for vitamin K, with the strongest selection being against rats with a high vitamin K requirement (e.g. Welsh type), and selection against rats with a moderate increase in vitamin K requirement (e.g. Scottish type) being markedly reduced (MacNicoll et al. 2001).

Thus, the benefit of exploiting a removal of anticoagulants from the environment as an alternative resistance management strategy will depend on the extent of pleiotropy of those resistant rat populations that are to be controlled.

This study is part of a larger study investigating and evaluating the pleiotropic effects of bromadiolone resistance in Danish rat populations. For this purpose, four enclosed populations (excluding reinvasion from resistant/sensitive rats) of free-ranging wild bromadiolone-resistant rats were established. Two populations were left untreated and the other two populations were treated with bromadiolone (0.005%) twice a year. The level of bromadiolone resistance was monitored by means of a blood clotting response (BCR) test for a period of 2 years. Here we present results obtained from the two non-treatment (not treated with bromadiolone) populations.

Materials and methods

Materials

Wild rats, *Rattus norvegicus*, were collected from two farm populations (A and B), where bromadiolone resistance was known to occur.

Before establishment of the experimental units, all animals were trapped and caged individually for 4 weeks in order to test for bromadiolone resistance. All rats from population A (n = 79) and 95% of those from population B (n = 77) were identified as resistant by blood clotting response (BCR) tests (A.-C. Heiberg and H. Leirs, unpublished data). Resistant rats from each locality were divided into two experimental groups, a non-treatment (untreated) and a treatment population, resulting in two non-treatment and two treatment populations. In each group, we introduced wild rats that were tested as sensitive to warfarin in order to ensure the presence of non-resistant alleles within the populations. Before introduction into the indoor breeding pens (13 m^2), all rats were weighed, sexed and marked with a subcutaneous passive integrated transponder (PIT) tag for later individual recognition. The wild, warfarin-sensitive rats, like the resistant farm rats, had been singly caged for a period of 4 weeks (during the resistance testing). All the introduced farm rats were assumed to be just as much strangers to each other as they would be to the warfarin-sensitive rats. We did not find any significant evidence for resistant farm rats being more successful than the sensitive rats in becoming established in the experimental populations (data not shown). Rats were at all times, when not treated with bromadiolone, fed on lab-pellets (Altromin No.1324, 3 mg vitamin K_3/kg). Items like carrots, maize and sprouting wheat were added regularly. The illumination cycle was 12/12 hours dark/light.

Experimental treatment

Every 6 months, all animals were captured and removed from the four pens. All individuals were checked for PIT tags and their weight and sex were registered. From the two non-treatment populations, animals were randomly selected for resistance testing. The proportion of animals removed in each trapping session varied between 30% and 50% depending on the number of individuals in the total sample. In the first trapping, animals were selected randomly among all individuals, whereas in later trappings, animals that were documented older than 1.5 years were removed together with individuals chosen randomly among new individuals. Though rats of 1.5 years of age still may be reproductively active, rats of that age will seldom occur in natural populations.

Those animals that were re-introduced into the pens were all, under anaesthesia, PIT tagged and blood samples from the ventral tail vein collected (blood samples were used for later DNA analysis to infer parentage in the populations; A.-C. Heiberg et al., unpublished data). All individuals were introduced into the re-established pens simultaneously.

Rats that were found dead between trappings (in all four pens) were removed and autopsied to find the possible cause of death.

Resistance testing

The rats that had not been re-introduced into the pens were kept individually in standard metal cages with mesh bottoms (31.5 × 26 × 19 cm). Rats were fed plain rye bread and water *ad libitum*. Female rats were kept in quarantine for 3 weeks to ensure that they were not pregnant during the resistance test. Bromadiolone-resistant individuals were identified by BCR test (Gill et al. 1994). Bromadiolone was supplied by Lipha Lyonaise (France).

To determine the population level of resistance in each trapping, we only considered individuals that had been born after the previous trapping event. However, the new individuals were not necessarily BCR tested when they were trapped for the first time. If an animal was released after the trapping, the BCR result of that animal was first obtained when the animal was removed from the population. This procedure was chosen as the results obtained in BCR have proven to be stable with respect to aging of the animal (A.-C. Heiberg et al., unpublished observations).

Autopsy

Animals that died during resistance testing or anticoagulant treatments and those animals found dead in between trapping sessions were autopsied in order to verify the cause of death, if possible. The cause of death was classified into four categories: (1) haemorrhage due to an anticoagulant treatment/BCR; (2) haemorrhagic symptoms with no anticoagulant treatment; (3) no anticoagulant poisoning symptoms, but other obvious sign, e.g. pneumonia or other inflammatory conditions, starvation (due to teeth damage); and (4) no cause of death found.

Results

The population level of phenotypic resistance in non-treatment A for males and females did not change over time (P_{males} = 0.65 and $P_{females}$ = 0.99, Pearsons χ^2, STATISTICA). Likewise, the level of resistance remained unchanged in the population when not differentiating between sexes (Pearson χ^2 = 0.89, df = 4, P_{total} = 0.93, STATISTICA) (Figure 1).

In non-treatment B, the population level of resistance for females remained unchanged ($P_{females}$ = 0.28) (Figure 1). All sensitive males that had been introduced initially died within the first month, thus presumably only phenotypically resistant males contributed to the next generation. The level of resistance remained constant (100%) over the study period. When testing for heterogeneity in the population irrespective of sex, we only included the data from the four trappings. No significant changes were observed (Pearson χ^2 = 3.81, df = 3, P_{total} = 0.28).

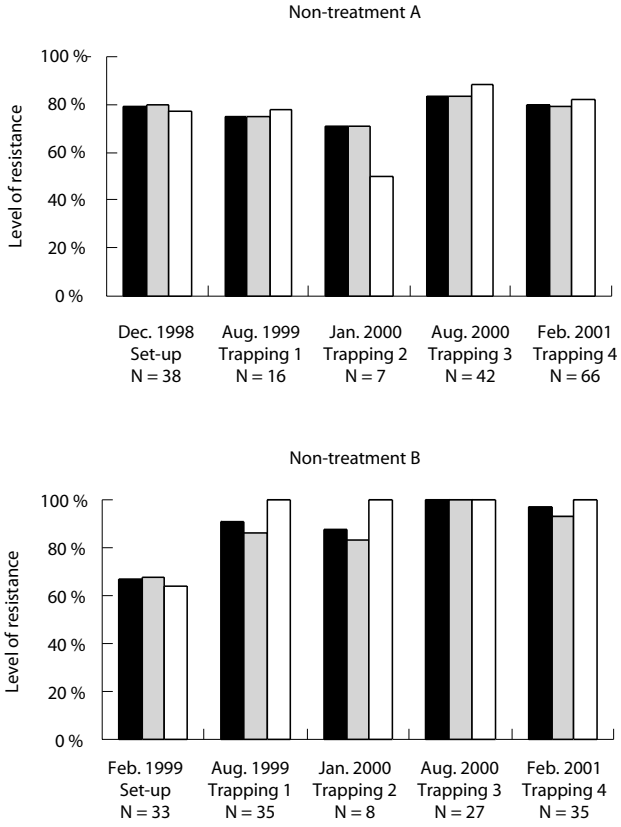

Figure 1. Level of observed phenotypic resistance within the two non-treatment populations, A and B. R_{total} (black bars) is the proportion of rats that were defined as bromadiolone resistant using the blood clotting response (BCR) test. $R_{females}$ (grey bars) and R_{males} (white bars) are the proportions of females and males, respectively, being defined as bromadiolone resistant. *N* is the number of rats tested using BCR.

Between the different trapping sessions we found animals with haemorrhagic symptoms (Table 1). Since these animals (including those animals from the treatment populations as they were found a minimum of 2 months after the last treatment) had not been exposed to anticoagulants before their death, these symptoms were taken as an indication of vitamin K deficiency. There is a general tendency (though not significant, except in non-treatment B) for males to be younger in age than females when dying with vitamin K deficiency symptoms.

Discussion and conclusion

Environmental conditions are important when the impact of selection against traits is to be evaluated. Rats often live in environments under constant change, thus the selection pressure and relative fitness of the different genotypes of the selected trait will change likewise (Mitton 1997). The experimental conditions that were examined in this study resembled those of farm rat populations in many ways. The environment of many rodent infestations in rural areas does provide, often unintentionally, excellent conditions for maintenance of anticoagulant resistance; e.g. farm buildings allowing rats to reproduce all year and abundance of good-quality and unprotected animal feed, which may be enriched with vitamin K (Kerins et al. 2001).

The level of resistance remained unchanged in the non-treatment populations when anticoagulant selection was removed. The presence of a stable vitamin K source may have resulted in an insignificant pleiotropic effect, as the vitamin K requirement of most of the resistant rats would have been met. Another explanation for the unchanged resistance level could be the small effective population sizes (N_e) in the investigated populations. Small N_e can render the direction of selection unpredictable over few generations due to random genetic drift (Falconer and Mackay 1996).

The N_e ranged between 8 and 25 breeding individuals in all four populations (A.-C. Heiberg et al., unpublished data), with large fluctuations in N_e from generation to generation. Knowing this, we simulated (a Wright-Fisher model) how genetic drift in 1000 populations with different N_e affected the frequency of the sensitive allele over 1, 2, 4, 6 and 10 generations given the relative fitness components of Partridge (1979) (absence of anticoagulant selection). For non-treatment A, we could ascribe the unchanged level of phenotypic bromadiolone resistance to the effects of random genetic drift, whereas the level of

Table 1. Animals found dead within the breeding pens between trapping/anticoagulant treatments with symptoms indicating vitamin K deficiency or antagonism. N_{dead} is the number of dead animals removed in total. $N_{A.S}$ is the number of animals with visible anticoagulant poisoning symptoms. The average age of individuals showing vitamin K deficiency was estimated based on the approximated age of the individuals. Age differences between males and females were tested with the non-parametric Kruskall–Wallis, Statistical Analysis System (SAS).

Treatment[a]	N_{dead}	$N_{A.S}$	$N_{dead/A.S}$	female $_{dead/A.S}$	male $_{dead/A.S}$	Average age (months ± sd)		Kruskall–Wallis
						female	male	*P*
Non-A	39	21	0.54	0.57	0.56	8.6 ± 5.6	5.8 ± 3.6	0.505
Treat-A	34	13	0.38	0.44	0.31	14 ± 5.0	8.6 ± 6.7	0.163
Non-B	74	39	0.53	0.39	0.63	9 ± 3.4	4.3 ± 2.9	0.001
Treat-B	49	23	0.47	0.36	0.52	6.8 ± 6.0	4.2 ± 1.3	0.737

[a] Non-A = rats from population A, not treated with bromadiolone; Treat-A = rats from population A, treated with bromadiolone (0.005%) twice a year; Non-B = rats from population B, not treated with bromadiolone: Treat-B = rats from population B, treated with bromadiolone (0.005%) twice a year.

resistance in non-treatment B could not be explained by the forces of drift or by selection. However, given the environmental conditions, the relative fitness components of Partridge (1979) might have been too low for both the homo- and heterozygous resistant rat in this experiment, indicating that selection against the resistant rats is weak.

Conversely, large numbers of rats died with haemorrhagic symptoms without being exposed to anticoagulants and, furthermore, the diet supplied to the rats contained 3 mg vitamin K_3/kg. These signs of vitamin K deficiency do suggest that bromadiolone resistance may have some marked disadvantages.

Homozygous resistant males from treatment populations A and B later showed that they were sensitive to a low vitamin K content diet (M.D.K. Markussen et al., unpublished results) whereas the resistant females showed moderate to no response to the vitamin K deficient diet. The haemorrhagic symptoms do, however, indicate that their vitamin K requirements were not met. The role of aging has not been investigated, but it could be speculated that the process of aging played a role when considering vitamin K requirement. Older rats may become more vulnerable to various diseases, which hypothetically could reduce their ability to fully utilise the vitamin K supplied in the diet.

We found that females dying with signs of vitamin K deficiency were generally older than males and that many of the females originating from the treatment populations had survived earlier treatments. The fact that females generally are less prone to vitamin K deficiency than males may explain the observed age difference, but most of the rats lived in the population for at least half a year before becoming vitamin K deficient. Thus it can be hypothesised that the death of these rats may be due to a reduced ability to utilise the vitamin K or that older resistant individuals experience a further increase in vitamin K requirement. However, conclusions on the importance of the aging process in the context of vitamin K requirement cannot be made based on these studies. More studies focusing on that aspect have to be done.

Though we were not able to see a reduced population level of bromadiolone resistance, the animals that apparently died due to vitamin K deficiency provide evidence for a pleiotropic effect of being resistant. The relatively short time span of the study (two years, $\approx$ 4–5 generations) may have been responsible for the fact that we did not see a reduction of bromadiolone resistance. Genetic drift in the relatively small populations could also explain why selection has no clear effect. We do, however, believe that the primary factor leading to the lack of response is a very weak selection resting upon the heterozygous resistant rat. Thus, removal of the anticoagulants alone as an alternative resistance management strategy will have no or only very limited effect.

References

Falconer, D.S. and Mackay, T.F.C. 1996. Introduction to quantitative genetics, 4th edition. Essex, Longman, 464 p.

Gill, J.E., Kerins, G.M., Langton, S.D. and MacNicoll, A.D. 1994. Blood clotting response test for bromadiolone resistance in Norway rats. Journal of Wildlife Management, 58, 454–461.

Hermodson, M.A., Suttie, J.W. and Link, K.P. 1969. Warfarin metabolism and vitamin K requirement in the warfarin-resistant rat. American Journal of Physiology, 217, 1316.

Kerins, G.M., Dennis, N., Atterby, H., Gill, J.E. and MacNicoll, A.D. 2001. Distribution of resistance to anticoagulant rodenticides in the Norway rat (*Rattus norvegicus* Berk.) in England 1995–98. In: Pelz, H.-J., Cowan, D.P. and Feare, C.J., ed., Advances in vertebrate pest management II. Proceedings of the 2nd European Vertebrate Pest Management Conference, Braunschweig, 6–8 September 1999. Fürth, Filander-Verl, (Zoological Library), Vol. 2, 149–159.

MacNicoll, A.D., Dennis, N.J., Atterby, H., Hudson, A., Langton, S., Kerins, G.M. and Gill, J.E. 2001. Fitness effects of different alleles of the warfarin resistance gene — implications for resistance management. In: Pelz, H.-J., Cowan, D.P. and Feare, C.J., ed., Advances in vertebrate pest management II. Proceedings of the 2nd European Vertebrate Pest Management Conference, Braunschweig, 6–8 September 1999. Fürth, Filander-Verl, (Zoological Library), Vol. 2, 171–180.

Mitton, J.B. 1997. Selection in natural populations. Oxford, Oxford University Press, 240 p.

Partridge, G.G. 1979. Relative fitness of genotypes in a population of *Rattus norvegicus* polymorphic for warfarin resistance. Heredity, 43, 239–246.

Partridge, G.G. 1980. Vitamin K deficiency syndromes in the warfarin-resistant brown rats (*Rattus norvegicus*). Laboratory Animals, 14, 193–195.

Smith, P., Townsend, M.G. and Smith, R.H. 1991. A cost of resistance in the brown rat: reduced growth rate in warfarin-resistant lines. Functional Ecology, 5, 441–447.

Warfarin susceptibility in the lesser bandicoot rat (*Bandicota bengalensis*)

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Abstract. Warfarin is a first-generation anticoagulant that relies on multiple feeding events to achieve lethality in susceptible rodents. For the bandicoot rat, warfarin-susceptibility baselines were established using the lethal feeding period (LFP) test methodology. Against a 0.003% warfarin formulation, LFP_{50} values of 2 and 4 days, and LFP_{99} values of 16 and 10 days were obtained for males and females, respectively. However, consumption of rodenticide was significantly reduced after the 4^{th} and 5^{th} day of test, at a time when animals would be expected to experience symptoms of warfarin toxicity. This would seriously compromise the Probit analysis, particularly for estimates of higher percentiles. Although the majority of animals were highly susceptible to warfarin, one female animal that survived a high dose of active ingredient (79.1 mg/kg) may bode for future resistance

Introduction

A number of rodenticides, including the anticoagulants brodifacoum, bromadiolone, chlorophacinone, diphacinone, and coumatetralyl, are registered in Pakistan, and are being marketed under different formulations and trade names. Total annual consumption of rodenticides (both acute and anticoagulants) during 1989–98 was reported to be between 0.1 and 45.6 t, according to the Pakistan Agricultural Pesticide Association.

The use of anticoagulant rodenticides is considered highly effective and safe due to their delayed mode of action and the availability of the complete antidote, vitamin K_1. The delayed action prevents the association of cause (the rodenticide) and effect (symptoms of toxicity), and as a result, conditioned bait aversion (or bait shyness) does not occur. The main drawback for these compounds was the development of physiological resistance, particularly in Norway rat (*Rattus norvegicus*) and house mouse (*Mus* sp.), which developed in populations following prolonged exposure (see Greaves 1994). Resistance has also been reported in other rodent species (i.e. *Rattus rattus*, *R. tiomanicus*), although the genetic basis of the resistance differs from that of Norway rat and house mouse (Chia 2000). The emergence of resistance motivated researchers to develop methods for its detection and monitoring in rodent populations. The lethal feeding period (LFP) test (WHO 1982) is commonly used for detection of resistance, and has been included by the European Plant Protection Organization (EPPO 1995) in their guidelines for testing rodents for resistance to anticoagulant rodenticides.

Like other South Asian countries, a complex of rodent species is responsible for indoor and outdoor infestations in Pakistan. The bandicoot rat is widely distributed in the region and is one of the more prominent pest species. Efficacy of a number of rodenticides (including anticoagulants) has been tested against this species in the field and under laboratory conditions (Mathur et al. 1992). Sensitivity to warfarin in the bandicoot rat has been reported to vary between geographically distinct populations: in Bombay, India (Deoras 1967; Renapurkar et al. 1973); in Karachi, Pakistan (Greaves and Rehman 1977); and in Rangoon, Burma (Brooks et al. 1980).

The present work was initially conducted to establish warfarin-susceptibility baselines for the bandicoot rat using the LFP test methodology (EPPO 1995). The baseline data could then be used as a basis to detect the emergence of physiological resistance in field populations.

Materials and methods

The study was carried out following the EPPO (1995) guideline for testing rodents for resistance to anticoagulant rodenticides. The rats were live-trapped from the crop and non-crop areas of the National Agricultural Research Centre (NARC), Islamabad, Pakistan (33°42'N, 73°07'E) between September 1995 and May 1996. The prevalence/ status of anticoagulant resistance was unknown in this

population, although they had not been exposed to an anticoagulant for at least 2 years before this study.

The animals were sexed, weighed and caged individually, with food and water freely available. The laboratory maintenance diet comprised locally milled wheat flour (40%), corn flour (40%), fishmeal (10%), full-cream dry powdered milk (5%), crude sugar (2%) and sunflower oil (3%). No supplementary vitamin K was provided. Animals were maintained in the laboratory for at least 3 weeks before testing. During this time, daily food and water consumption was monitored and the animals were kept under observation to ensure they were healthy and to acclimatise them to the test conditions. Animals that were pregnant, sick, poor feeders, or were outside the body weight range of 150–350 g were not included in the study. The room temperature was maintained at 23–25°C with a natural day/night light regime.

The warfarin baits were prepared from 1% powdered concentrate (Sorex Ltd, St Michaels Trading Est., Widnes, Cheshire WA8 8TJ, England), and the bait concentrations (0.003%, 0.005% or 0.025%) were freshly formulated as required for each test.

In the light of earlier reports on warfarin susceptibility in the bandicoot rat (Deoras 1967; Brooks et al. 1980), feeding tests were initiated using 0.005% warfarin bait. In an initial ranging study, two animals of each sex were presented the bait for feeding periods of 2, 3, 4, 5 and 6 days. Complete mortality was achieved with the exception of four animals that survived feeding periods of 2 and 3 days. Survival was insufficient for effective Probit analysis (Finney 1971).

In accordance with the EPPO (1995) guidelines, the warfarin content of the test formulation was reduced to 0.003%, in order to provide sufficient feeding periods with incomplete survival. Subsequently, the group sizes for critical feeding periods were increased to 10 male or 10 female animals (EPPO 1995). For each test animal, either survival or the day of death was recorded. Survivors were observed for a further 21 days post-test observation period, and animals that died were examined for evidence of haemorrhage.

Surviving bandicoot rats were allowed to recover for 30 days, and subsequently subjected to a field-strength warfarin formulation (0.025%) for a 4-day no-choice feeding test. Animals that survived the field-strength formulation (plus the 21-day post-test observation period) were again offered the field-strength formulation in a no-choice feeding regime until death.

The lethal feeding period response data were subjected to Probit analysis, using Proc Probit (Probit – log days) in SAS (release 6.8) for WINDOWS. Other statistical analyses were performed using computer-based packages MINITAB (32 bit, release 10.51 Xtra) and Microsoft EXCEL.

Results and discussion

The feeding test results for bandicoot rats given 0.003% warfarin bait for feeding periods of between 1 and 7 days are summarised in Table 1. Complete mortality was achieved following a 6 and 7 day feeding period for males and females, respectively. As the response of males differed significantly from that of females ($\chi^2 = 5.0$, df = 1, $P = 0.025$), Probit analysis was performed and lethal feeding period percentiles were calculated separately for

Table 1. Mortality in the bandicoot rat after no-choice feeding on bait containing 0.003% warfarin for various numbers of days.

Sex/Feeding days	Body weight (g) mean ± se	Mortality (dead tested)	Amount of active ingredient (mg/kg) consumed		Daily intake of warfarin (mg/kg/day) mean ± se (*n*)	Mean days to death
			Survivors mean ± se (range)	Non-survivors mean ± se (range)		
Males						
1	289.8 ± 9.3	3/10	2.2 ± 0.2 (1.6–2.8)	2.9 ± 0.5 (2.2–3.9)	2.61 ± 0.12 (61)	6.7
2	261.2 ± 17.7	5/10	4.2 ± 0.3 (3.1–5.1)	4.8 ± 0.3 (4.0–5.7)	3.01 ± 0.16 (51)	7.6
3	255.5 ± 19.9	7/10	6.6 ± 0.6 (5.4–7.6)	9.3 ± 1.2 (6.0–15.3)	3.18 ± 0.18 (41)	7.0
4	230.0 ± 13.6	6/10	14.6 ± 2.7 (11.0–22.7)	14.1 ± 2.1 (9.2–23.5)	3.05 ± 0.21 (31)	8.8
5	211.8 ± 16.2	9/10	12.4	16.0 ± 1.5 (9.0–25.8)	2.28 ± 0.21 (20)	7.7
6	265.9 ± 9.2	11/11	–	13.2 ± 0.9 (7.1–17.3)	1.79 ± 0.35 (8)	7.0
Females						
2	240.5 ± 9.0	1/10	4.8 ± 0.2 (3.9–5.7)	7.0	2.78 ± 0.11 (60)	4.0
3	235.0 ± 11.9	3/10	8.9 ± 0.9 (6.6–12.7)	8.7 ±1.1 (7.2–10.9)	3.02 ± 0.14 (50)	8.7
4	220.0 ± 17.8	8/10	13.7 ± 3.1 (10.7–16.8)	11.5 ± 1.3 (7.4–16.8)	2.90 ± 0.13 (39)	7.4
5	227.8 ± 11.3	8/10	11.6 ± 0.7 (11.1–12.1)	13.3 ± 1.3 (9.3–21.4)	2.57 ± 0.14 (28)	7.4
6	228.4 ± 10.9	8/10	22.1 ± 1.4 (20.8–23.5)	16.1 ± 1.1 (13.5–22.6)	2.05 ± 0.23 (19)	8.0
7	241.4 ± 16.6	11/11	–	14.3 ± 2.4 (3.4–30.3)	0.98 ± 0.38 (9)	7.5

each sex. Against a 0.003% warfarin formulation, LFP_{50} values of 1.9 and 3.4 days, and LFP_{99} values of 15.5 and 9.1 days were obtained for males and females, respectively. EPPO (1995) recommend the use of the LFP_{99} (rounded up to the next whole day) as the discriminating feeding period to identify anticoagulant resistance (the resistance checking test). On this basis, the discriminating feeding period for warfarin resistance in the bandicoot rat is 16 days and 10 days for males and females, respectively.

The mean time from initial feeding on the warfarin formulation to death was 7.7 ± 0.25 days (n = 41) and 7.6 ± 0.30 days (n = 39) for males and females, respectively. No significant difference between the sexes was observed (F = 0.2, df = 79, P = 0.72). Of the 122 rats tested, 88 (72.1%) were affected by the poison (with external bleeding and/or the 'stop feed' effect) and of these, 80 animals died and 8 animals recovered completely and survived the test. Of the 80 animals that died, three developed symptoms of poisoning (the 'stop feed' effect) on the third day of the test.

For the bandicoot rat, males would appear more susceptible to warfarin than females. Of animals dying after the consumption of less than 5 mg/kg of warfarin, 14.6% (6/41) were males and 5.1% (2/39) were females; and the maximum warfarin dose survived by females (23.5 mg/kg) was greater than that survived by males (22.7 mg/kg). A similar sex difference has been reported for the Norway rat (Greaves and Cullen-Ayres 1988).

The results for the screening of the survivors of the LFP test against field-strength warfarin (0.025%) are summarised in Table 2. The only survivor was one female that consumed a warfarin dose of 79.1 mg/kg. In this study, the maximum warfarin dose consumed by all other animals that survived a feeding test was 23.5 mg/kg. The above female has survived a dose more than three times greater than that survived by all other animals tested.

Considerable variation in sensitivity to warfarin for different populations of bandicoot rat has been reported (Deoras 1967; Renapurkar et al. 1973; Greaves and Rehman, 1977; Brooks et al. 1980). Previous studies on warfarin susceptibility in the bandicoot rat showed two levels of susceptibility. In Rangoon, there was high mortality after a 6-day feeding period with single male and female survivors consuming 3.0 and 2.7 mg/kg warfarin, respectively (Brooks et al. 1980), while in Karachi, male and female survivors consumed maximum doses of 97 and 87 mg/kg warfarin respectively (Greaves and Rehman 1977). The present population would appear to be more tolerant to warfarin than the Rangoon population but more susceptible than the Karachi population. Brooks et al. (1980) considered these variations in susceptibility to be attributable to the selection pressure resulting from the consistent use of first-generation anticoagulants, to geographical variations, and to the distribution of bandicoot rats as isolated races in both urban and agricultural environments.

In the present study, one can speculate that survival of the female animal and its potential descendants following a prolonged warfarin treatment could initiate a resistance focus. The amount of warfarin consumed by this female rat is similar to that consumed by survivors in the Karachi study (Greaves and Rehman 1977).

In this study, using a 0.003% warfarin formulation, complete mortality was achieved with a feeding period of 6 and 7 days for males and females, respectively, thus demonstrating that bandicoot rats are highly susceptible to warfarin. However, Probit analysis calculated LFP_{50} values of 1.9 days and 3.4 days, and LFP_{99} values of 15.5 days and 9.1 days for males and females, respectively. The LFP_{99} values are much longer than expected, particularly for male animals.

Consumption of test bait (and thus active ingredient uptake) was reduced as the test progressed (Table 1). Among the 88 affected rats, 9 males and 14 females exhibited the 'stop feed' effect, and the majority of these belonged to test groups that were fed warfarin for 5 days or more. This 'stop feed' phenomenon has also been recorded and described in both the Norway rat and the house mouse (Rowe and Redfern 1964; Drummond and Wilson 1968; Lund 1988).

In the analysis of the susceptibility baseline data, Probit analysis will assume that the incremental increase in feeding period will be equal throughout the test period. However, in the present study (Table 1), the incremental increase of bait consumed was reduced on the 5th, 6th and

Table 2.Mortality in the bandicoot rat after no-choice feeding on bait containing 0.025% warfarin for 4 days.

Sex	Body weight (g) mean ± se	Mortality (dead/tested)	Amount of active ingredient (mg/kg) consumed	
			Non-survivors mean ± se (range)	Survivor
Males	353.0 ± 17.2	6/6	63.1 ± 11.3 (54.6–81.1)	–
Females	308.4 ± 13.5	12/13	60.9 ± 7.7 (43.8–72.4)	79.12[a]

[a] Subsequent feeding till death on warfarin (0.025%) resulted in mortality on day 8 after consuming 82.77 mg/kg. Daily intake was: 8.75, 14.29, 16.79, 14.46, 12.77, 8.30, 7.23 and 0.18 mg/kg.

7^{th} days. This would seriously compromise the Probit analysis, particularly for estimates of higher percentiles. The problem would appear to be greater for males than for females, and would account for the lower LFP_{50} value and higher LFP_{99} value of males compared to females, despite the fact that dose mortality data indicates that males are more susceptible to warfarin than females.

The test procedures suggested by WHO (1982) and EPPO (1995), requiring the strength of the anticoagulant rodenticide to be adjusted so that some of the susceptible population will survive after 4 to 6 days feeding on anticoagulant, is considered flawed, because of the 'stop feed' effect. One possible option might be to assess mortality on the basis of active ingredient intake rather than duration of the feeding period. However, a reduced anticoagulant strength could undermine the efficacy of the compound in use due to possible metabolic clearance of low daily doses of anticoagulant—an aspect that may not be related to genetic resistance.

Lethal feeding period tests are a useful tool for the assessment of physiological resistance, and can be used to provide a realistic assessment of the likely impact of resistance in the field situation. However, where feeding periods extend beyond 4 days, the 'stop feed' effect can affect results, either by causing an overestimation of the LFP_{99} discriminating dose for susceptible animals, or by misclassifying a susceptible animal as resistant in the subsequent application of the resistance checking test.

References

Brooks, J.E., Htun, P.T. and Naing, H. 1980. The susceptibility of *Bandicota bengalensis* from Rangoon, Burma to several anticoagulant rodenticides. Journal of Hygiene, Cambridge, 84, 127–135.

Chia, T.H. 2000. Growth, distribution and susceptibility of major rat species to anticoagulant rodenticides and the inheritance of resistance to warfarin in *Rattus tiomanicus* in oil palm plantations in Peninsular, Malaysia. PhD thesis. Reading, UK, University of Reading.

Deoras, P.J. 1967. Tolerance status of some rats to an anticoagulant poison. Current Science, 36, 207–208.

Drummond, D.C. and Wilson, E.J. 1968. Laboratory investigations of resistance to warfarin of *Rattus norvegicus* Berk. in Montgomeryshire and Shropshire. Annals of Applied Biology, 61, 303–311.

EPPO (European Plant Protection Organization) 1995. Guideline for the evaluation of resistance to plant protection products: Testing rodents for resistance to anticoagulant rodenticides. EPPO Bulletin, 25, 575–593.

Finney, D.J. 1971. Probit analysis, 3^{rd} edition. Cambridge, Cambridge University Press, 333 p.

Greaves, J.H. 1994. Resistance to anticoagulant rodenticides. In: Buckle, A.P. and Smith, R.H., ed., Rodent pests and their control. Wallingford, UK, CAB International, 197–217.

Greaves, J.H. and Cullen-Ayres, P.B. 1988. Genetics of difenacoum resistance in the rat. In: Suttie, J.W., ed., Current advances in vitamin K research. New York, Elsevier Science Publishers, 381–388.

Greaves, J.H. and Rehman, A.B. 1977. The susceptibility of *Tatera indica*, *Nesokia indica* and *Bandicota bengalensis* to three anticoagulant rodenticides. Journal of Hygiene, Cambridge, 78, 75–84.

Lund, M. 1988. Detecting and monitoring of resistance to anticoagulant rodenticides in populations of brown rats (*Rattus-norvegicus*) in Denmark. In: Suttie, J.W., ed., Current advances in vitamin K research, New York, Elsevier Science Publishers, 399–405.

Mathur, R.P., Kashyap, N. and Mathur, M. 1992. Bioefficacy of anticoagulant rodenticides. In: Prakash, I. and Ghosh, P.K., ed., Rodents in Indian agriculture. Jodhpur, India, Scientific Publishers, 517–583.

Renapurkar, D.M., Menon, T.U.K., Bhat, V.M. and Sant, M.V. 1973. Tolerance in *Bandicota bengalensis* to warfarin. Pesticides, Bombay, 7, 23–27.

Rowe, F.P. and Redfern, R. 1964. The toxicity of 0.025% warfarin in wild house-mouse (*Mus musculus* L.). Journal of Hygiene, Cambridge, 62, 389–393.

WHO (World Health Organization) 1982. Instructions for determining the susceptibility or resistance of rodents to anticoagulant rodenticides. WHO Vector Biology and Control Series 82, 843, 9 p.

Factors influencing the occurrence of rodent infestations in an inner city area of Manchester

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Abstract. Cheetham Hill is an inner city area of Manchester, England. A study area that was typical of other areas of the city was defined which contained 253 domestic properties. The area has a diverse mix of domestic properties ranging in age and type from pre-1919 terraces to more recently built detached/semi-detached dwellings in public and private ownership. Tracking plates were used to detect rat activity externally, but little evidence was found. Only two properties in the area were found to have indoor rat activity. A qualified surveyor gained access to 117 properties to undertake a thorough constructional survey. Fifty per cent of the properties had indoor mouse infestations. The factors associated with these indoor infestations were examined. Variables that were significantly associated with indoor mouse infestations were screened and allocated to one of four models. Binary logistic regression was used to explore the ability of these models, including a total model, to predict the likelihood of indoor mouse infestations. All five models significantly improved the ability to predict indoor mouse infestations in the study area. Whilst the model which had all variables included was the most reliable in predicting infestation, those which relied on general factors (tenure of the property, date of construction, and type of dwelling) or the external structure (state of the damp-proof course, external front and back overall assessment, gaps on the door thresholds, and the presence of airbricks) also proved useful. These models could be used to investigate other urban areas to confirm their reliability in predicting indoor mouse infestations. The need for a review of the way in which rodent control services are resourced and delivered in the United Kingdom is discussed.

Introduction

The two main commensal rodent species in the United Kingdom (UK) are *Mus domesticus* and *Rattus norvegicus.* Both pose a potential threat to public health through the diseases they may carry and, therefore, an understanding of their distribution and potential contact with man is important in trying to estimate the actual risks posed. The English House Condition Survey (EHCS) is undertaken every 5 years and examines the state of the housing stock in the UK. The 1996 survey form included questions relating to rodent infestations and provided an important indication of the levels of rodent infestations associated with domestic properties. This survey reported modest infestation rates of 1.83% for mice living indoors, 0.23% for rats living indoors, and 1.6% for rats living outdoors (Langton et al. 2001).

Colvin and Jackson (1999) emphasised the need to define the characteristics within a habitat that favour infestation and Advani (1995) demonstrated that, in urban environments, areas with inadequate sanitary and building maintenance measures had higher numbers of rats. Socio-economic factors were also found to influence the ecology of commensal rodents (Childs et al. 1991).

In the UK, a plethora of organisations is involved in controlling commensal rodents in the urban environment (Murphy and Oldbury 2002). Local authorities in the UK have powers to enforce statutory instruments to protect public health, and although there is no statutory requirement for them to undertake treatments to control rodents in domestic premises, many local authorities do provide such a service. The way in which this service is operationalised varies across the UK with local political pressures and sensitivities determining decisions regarding whether charges are levied for the service. Charging is often related to historical (and often erroneous) views about rats and mice, with rats being classified as public health pests (and therefore usually treated free of charge in domestic premises) and mice as nuisance pests (with a charge made for domestic treatments). Some local authorities attempt to offset the cost of their public health pest control activities by charging commercial rates for treatment of nuisance pests such as wasps, garden ants and mice. In addition to the services that may be offered by local authorities, private pest control companies offer services to eradicate pests in domestic properties, and householders are able to purchase rodenticides for personal use.

Local authorities that do undertake domestic infestation treatments are often hampered in their efforts to effectively control domestic mouse infestations. Whilst rigorous legislation relating to food premises exists which provides authorised officers of the local authority (usually

Environmental Health Officers, EHOs) with powers of entry, the law relating to commercial non-food and domestic premises is relatively weak. The main piece of legislation used in these settings is the *Prevention of Damage by Pests Act 1949* (PDPA). This legislation was introduced primarily to protect agricultural crops against rodent damage and its fundamental weakness is that it does not furnish EHOs with powers of entry. Although some local authorities have introduced local legislation to provide such powers of entry (for example, the *Greater Manchester Act 1981*), many do not have such legislation in place. Thus, if an infestation is confirmed within a terraced property, EHOs are often unable to gain access to all properties to treat the block if the owner refuses entry.

A tool to predict the likely presence of domestic mouse infestations would prove useful in two ways. Firstly, it could be used as supporting evidence to convince a Magistrate of the need to issue a warrant allowing access to properties to confirm the presence of an infestation and specify measures to eradicate the infestation. Secondly, and more importantly, it would provide evidence to those who set the resource levels available for pest control work that there is a need to undertake block treatments in certain situations to ensure long-term and cost-effective control. Meyer and Drummond (1980) raised concerns about the effectiveness of pest control services that only react to public reports of infestations. By treating individual premises in an infested block, the likelihood of re-infestation from neighbouring properties is high. While they acknowledged that the initial costs of undertaking block treatments was significant, they found that once the infestation had been reduced by the first systematic treatment, the extra cost of keeping it low was financially justified.

This paper examines the reliability of using external and internal factors in predicting the likelihood of the presence of indoor mouse infestations.

Materials and methods

The research area in Cheetham Hill, Manchester, is a typical inner city residential area with a mixture of privately and publicly owned domestic properties ranging in age from pre-1919 terraces to post-1964 detached and semi-detached properties. The research area encompassed 253 residential properties. A qualified surveyor gained access to 117 properties and surveyed them internally and externally. Only 2 of the 253 properties in the area had evidence of rats inside the property, and only 4 of the196 tracking plates placed externally throughout the study site showed evidence of rats outside the properties (see Taylor and Quy 1973 for techniques used). The analysis presented is, therefore, based on evidence of mouse activity inside the properties.

The surveyor inspected each property internally and externally and scored the general area with regard to four general aspects of the properties (described below). The surveys were undertaken between January and May 2002. Residents either volunteered or were recruited during contact with the research team and appointment times convenient to the resident were agreed. As the same surveyor undertook all of the surveys, consistency was assured. He did not attempt to estimate the size of the population but recorded evidence (presence of rodent droppings, hairs, gnawing, runs, smells, damage to goods, footprints/tail swipes) of internal mouse infestations. In addition to searching for signs of rodent infestation, he also asked the resident whether he/she thought the property was infested and to show him the signs of infestation. A survey report for each property was completed, and data were compiled in an SPSS electronic database. Cross-tabulations were carried out against presence or absence of indoor mouse infestations, and where significant associations were found, the variables were screened and spurious results excluded. Variables that were significant, plausible and relatively easy to assess in the field were grouped into four categories (see Table 1 for details of the characteristics included in each model):

- general characteristics of the property;
- external structure;
- general food hygiene within the kitchen area; and
- general environment external to the property.

Using these categories, four models were tested using binary logistic regression to examine the goodness of fit in predicting indoor mouse infestations. In addition, all variables used in the models were entered into a total model.

Results and discussion

Fifty per cent of the properties surveyed were found to be infested with mice indoors. This is significantly higher than the levels of indoor mouse infestations reported in the EHCS ($\chi^2 = 933$; $p < 0.001$). Whilst the sample size in Cheetham Hill is modest, this difference may highlight a potential problem with the way in which the EHCS data were collected and weighted. Meyer and Drummond (1980) reported the effects of clumping in mouse infestations, and the EHCS, whilst giving a good indication of infestations across the UK, may miss the clumping effect, particularly in urban areas with a high proportion of older terraced properties.

The relationship between specific variables and the presence of mouse infestations was explored using a chi-square analysis (Table 1). Whilst individually these associations are valuable and provide important information about the factors which may influence the presence of an indoor mouse infestation, using them within a model provides a mechanism to examine the relative importance of difference characteristics within the environment. Results from the four models plus the total model showed that for each model the drop in the –2 log-likelihood statistic was significant (Table 2), confirming that each significantly improved the ability to predict the presence of domestic mouse infestations. The Hosmer and Lemeshow test statistics were all non-significant, confirming a good fit between the logistic equation and the observed data.

Table 1. Variables related to four general aspects of the properties surveyed with χ^2 statistics, significance levels and percentage mouse infestation for each variable (df = degrees of freedom, *n* = number in sample, LA = local authority).

GENERAL CHARACTERISTICS (Model 1)			**KITCHEN (Model 3)**		
Tenure of the property (χ^2 = 9.04, 2 df, p = 0.011)			*Kitchen food storage* (χ^2 = 15.85, 2 df, $p < 0.001$)		
Variable	*n*	% infested	Variable	*n*	% infested
Privately owned	84	48	Good	34	23
Privately rented	23	71	Satisfactory	69	58
LA rented	10	20	Poor	14	79
Date of construction (χ^2 = 42.14, 3 df, $p < 0.001$)			*Kitchen refuse storage* (χ^2 = 20.52, 2 df, $p < 0.001$)		
Pre-1919	60	77	Good	34	23
1919–1939	6	67	Satisfactory	69	55
1940–1964	3	67	Poor	14	93
Post-1964	48	15			
Dwelling type (χ^2 = 31.7, 1 df, $p < 0.001$)			*Kitchen under-cupboard access* (χ^2 = 9.77, 1 df, p = 0.002)		
Detached/semi-detached	43	16	Yes	73	62
Terraced/flats	74	70	No	44	32
EXTERNAL STRUCTURE (Model 2)			*Kitchen overall hygiene* (χ^2 = 14.35, 2 df, p = 0.001)		
Damp-proof course (front and back) (χ^2 = 25.58, 1 df, $p < 0.001$)			Good	34	23
			Satisfactory	64	59
Satisfactory	72	32	Poor	19	68
Unsatisfactory	45	80			
External front and back overall assessment (χ^2 = 5.4, 1 df, p = 0.02)			**GENERAL ENVIRONMENT (Model 4)**		
Satisfactory	100	46	*Vacant properties* χ^2 = 19.09, 1 df, $p < 0.001$)		
Unsatisfactory	17	76			
Gaps on external door thresholds (χ^2 = 14.11, 1 df, $p < 0.001$)			Little problem	51	27
			Substantial problem	66	68
Gaps present	30	80	*Industrial waste/rubbish* (χ^2 = 19.09, 1 df, $p < 0.001$)		
No gaps	87	40			
Airbricks (χ^2 = 11.86, 1 df, p = 0.001)			Little problem	51	27
			Substantial problem	66	68
No airbrick present	50	32	*Domestic waste/rubbish* (χ^2 = 19.09, 1 df, $p < 0.001$)		
Airbrick present	67	64			
			Little problem	51	27
			Substantial problem	66	68
			Evidence of residents feeding pigeons (χ^2 = 17.57, 1 df, $p < 0.001$)		
			Little problem	50	28
			Substantial problem	67	67

Table 2. Statistics for binary logistic regressions (models 1–4 and total model).

	Model 1	Model 2	Model 3	Model 4	Total model
Initial –2 log-likelihood	162.2	162.2	162.2	162.2	162.2
Model –2 log-likelihood	104.1	123.7	130.5	141.9	74.2
Chi squared	58.1	38.5	31.6	20.32	88.0
Significance	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Hosmer Lemeshow test	p = 0.992	p = 0.838	p = 0.997	p = 0.964	p = 0.858
R_L^2	0.358	0.237	0.195	0.125	0.542
% sample correctly classified	82.1	72.6	69.2	70.1	83.8

The R_L^2 statistic (the proportional reduction in the absolute value of the log-likelihood) confirmed that whilst the total model was best at predicting the outcome variable, model 1 provided the next best predictor of internal mouse infestation. The ability of the models to correctly classify each case ranged from 69.2–83.8%, with the total model again proving to be the most reliable.

Although the total model was the most reliable, the collection of all the data specified in this model is resource intensive and in some instances, where access to the property is denied, impossible. The use of external characteristics that are relatively easy to assess may provide a useful indication of the likelihood of internal mouse infestations. The high prevalence of infestations in older, privately rented, terraced properties with external indicators of poor general maintenance concurs with previous studies and these may be more useful indicators of infestation than internal hygiene measures. The problems of leaving potential pockets of infestation within blocks are well recognised (Rennison and Shenker 1976). However, the constraints of the current legal framework in the UK, together with the variability in charging policies, result in operational difficulties when attempting to treat whole blocks.

The failure of those charged with setting public health budgets within local authorities to recognise the long-term advantages of block treatments results in a reactive service dominating the approach to treating domestic infestations in the UK. This is further complicated by the vexed issue of charging for domestic mouse infestation treatments. Indeed, some local authorities are scrutinising their pest control services and deciding whether to privatise them. This is unlikely to improve the coordination and delivery of public health services related to urban rodent control.

These models have provided a reliable indicator of the likelihood of infestation, but caution must be applied to their applicability in other urban areas. The sample size used in the models is modest and the factors found to influence indoor mouse infestations may be unique to Cheetham Hill. Further rigorous testing of the models in other urban settings is required to confirm their reliability and to enable others to use them as a tool for arguing for the need to undertake block treatments. More intensive analyses of the results will also refine the relative importance of the variables included in each model.

Conclusions

The fragmented approach to urban rodent control in the UK is cause for concern. The primary aim of local authorities is to protect public health, but the current legislative framework for rodent control and the manner of resourcing the service make it difficult to ensure that treatments are effective in protecting human health. This is further complicated by a lack of coordination between those providing pest control services in the public and private sectors. The results of the Cheetham Hill study confirm the need for a holistic approach to block treatments. Meyer and Drummond (1980) emphasised the need for such an approach over two decades ago, but little progress in implementing such a policy has been made. Urban pest control is often viewed as a low priority, and there is, therefore, little hope of a review of the legislative framework. Sadly, a serious outbreak of rodent-borne disease within an urban setting is likely to be the only driver to provide the impetus for such a review. Although no evidence of behavioural or physiological resistance to rodenticide baits was found in the mouse populations in Cheetham Hill, resistance has been confirmed in other mouse populations within the UK (Humphries et al. 1992), and if these resistant populations increase, their avoidance of bait and bait stations may further hamper control measures.

References

Advani, R. 1995. Mouse populations and their control in New York City. International Biodeterioration and Biodegradation, 36, 135–141.

Childs, J.E., Glass, G.E. and Le Duc, J.W. 1991. Rodent sightings and contacts in an inner city population in Baltimore, Maryland, USA. Bulletin of the Society of Vector Ecology, 16, 245–255.

Colvin, B.A. and Jackson, W.B. 1999. Urban rodent control programs for the 21st century. 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, 243–257.

Humphries, R.E., Meehan, A.P. and Sibly, R.M. 1992. The characteristics and history of behavioural resistance in inner-city house mice (*Mus domesticus*) in the UK. In: Borrecco, J.E. and Marsh, R.E., ed., Proceedings of 15th Vertebrate Pest Conference. University of California, 161–164

Langton, S.D., Cowan, D.P. and Meyer, A.N. 2001. The occurrence of commensal rodents in dwellings as revealed by the 1996 English House Condition Survey. Journal of Applied Ecology, 38, 699–709.

Meyer, A.N. and Drummond, D.C. 1980. Improving rodent control strategies in Lambeth. Environmental Health, 88, 77–81.

Murphy R.G. and Oldbury D.J. 2002. Rat control by local authorities within the UK. In: Jones, S.C., Zhai, J. and Robinson, W.H., ed., Proceedings of the 4th International Conference on Urban Pests, Charleston, South Carolina, USA, 6–10 July 2002, 413–420.

Rennison, B.D. and Shenker, A.M. 1976. Rodent infestation in some London Boroughs in 1972. Environmental Health, 84, 9–13.

Taylor, K.D. and Quy, R.J. 1973. Marking system for the study of rat movements. Mammal Review, 3, 30–34.

Investigating residents' perceptions of urban rodents in Manchester, UK

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Abstract. The need to understand and explore the perceptions about urban rodents in communities is an important and often neglected area of urban rodent control programs. This study investigated the perceptions of a group of residents living in an inner city area of Manchester about urban rodents. The study area contained 253 domestic properties, and a questionnaire was sent to all these properties. A response rate of 88.5% was achieved. Forty-four per cent of residents stated that they currently had mouse infestations in their property, 44% stated they did not, and the remaining 12% were unsure. Residents were asked to indicate their levels of agreement with nine statements about rodents. The vast majority clearly understood the potential risks to health posed by rodents and that infestations were likely to spread through blocks. The majority of respondents agreed with the statement that poisons were the best way to get rid of mice (65%) and rats (71%), suggesting that they may overestimate the efficacy of such an approach and underestimate the impact of environmental management. This view was supported by analysis of their approaches to treatments, with a heavy reliance on the use of poisons and little attempt to undertake environmental management. Significant differences in opinions were found when the sample was split into those with and without experience of domestic mouse infestations. This study underlines the importance of providing communities with clear, consistent advice on the biology of urban pests and coordinated approaches to control. The need for fundamental research on the biology and control of rodents in the urban environment is acknowledged.

Introduction

The need to understand and explore the risk perceptions of communities is an important and often neglected area of urban rodent control programs. Only by establishing these factors can effective risk communication with the public be successfully undertaken. Previous attempts to involve local residents in control programs have reported varying degrees of success (Margulis 1977; Colvin and Jackson 1999; Lambropoulos et al. 1999). However, if communities are not centrally involved by ensuring their beliefs and perceptions of urban rodents are incorporated into control programs, then they may believe that rodent control is someone else's responsibility and that they have little to contribute to control programs. A small, but growing, body of empirical work in risk communication and related fields has investigated the effects of different message formats. No single presentation format has been found to be unequivocally the best, and the preferred format appears to vary depending on whether the purpose of the risk communication effort is to educate, to affect risk perceptions, or to motivate people to take appropriate actions. Characteristics such as the audience's level of knowledge and education; their mental models, attitudes and beliefs about the issue at hand; their level of receptivity and openness to the ideas being communicated; and their concerns about the issue will also affect the way in which risks are communicated (Bier 2001).

Rowan (1991) identified five possible goals of risk communication: building trust in the communicator; raising awareness (e.g. of the potential disease hazard of rodents); educating; reaching agreement (e.g. on a particular strategy for ensuring long-term control of rodent infestations); and motivating action (e.g. encouraging residents to adopt an integrated control strategy to reduce levels of infestation). Because of this multiplicity of purposes, different strategies of risk communication may be appropriate for different goals.

The success of both *Mus domesticus* and *Rattus norvegicus* can be largely attributed to their ability to live in close association with man (Rowe 1973; Shenker 1973; Childs et al. 1991). Although rats and mice have been found to harbour a wide array of pathogens, the actual magnitude of the public health threat posed by rodents remains unclear (Gratz 1994; Childs et al. 1998). An understanding of the distribution, behaviour and potential contact of urban rodents with humans is essential in trying to estimate this public health risk. Different perceptions in

the attitudes of the public to rats and mice may influence the way in which they implement their own control strategies and such actions may inadvertently facilitate the establishment of chronic infestations. This study examined the perceptions of residents to rodents and examined the beliefs they have about approaches to treatments.

Materials and methods

Cheetham Hill is an inner city area of Manchester with a history of pockets of chronic mouse infestations, which local residents regularly reported to the politicians representing that area. However, a review of Manchester City Council's pest control section records found little evidence of the reporting of these infestations. The charging policies of local authorities on rodent treatments vary throughout the United Kingdom (UK) and are often related to historical (and often erroneous) views about rats and mice, with rats being classified as public health pests (and therefore usually treated free of charge in domestic premises) and mice as nuisance pests (with a charge made for domestic treatments). Whilst Manchester City Council's pest control section does undertake domestic mouse infestation treatments, up until May 2002 a significant charge was levied for such treatments (apart from those occurring in Council-owned properties) and may partly explain the low numbers reported to them.

A site within Cheetham was selected and the boundaries were defined to ensure that the study area reflected a 'typical' inner city Manchester area in terms of property types (including terraced, semi-detached, detached and cottage flats ranging in age from pre-1919 terraces to post-1964 semi-detached houses), ownership (public/private) and the demographics of the population. The study site contained 253 residential properties. Community events before the fieldwork commenced, followed by regular newsletters, ensured that the residents within the study site were aware of the aims of the project. All householders in the research area were asked to complete and return a questionnaire that sought general and specific information on personal details, experience of mouse infestations and general beliefs about rodents. All data from the questionnaire were entered into a SPSS database for analysis.

Results and discussion

Two hundred and twenty-four questionnaires were returned, giving a response rate of 88.5%. This high response rate was achieved by sending out further questionnaires to non-respondents and by the efforts of community members in encouraging non-respondents to complete and return them.

Mouse infestations

Forty-four per cent of respondents reported that they currently had a mouse infestation in their property, 44% stated that they did not, and 12% reported that they did not know. Those respondents who did not currently have an infestation were asked whether they had experienced mouse infestations in the past and 41% stated that they had. The reliability of this information was validated by comparing it with the results from mouse tracking plates left in 202 properties, which confirmed mouse activity in 73 (36%). Whilst lower than that estimated by the residents, it does show that the data provided by the residents are reasonably reliable. The overall level of mouse infestation is considerably higher than that quoted by Langton et al. (2001) of 1.83%. Whilst the two studies have fundamental differences in the sampling techniques used, the differences in infestation rates are striking and suggest that the random sampling of properties reported by Langton et al. (2001) may miss concentrated pockets of mouse infestation.

Rat infestations

Although the project focused primarily on mouse infestations, several questions related to rats. Respondents were asked whether they thought rats had been present in the research area during the previous 12 months. Forty-eight per cent thought rats had been present, 45% did not know and only 7% believed there were no rats present. They were asked to clarify what information they had used to come to this view. The most common evidence, cited by 59% of respondents, was that someone else had told them. Fifty six per cent stated that they had seen rats, 15% stated they had heard them, and 3% gave other reasons. Residents were asked to indicate on a map the areas where they had seen rats. Of the 274 rat tracking plates were placed in the study area (6.65 ha) for four days (see Taylor and Quy 1973 for techniques), only four plates showed positive rat activity. This would suggest that residents may overestimate the presence of rats and may amplify the risks posed by rats. Only 31% of those who believed rats were present had reported it to anyone, despite the fact that the local authority provides free treatments to control domestic infestations.

Concerns about the presence of rodents

Respondents' concerns about rodent infestations were explored. Residents were asked to indicate their level of concern about mouse and rat infestations. Seventy per cent indicated that they were very concerned about mouse infestations, 20% reported they were concerned, and 4% reported they were not concerned. Eighty-one per cent stated they were very concerned about rat infestations, 15% stated they were concerned, and 3% reported they were not concerned. There was a significant relationship between levels of concern about rats and mice ($\chi^2 = 107.6$, df = 4, $p < 0.0001$). Results from intensive tracking show little evidence of rats in the area, but high levels of mouse infestations, yet high levels of concern about both species were found.

Respondents were asked to specify why they were concerned about mouse infestations (n = 132) and the largest group (47%) cited diseases or that they were

unhealthy. Fifteen per cent mentioned that they were concerned about the problems they brought to the area and 14% stated that they did not like them.

Respondents were asked to consider nine statements and to indicate on a four-point scale their agreement with each statement (Table 1). The analysis that follows was based on the valid responses, and missing cases were ignored.

The link between the presence of rodents and the transmission of disease was well understood by respondents with 96% and 99%, respectively, agreeing or completely agreeing that people could catch diseases from mice and rats. However, anecdotal evidence suggests that residents are unclear as to the nature of these risks and may be overestimating the actual risks posed. Cheetham Hill has suffered from chronic pockets of mouse infestations for many years and it was, therefore, predictable that the majority of respondents (73%) would acknowledge the difficulties of eradicating such infestations.

The high levels of agreement that if their neighbour has mice then they are likely to get mice (94%) suggests that respondents appreciate the importance of constructional features in facilitating infestations and the need to treat all properties in a block.

There was a fairly even split between those who agreed (52%) and disagreed (48%) with the statement that mice are more likely to live in dirty houses, which suggests that not all of the respondents may appreciate the need for high levels of hygiene when attempting to eradicate mouse infestations.

Chemical poisons will usually form an essential element of a rodent control strategy, but analysis of the responses on whether using poisons is the best way to get rid of rats (71%) and mice (65%) suggests that residents may overestimate their efficacy in controlling rodent populations. The importance of environmental improvements may need to be emphasised.

Whilst the majority of respondents believed that poisons should be removed when mice were not present, over a third (35%) agreed or completely agreed that leaving poisons down all the time was a good strategy to adopt. Respondents may not be aware that leaving poisons down may result in the poison losing potency and may also encourage the development of resistant mouse populations.

There was clear confusion about where rats are likely to live, with 71% agreeing that rats live inside houses. This may have been influenced by media reports, which frequently cite rodents gaining entry to premises via toilets etc. This may also partially explain the high levels of concern regarding the presence of rats in the area.

To investigate whether views varied between those respondents who had experience of infestations (either currently or previously) and those who had not, the respondents were split into two groups: those with (n = 154) and without (n = 64) infestation experience. The responses to the nine questions were collapsed into two categories (completely agree/agree and disagree/completely disagree) and chi-squared tests applied. No significant differences were found to the responses for: disease transmission from mice (p = 0.174) and rats (p = 0.843); risk of infestation from neighbouring property (p = 0.0550); leaving poisons down all the time (p = 0.913); using poisons is the best way to get rid of rats (p = 0.218); or that rats live inside houses (p = 0.55). Significant differences between those with and without previous experience of mouse infestations were found in the responses to: easy to get rid of mice (χ^2 = 6.45, df = 1, p = 0.011); mice more likely to get live in dirty

Table 1. Analysis of the responses to nine statements about rodents (n = 224; CA = completely agree, A = agree, D = disagree, CD = completely disagree). The percentages presented relate to valid cases; the number of missing cases is shown below each statement.

Statement	CA	A	D	CD
People can catch diseases from mice	137	61	7	1
(Missing cases = 18)	66%	30%	3%	<1%
People can catch diseases from rats	153	51	3	0
(Missing cases = 17)	74%	25%	1%	–
It is easy to get rid of mice	14	41	100	48
(Missing cases = 21)	7%	20%	49%	24%
If my neighbour has mice I will get mice too	99	93	13	0
(Missing cases = 19)	48%	45%	6%	–
Mice are more likely to live in dirty houses	50	54	77	20
(Missing cases = 23)	25%	27%	38%	10%
Using poisons are the best way to get rid of mice	48	78	55	14
(Missing cases = 28)	25%	40%	28%	7%
Using poisons are the best way to get rid of rats	73	66	37	20
(Missing cases = 28)	37%	34%	19%	10%
Always leave poisons down, even if you don't have mice at the moment	27	39	73	50
(Missing cases = 35)	14%	21%	39%	26%
Rats live inside houses	70	68	49	6
(Missing cases = 31)	36%	35%	25%	3%

houses ($\chi^2 = 4.16$, df = 1, $p = 0.041$) and using poisons is the best way to get rid of mice ($\chi^2 = 6.7$, df = 1, $p = 0.01$).

Respondents were asked how they thought the mice had got into their property ($n = 132$). The largest proportion (48%) stated that they did not know. Other reasons included via floorboards (15%), outside doors (11%), general holes (7%), and the cavity walls (5%). Residents were also asked where they thought the mice were coming from ($n = 149$). The largest proportion thought that mice were coming from the garden or outside (34%). Thirty-two per cent thought mice were coming from next door and 20% stated that they did not know where the mice were coming from.

Control measures

Analysis of the approaches adopted by those in the study area to control mouse infestations was undertaken. Of the 154 respondents who had experienced infestations either currently or previously, 77% had attempted to get rid of the mice themselves. Respondents were given four options (use of live-traps, snap-traps, poisons and 'other' methods) and asked to indicate all the methods they had used. Results are presented in Table 2. Poisons were used by 62% of the respondents, traps (either live or snap) by 56% of respondents and other methods by 13%. Only two respondents mentioned the need for improved hygiene and maintaining the fabric of the building. Thirty-six respondents reported that they had not attempted to control the infestation. It is unclear what influenced their decisions not to undertake treatments themselves.

Table 2. Control strategies adopted by respondents ($n = 116$).

Control measure	*n*	%
Poison only	36	31
Poison and snap-trap	18	15
Snap-trap only	16	14
Live-trap only	10	9
Other combination	7	6
Poison and live-trap	9	8
Live-trap, snap-trap and poison	9	8
Other methods only	8	7
Live-trap and snap-trap	3	3

Conclusions

Colvin and Jackson (1999) emphasised the importance of coordinated efforts supported by technical leadership at the local level in promoting successful urban rodent control programs. The results of this study underline the importance of clear, consistent information from those coordinating urban rodent control. Misconceptions regarding the risks posed by rodents, the most effective strategies for control and the importance of environmental management need to be fully explored and appropriate educational material developed and delivered. However, without the underpinning research to establish the actual risks posed by urban rodents, it is difficult to communicate these risks effectively.

Inconsistencies in the approach to the control of rats and mice as a result of political pressures mean that residents receive mixed messages about the risks rodents may pose and the most appropriate approaches to control. If residents believe that the use of poisons is the best way to gain control, then they will put little effort into environmental management—therefore they need information that is reliable and consistent on integrated rodent pest management and the contributions they can make to long-term control. If they do not feel any sense of ownership to the problems associated with infestations, then approaches to coordinated control will remain piecemeal and rodent populations will continue to exploit the plethora of niches available in the urban environment.

References

Bier, V.M. 2001. On the state of the art: risk communication to the public. Reliability Engineering and System Safety, 71, 139–150.

Childs, J.E., Glass, G.E. and LeDuc, J.W. 1991. Rodent sightings and contacts in an inner city population of Baltimore, Maryland, USA. Bulletin of the Society of Vector Ecology, 16, 245–255.

Childs, J.E., McLafferty, S.L., Sadek, R., Miller, G.L., Khan, A.S., DuPree, E.R., Advani, R., Mills, J.N. and Glass, G.E. 1998. Epidemiology of rodent bites and prediction of rat infestation in New York City. American Journal of Epidemiology, 148, 78–87.

Colvin, BA. and Jackson, W.A. 1999. Urban rodent control programs for the 21st century. 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, 243–257.

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

Lambropoulos, A.S., Fine, J., Perbeck, A., Torres, D., Glass, G.E., McHugh, P. and Dorsey, E.A. 1999. Rodent control in urban areas. Environmental Health, Jan–Feb, 12–17.

Langton, S.D., Cowan, D.P. and Meyer, A.N. 2001. The occurrence of commensal rodents in dwellings as revealed by the 1996 English House Condition Survey. Journal of Applied Ecology, 38, 699–709.

Margulis, H.L. 1977. Rat fields, neighbourhood sanitation, and rat complaints in Newark, New Jersey. Geographical Review, 67, 221–231.

Rowan, K.E. 1991. Goals, obstacles and strategies in risk communication: a problem solving approach to improving communication and risks. Journal of Applied Communication Research, 19, 300–329.

Rowe, F.P. 1973. Aspects of mouse behaviour related to control. Mammal Review, 3, 58–63.

Shenker, A.M. 1973. The house mouse in London. Mammal Review, 3, 64–69.

Taylor, K.D. and Quy, R.J. 1973. Marking system for the study of rat movements. Mammal Review, 3, 30 –34.

Effects of the addition of L-histidine on the toxicity of zinc phosphide in laboratory rats and mice

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Abstract. The efficacy of rodenticidal compounds can be enhanced greatly if the acceptance or palatability is improved. In this study, the effect of the addition of L-histidine (which yields histamine, a very active substance physiologically for decarboxylation and a useful acid-secreting stimulant) on the toxicity of the rodenticide zinc phosphide was determined using laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*). The animals were fasted for 0, 6, 12, 18 or 24 h and then fed *ad libitum* with baits containing zinc phosphide (2%) alone or zinc phosphide (2%) plus L-histidine (0.004%).

Feeding of zinc phosphide alone resulted in 100% mortality in rats (n = 8) and mice (n = 8) when the fasting period was less than 24 or 18 h, respectively. One of eight rats fasted for 24 h, and one of eight mice fasted for either 18 or 24 h, survived. There was 100% mortality in all rats and mice fed zinc phosphide plus L-histidine. Uptake of this bait by rats was significantly greater and the time to death shorter than in the groups fed zinc phosphide only.

Introduction

In rodent pest management programs, poison baiting is the most widely used technique throughout the world (Gratz 1973; Muktha Bai 1996). Although rodenticides can be incorporated either in bait, dust or water formulations (Pratt 1983), they are generally included in food baits to achieve good control. Much effort has been made to improve the palatability of rodent baits to ensure maximum ingestion by the target rodent pests and thereby improved efficacy. A survey of the literature indicates that several attempts have been made to improve the palatability of various rodenticides, including alpha-chlorohydrin (Ericsson et al. 1971), alpha-chlorolose (Greaves et al. 1968; Cornwell 1970), norbormide (Greaves et al. 1968; Cornwell 1970; Jackson 1974), strychnine (US Patent 1960), warfarin (Cornwell 1970; Abrams and Hinkes 1974), and zinc phosphide (Cornwell 1970; El-Sebae et al. 1978; Anonymous 1986). These studies have involved a variety of methods such as encapsulation and micro-encapsulation. The results obtained have shown, in most cases, some improved palatability, but mortality was reduced. However, there is limited information available regarding the effect of compounds/additives having different pharmacological or physiological modes of action on the palatability of rodenticides.

Recent outbreaks of hantavirus pulmonary syndrome (HPS) and resistance to second-generation anticoagulant rodenticides have demonstrated a need for use of acute rodenticides in rodent pest management programs (Childs et al. 1994). A more effective formulation of these acute rodenticides would be appropriate. In this study, the responses of laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*) to zinc phosphide (2%) (an acute rodenticide) were determined after they had been deprived of food for different periods of time (0–24 h). These responses were compared with those of fasted rats and mice fed zinc phosphide bait (2%) also containing L-histidine (0.004%). In the stomach, the histidine is decarboxylated to yield histamine, which stimulates acid secretion and aids the liberation of the phosphine gas.

Materials and methods

Baits

Zinc phosphide (technical grade, 94% purity; Tata Fison, Bombay) and L-histidine (Fluka Ag, Switzerland) were used. These were mixed thoroughly with the basal diet (wheat flour, 26.6%; ragi flour, 26.6%; chickpea flour, 26.7%; peanut oil, 10%; casein, 6.7%; calcium carbonate, 0.7%; shark liver oil, 0.7%; and common salt, 2%) to the required concentrations of (i) 2% zinc phosphide or (ii) 2% zinc phosphide plus 0.004% L-histidine.

Animals

Adult albino rats (*Rattus norvegicus:* CFT-Wistar strain; males, 180–220 g; females, 160–190 g) and adult albino

mice (*Mus musculus*: males, 25–35 g; females, 18–30 g) were maintained under 12 h dark and 12 h light periods at 25°C ± 5°C in the animal house at the Central Food Technological Research Institute. Ten groups of eight rats (four males and four females) each were housed individually in polypropylene cages (410 × 282 × 150 mm) and were provided with food and water ad libitum. Similarly, mice were also divided into ten groups of eight animals each but were housed in groups of four per cage (290 × 220 × 140 mm). All the animals were acclimatised for a period of 7 days. These experiments were approved by the Institute's Animal Ethics Committee.

Test procedure

All animals were held on a standard diet with water *ad libitum* for 5–7 days before the experiment commenced. The 10 groups of rats and mice were then deprived of food for a specific period (0, 6, 12, 18 or 24 h). For each period, two groups of animals (for both rats and mice) were used, and at the end of the fasting period they were given either baits containing 2% zinc phosphide alone or 2% zinc phosphide plus 0.004% L-histidine. The baits were placed in the cages for one night only and the next morning the residues were weighed and intakes calculated. The animals were closely monitored for symptoms (such as restlessness, heavy breathing, ataxia, paralysis of hind limbs etc.), mortality and time to death throughout the experimental period. The survivors were observed further for a period of 3 weeks while they were maintained on stock diet and water *ad libitum* and the results obtained were statistically analysed. The results of rats fed zinc phosphide and zinc phosphide plus L-histidine for different fasting periods were compared for parameters such as body weight, bait intake, and active ingredient intake using analysis of variance, followed by Duncan's new multiple range test whenever significant results were obtained (Douglas 1991).

Results

Laboratory rats (*R. norvegicus*)

Although at 'zero' h of fasting the mean ingestion of the bait was low (1.06 ± 0.5 g/rat) compared to the previous day's food intake of 15.2 ± 0.9 g/rat, all rats died within 8 h (range: 6–7.30 h) (Table 1). For fasting periods of 6, 12, 18 and 24 h, the mean ingestion of bait per rat was greater (2.6 ± 1.2, 3.5 ± 1.3, 4.1 ± 2.0 and 3.25 ± 1.6 g, respectively), and mortality was 100%, except in the group fasted for 24 h before exposure to the bait, where one rat survived. The time to death ranged from 4–20 h (Table 1).

The groups of rats given the baits containing zinc phosphide plus L-histidine after the period of fasting ingested almost twice as much of this bait. This was significantly different from the corresponding values of animals given zinc phosphide alone. The average time to death was reduced to approximately 6 hours and all rats died (Table 1).

Table 1. Response of laboratory rats (*Rattus norvegicus*) to baits containing zinc phosphide (2%) either alone or with added L-histidine (0.004%) (values are mean ± se of eight rats in each group). Means of the same column followed by different letters differ significantly ($p < 0.05$) according to Duncan's new multiple range test (** = very highly significant ($p < 0.001$), * = highly significant ($p < 0.01$), ns = not significant ($p > 0.05$). The parameters were also compared with the corresponding values of zinc phosphide (2%) fed animals using student's *t*-test.

Body weight (g)	Fasting period (h)	Food intake before fasting (g)	Poison bait intake (g)	Intake of active ingredient (mg/kg body weight)	Mean time to death (h) (range)	Mortality (%)
Zinc phosphide (2%)						
208.5 ± 10.7a	0	15.2 ± 0.9a	1.06 ± 0.5a	102.7 ± 47.5a	7.10 (6–7.30)	100
210.5 ± 13.8a	6	16.1 ± 2.0a	2.62 ± 1.2b	241.7 ± 121.4ab	12.20 (6–15)	100
207.2 ± 8.6a	12	17.4 ± 2.4a	3.50 ± 1.3b	330 ± 124.5bc	12.20 (7–20)	100
208.1 ± 6.3a	18	16.5 ± 2.2a	4.12 ± 2.0b	397.7 ± 192.7c	14.0 (4–20)	100
207.9 ± 5.5a	24	18.7 ± 5.8a	3.25 ± 1.6b	309.6 ± 148.2bc	12.0 (4–20)	87.5
sem: ±3.26		±1.13	±0.49	±47.97		
Zinc phosphide (2%) plus L-histidine (0.004%)						
169.9 ± 14.1a**	0	16.0 ± 2.9a*	3.62 ± 0.9a**	399.7 ± 195a**	4.0 (2.30–8)	100
170.2 ± 14.8a**	6	17.6 ± 2.6a*	7.12 ± 1.1b**	834.6 ± 80.2b**	6.16 (3–12)	100
166.8 ± 11.9a**	12	16.0 ± 2.3a*	6.2 ± 1.5b**	745 ± 142.2b**	6.0 (4–12)	100
168.8 ± 13.2a**	18	17.0 ± 2.0a*	7.2 ± 1.5b^{ns}	841.8 ± 118.4b**	6.32 (3–12)	100
167.9 ± 12.3a**	24	16.9 ± 1.6a*	7.2 ± 1.1b^{ns}	851.2 ± 93.5b**	6.45 (4–10)	100
sem: ±4.80		±0.82	±0.44	±40.64		

Albino mice (*M. musculus*)

The responses of the mice to baits containing zinc phosphide were similar to those of the rats. All mice died in the groups fasted for 12 h or less, and the time to death ranged from 5–11 h. One mouse survived in each group where the fasting period was longer than 12 h (Table 2), and time to death ranged from 8–24 h. While the bait intake of individual mice could not be recorded, as they were housed in groups of four per cage, it was noted that in all the groups, all of the bait (10 g/group) was consumed. For the groups of mice fed baits containing zinc phosphide plus L-histidine, all animals died and the time to death ranged from 4–12 h (Table 2).

Table 2. Response of laboratory mice (*Mus musculus*) to baits containing zinc phosphide (2%) either alone or with added L-histidine (0.004%). (Values are mean ± se of eight mice in each group). Mice were kept in groups of four/cage, therefore bait intake by individual mice could not be recorded.

Body weight (g)	Fasting period (h)	Mean time to death (h)	Mortality (%)
Zinc phosphide (2%)			
26.9 ± 1.2	0	8.52 (8–10)	100
26.9 ± 1.5	6	7.0 (5–7)	100
26.9 ± 1.2	12	10.0 (8–11)	100
27.4 ± 1.9	18	12.30 (8–16)	87.5
28.8 ± 4.0	24	22.0 (22–24)	87.5
Zinc phosphide (2%) plus L-histidine (0.004%)			
29.0 ± 2.2	0	7.50 (4–10)	100
30.4 ± 2.4	6	8.0 (4–10)	100
29.8 ± 0.7	12	10.0 (6–12)	100
30.2 ± 2.0	18	10.0 (6–12)	100
33.2 ± 3.0	24	11.0 (10–12)	100

Discussion

This study has demonstrated that fasting animals before testing the efficacy of new bait formulations may not necessarily lead to increased consumption of baits or a reduction in the time to death. This phenomenon has been observed previously (Hollander 1955; Bell et al. 1965). For research and development studies of new formulations of rodenticides, it may be wise to undertake a pilot experiment to determine the most appropriate period of food deprivation before full evaluation of new compounds.

When zinc phosphide baits have been used in large-scale rodent control programs, a common criticism has been the level of bait consumption by free-living rodent populations in the presence of alternative food sources. In such situations, rodents may be expected to consume smaller quantities of toxic bait and survivors may develop ‘bait shyness’ (Muktha Bai et al. 1980; Prakash 1988). While the success of baiting programs is always closely associated with consumption of toxic baits, it is reasonable to assume that the higher the bait consumption, the higher the level of mortality. However, the results of our present studies have also clearly indicated that addition of L-histidine to zinc phosphide improves significantly the palatability, reduces the time to death, and enhances the mortality of rats and mice. This could be a significant achievement in the development of a new formulation of zinc phosphide and its wider application, because other methods like encapsulation or micro-encapsulation (El-Sabae et al. 1978) or coating with paraffin wax or steric acid (Chyun 1973) have not improved the mortality, although acceptance/palatability was enhanced.

It is well known that the toxicity of zinc phosphide, which is hydrolysed by the acid present in the stomach of animals which have ingested zinc phosphide baits, is due to the liberation of phosphine (Hayes and Laws 1991). In our studies, the rats with no fasting period before being fed with zinc phosphide bait showed 100% mortality with a mean time to death of 7.1 h. However, feeding rats (0 h fasting) with zinc phosphide plus L-histidine resulted in a higher intake of bait/rat (3.60 ± 0.9 g) and also reduced the mean time to death to 4 h. This could be attributed to the action of L-histidine plus the presence of food in the stomach and the secretion of acid in the animals (Feinburg et al. 1950; West and Todd 1961, pp. 1113–1115; Bell et al. 1965; Muktha Bai 1979). This was further corroborated in our experiments by the results observed for the shorter time to death of rats given histidine in bait compared to those given bait without histidine.

In rodent pest management programs, much emphasis has been placed on increasing acceptance of toxic zinc phosphide baits in the absence of improving the efficacy of rodenticides by adding compounds/additives which help to release the toxic gas phosphine. In the present studies, the results indicate the beneficial effect of adding L-histidine (0.004%) to zinc phosphide (2%) baits. There was a significant improvement in palatability as measured by bait consumption, an increase in mortality, and a decrease in the time to death after bait consumption. The addition of L-histidine could minimise the secondary hazards arising from consumption of carcasses of poisoned rats due to the presence of unreacted toxicant in the rodent's stomach. Indeed, Rudd and Genelly (1956) have reported that several days are required for the complete breakdown of zinc phosphide in the stomach. Thus, the possibility of secondary poisoning occurring during that time could be prevented by the addition of L-histidine.

Thus, adding L-histidine (0.004%) to zinc phosphide (2%) baits may be more effective for both rats and mice living in free conditions with access to alternative food sources, because there will be an increase in the efficacy of baits through a reduction in the time to death and a minimisation of secondary effects on non-target species.

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References

Abrams, J. and Hinkes, T.M. 1974. Acceptance and performance of encapsulated warfarin. Pest Control, 42(5), 14–16.

Anonymous 1986. New zinc phosphide coating process. International Pest Control, 27(5), 127.

Bell, G.H., Davidson, J.N and Scarborough, H. 1965. Text book of physiology and biochemistry, sixth edition. Edinburgh, The English Language Book Society and E&S Livingstone Ltd, 1140 p.

Childs, J.E., Ksiazek, T.G., Rolin, P.E., Krebs, J.W., Zaki, S., Nichol, S.T., Peters, C.J. and Glass, G.E. 1994. Hantaviruses and their rodent reservoirs in the United States. In: Helverson, W.S. and Crabb, A.C., ed., Proceedings of the 16th Vertebrate Pest Conference. Davis, University of California, 188–191.

Cornwell, P.B. 1970. Studies in microencapsulation of rodenticides In: Vertebrate pest conference, 4. Davis, University of California, 83–97.

Chyun, S.P. 1973. Studies on the ecology and control of *Rattus norvegicus* Berkenhout in Korea. Seoul, Korea, Dong-Guk University, 30 p.

Douglas, M. 1991. Design and analysis of experiments, third edition. New York, John Wiley and Sons, 260 p.

El-Sebae, A.H., Ibraheim, S.M., El-Fiki, S.A. and Srinivastava, S.N. 1978. Microencapsulation of methomyl, zinc phosphide and copper sulfate—methodology and activity. In: Geissbuble, H., ed., Proceedings of the fourth international congress on pesticide chemistry. New York, Pergamon Press, 763–765.

Ericsson, R.J., Downing, H.E., Marsh, R.E. and Howard, W.E. 1971. Bait acceptance by rats of microencapsulated male sterilant alphachlorohydrin. Journal of Wildlife Management, 35, 573–576.

Feinburg, S.M., Malkid, S. and Feinburg, A.R. 1950. The antihistamines. Chicago, The Year Book Publishers, 20–22.

Gratz, N.G. 1973. A critical review of currently used single-dose rodenticides. Bulletin of the World Health Organization, 48, 469–477.

Greaves, J.H., Rowe, F.P., Redfern, R. and Ayres, P. 1968. Microencapsulation of rodenticides. Nature, 219, 402–403.

Hayes, N.J., Jr and Laws, E.K., Jr 1991. Handbook of pesticide toxicology, volume 2. New York, Academic Press, 508 p.

Hollander, F. 1955. The regulation of hunger and appetite. Annals of New York Academy of Sciences, 63, 1–144.

Jackson, W.B. 1974. Use of microencapsulation to enhance rodenticide acceptance. Paper presented at the Controlled Release Pesticide Syposium, University of Akron, 16–18 September 1974.

Muktha Bai, K. 1979. Potentiation of warfarin toxicity to roof rats (*Rattus rattus*) by L-histidine and by vitamin K adsorbers. Pesticide Science (UK), 10, 221–226.

Muktha Bai, K. 1996. Commensal rodents as pests and methods for their control—a critical apprasial. Journal of Food Science and Technology, 33, 175–196.

Muktha Bai, K., Krishnakumari, M.K., Ramesh, H.P., Shivanandappa, T. and Majumder, S.K. 1980. Short term toxicity study of zinc phosphide in albino rats (*Rattus norvegicus*). Indian Journal of Experimental Biology, 18, 854–857.

Pratt, H. 1983. Rodenticides—what to use where, when and how. Pest Control, 51(10), 19–20, 22–24.

Prakash, I. 1988. Bait shyness and poison aversion. In: Prakash, I., ed., Rodent pest management. Boca Raton, Florida, CRC Press, 321–329.

Rudd, R.L. and Genelly, R.E. 1956. Pesticides: their use and toxicity in relation to wild life. Bulletin of the California Department of Fish and Game, 7, 209 p.

US (United States) Patent 1960. US Patent No. 2957806 (Pesticide: H.R. Shuyler, 25 October 1960).

West, E.S. and Todd, W.R. 1961. Text book of biochemistry, 3rd edition. New York, The Macmillan Company, 1423 p.

Roof rat invasion of an urban desert island

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Abstract. Roof rats have invaded the Phoenix metropolitan area. Although the desert surrounding Phoenix is formidable to roof rats, residential and urban development has probably sufficiently altered habitat to render it suitable for roof rats. Ongoing community and government campaigns are reducing the resources necessary for rat survival and are working to suppress rat populations. Whether these efforts will be adequate to eradicate roof rats from the area is unknown. Rat activity has declined over the past several months. However, it is difficult to assess whether this reduced activity reflects decreased rat numbers or if rats have become less active during the summer heat.

Introduction

Roof rats (*Rattus rattus*) first arrived in the contiguous United States on sailing vessels along with early explorers and colonists (Lowery 1974). Their distribution had expanded considerably along routes of commerce by the late 1700s (Jackson 1982). Subsequently, roof rat distribution declined, particularly from northern and inland areas, as their populations were gradually displaced by Norway rats (*Rattus norvegicus*) (Jackson 1982). The current distribution of roof rats within the continental United States is along the lower half of the East Coast, throughout the Gulf States, and along the Pacific Coast. States located within the interior of the United States are generally free of roof rats. However, infested cargo may produce isolated infestations (Marsh 1994).

Roof rats have appeared sporadically in Arizona. The first known roof rat in Arizona occurred during 1890 with dual invasions of Tucson and along the Colorado River near Yuma (Cockrum 1960). Two years later, roof rats were reported in Cochise County (Hoffmeister and Goodpaster 1954). Roof rats did not appear again until a series of small invasions during 1900 in Yuma and Tucson and towns located in the San Pedro and Santa Cruz valleys, and then a brief emergence near Miami during 1922 (Cockrum 1960). They did not persist after these initial invasions. Their failure to establish is most likely attributable to poor habitat—specifically, sparse availability of desirable vegetation and limited water resources. Cockrum (1960) reported Arizona to be roof rat free in his book on Arizona mammals. However, an increasing human population and associated urban and residential development is changing the Arizona landscape. Introduced plants and increasing irrigation are probably leading to an increase in rat habitat. During the 1970s, an outbreak of roof rats occurred in the warehouse district of Globe, Arizona. An eradication program implemented by local authorities continued for 3 years before Globe was claimed to be roof rat free (Hoffmeister 1986).

In early December 2001, a resident notified the Maricopa County Environmental Services Department that he had seen a rat outside his home in Phoenix, Arizona. The Department's Vector Control Program responded by placing live-traps in the vicinity of the resident's home. Shortly thereafter, a rat that had been electrocuted while crossing a power-line in the same neighborhood was positively identified as a roof rat. Subsequently, a live roof rat was captured on 19 December 2001. Expanded rat trapping and neighbourhood reports suggested roof rats occupied approximately 15 km^2 by early January 2002. This area was expanded to include 41 km^2 a couple of weeks later.

The objective of this paper is to describe why the current rat infestation may be more problematic than those occurring before it, initial reactions to the infestation, and preliminary results of control measures.

Rat infestation of Phoenix

Human emigration into Arizona has significantly altered resource availability over the past few centuries, often expanding suitable roof rat habitat. Early rat populations probably faded because necessary resources were sparse. Several changing environmental attributes in the Phoenix

metropolitan area may be enhancing the potential for current invading rats to establish successfully. Water is probably no longer a limiting factor across most residential and agricultural areas of Arizona. For example, irrigation channels and ditches, flood irrigation of crops and lawns, drip irrigation of flowerbeds, sewers, leaking faucets, and pet dishes—among other avenues—provide excellent water sources for rats.

Plant communities also have been significantly altered. Roof rat distribution has been correlated with introduced plants. Rat populations on the west coast have expanded considerably because rats have utilised blackberry (*Ribes* spp.) associated with old mining camps (Jameson and Peeters 1988), and the lush vegetation planted along freeways and urban housing developments (Jackson 1982). Exotic plants were first introduced to the Sonoran Desert by the Spanish in 1540 when wheat and other crop seeds were distributed to Native Americans (Tellman 2002). Today, many plants introduced for landscaping or agricultural production provide at least adequate, if not excellent, food and cover for roof rats. At present, an estimated 233 non-native plant species contribute to the flora composition (Wilson et al. 2002). Introduced ornamentals used for landscaping further contribute to a changing plant community. Citrus and nut trees in yards, and interlocking hedges and vines draping over fences are common within the residential neighbourhoods most recently infested by roof rats. Other sources of rat food commonly found include poorly stored food, pet food and garbage. These readily available food sources combined with improved cover and water greatly increase the potential for the new invaders to become established as compared to opportunities afforded rats during prior invasions.

Altered fauna populations also may benefit roof rat establishment. Natural predators and species normally competitive with roof rats may be less abundant. Snakes have been largely displaced, or populations suppressed, in urban neighbourhoods (Rosen and Schwalbe 2002). Domestic cats have contributed to the disappearance of many wildlife species, including competitive rat species (Rosen and Schwalbe 2002). Roof rats do not compete well with Norway rats (Jackson 1982), and most likely do not compete well with wood rats (*Neotoma* spp.). Roof rats may fare better where populations of these species are sparse. The arboreal nature of roof rats may make them less vulnerable to cats and other urban predators than some other rat species.

Potential problems inflicted by roof rats also have increased as the Sonoran Desert has been developed. Foraging roof rats can inflict significant negative impact on citrus and nut crops (Marsh 1994). Acreage devoted to citrus and nut production in Arizona continues to increase. Mean annual production over the past five years is valued at nearly US$150 million. If roof rats became established within these orchards, subsequent consequences could be devastating to these industries. Another potential problem is contamination of stored feeds or animal facilities. Rats living in attics, walls, and basements commonly gnaw on electrical wiring, causing communication and power disruptions. Exposed and frayed wires then pose threats for electric shock or fire (Cogelia et al. 1976). Rats also serve as vectors and reservoirs for diseases communicable to humans (Chin 2000). Therefore, public health is always a concern when rat infestations occur in residential neighbourhoods.

Initial response

Successful urban rodent control needs to focus on long-term strategic, comprehensive approaches that incorporate multiple tactics and partnerships among government agencies, community groups and pest control companies (Colvin and Jackson 1999). Whenever possible, such control programs should focus on altering habitat and reducing its potential for attracting and supporting pest species. Otherwise, benefits derived from control measures will be short-lived and frequently repeated (Davis 1972).

Government agencies, primarily county, began formulating a response plan soon after officials suspected a potential roof rat infestation. The first response to the rat sighting was to identify the species. Once roof rats were confirmed, efforts were initiated to confirm boundaries of the area infested by rats. This area quickly expanded from 15 km^2 to 41 km^2, centered on the Arcadia–Camelback Mountain area of Phoenix. Whether this expansion reflected increased rat dispersal or merely better surveys is unknown. A contingency plan addressing an influx of roof rats to the Phoenix area did not exist. In retrospect a plan would have been beneficial.

The Maricopa County Vector Control Office sponsored a series of meetings during January 2002 to gather agency support, share information, and begin developing a response plan. A wide spectrum of interested groups and agencies were represented at these meetings. Subsequently, Maricopa County assumed a lead role in developing and implementing a plan to address real and perceived problems caused by roof rats.

Maricopa County issued a news release that urged citizens to cover trash containers, use rat-proof containers to store food items, eliminate rat access to pet foods, pick up fallen citrus, and harvest fruits remaining on trees. The release also announced an upcoming public meeting scheduled to explain the situation and to address public questions. At the meeting, hundreds of local residents were provided an overview of roof rat ecology and management, and advised to clean up yards, remove citrus fruits from their property, and to use traps or baits to manage local rat populations. Residents also were told that the City of Phoenix would haul away unwanted citrus and assist in organising campaigns to clean up public and common-ground areas.

Direct measures to combat roof rats were implemented by mid-February 2002. More than two-dozen groups participated in the rat eradication effort. The City of Phoenix provided bulk trash bins for residents. The Arizona Department of Health Services, in cooperation

with Maricopa County Environmental Services, began testing roof rats for hantavirus, bubonic plague, and tularemia. Food banks and family assistance programs accepted undamaged discarded citrus from clean-up campaigns. Several neighbourhood groups were organised to clean common areas or assist those residents less capable of picking fruits or cleaning debris from their properties. Personal-use bait stations and snap-traps were distributed by county and volunteer groups until supplies were depleted. Home-owner associations sold additional bait stations at the cost of materials. Educational programs continued, ranging from leaflets to group meetings, urging residents to take necessary steps to deny rat access to cover and food.

Maricopa County Vector Control implemented a baiting program to suppress and hopefully eliminate rat populations. Their target area, including a buffer zone, was approximately 60 km^2. Certified County employees, assisted by volunteer apprentices, affixed approximately 6000 bait stations 2–2.5 m above the ground on utility poles. Utility poles were spaced 30–60 m apart and were located primarily along alleys. Stations were initially installed in areas considered 'hot spots' and in the 0.75 km buffer zone established along the outside perimeter of the infested area. Bait stations were constructed of polyvinyl chloride (PVC) pipe (30 cm long and 10 cm diameter) capped on both ends, and a hole drilled in the middle to permit rat access, but minimise non-target exposure. Each station was treated with 225 g of bait containing 0.005% bromadiolone. The Vector Control group monitored stations at least once a month, replacing any bait that had been removed.

Preliminary results and discussion

An integrated plan was developed to eradicate, or at least abate, roof rat establishment in the Phoenix area. Numerous community groups banded together to remove potential rat food and rat habitat. One optimistic volunteer considered the "rats a blessing, not a curse, in that they have brought us closer as a community…and are pushing us in a direction we need to go, and that's cleaning up our properties." The 'NEIGHBOR to NEIGHBOR' campaign picked, and donated to food banks, approximately 31.5 t of citrus through their efforts to rid neighbourhoods of rat food. Their future goal is to collect and donate more than 750 t of citrus next season. Resident and volunteer groups deposited almost another 100 t of waste citrus and debris in dumpsters distributed and serviced by the city. These efforts have greatly decreased availability of food and cover for rats. Unfortunately, some residents have not participated in the clean-up campaign, leaving pockets of citrus and other desirable rat habitat attributes. It is unknown whether these havens will enable rats to establish and disperse throughout the community in the future. Community organisations also have worked with residents to set bait stations and traps on private land inaccessible to county officials.

City, county, state, and federal governmental agencies have all contributed to roof rat eradication. Public awareness programs have greatly enhanced public involvement in rat proofing their homes, installing traps and bait stations on private land, and monitoring for rat activity. The Arizona Department of Health Services has tested rats and has thus far not found evidence of disease communicable to humans. Maricopa County Vector Control has taken the lead role to suppress roof rat populations. Over 1 t of bait has been distributed through approximately 6100 bait stations mounted on the utility poles. Few stations (less than 0.5%) have been vandalised or otherwise damaged. Vector Control also has set rat traps in areas believed to contain high rat populations or where bait stations may pose perceived problems. Other agencies have enhanced control efforts by contributing funds, labour, equipment, and expertise.

The efficacy of these programs to eradicate roof rats is largely unknown. Rat activity appears to have declined, according to indicators such as bait disappearance, trapped rats, and residential calls to hotlines. Whether this reduced activity means suppressed populations or merely reflects less movement by rats during the higher summer temperatures is difficult to ascertain. A more accurate measure of program success will occur next winter, when temperatures drop and citrus trees bloom and begin producing fruit.

Conclusions

Roof rats and other rodents have been introduced to new localities throughout the world. Invading roof rats have established and wreaked havoc on many island ecosystems (Atkinson 1989). Urban and residential development may be creating islands of habitat suitable for roof rat survival. While ships were required to transport invasive species among islands, their movement across inhospitable terrestrial sites should be relatively easy, given the rapid transport of goods and constant movement of vehicles. Therefore, municipalities may need to consider whether development is creating habitat for invasive species and the likelihood these species will be introduced. If conditions favour a species capable of causing devastating impacts to a region, then contingency plans may need to be considered. Under some conditions, it may be reasonable to establish monitoring programs for early detection, e.g. a monitoring program for early detection of roof rats in Arizona citrus orchards. However, it is understandable why government agencies are hesitant to extend limited resources to address concerns with species supposedly non-indigenous to their locality.

References

Atkinson, I.A.E. 1989. Introduced animals and extinctions. In: Western, D. and Pearl, M.C., ed., Conservation for the twenty-first century. New York, Oxford University Press, 54–79.

Chin, J. 2000. Control of communicable diseases manual. Washington, D.C., American Public Health Association, 624 p.

Cockrum, E.L. 1960. The recent mammals of Arizona: their taxonomy and distribution. Tucson, The University of Arizona Press, 276 p.

Cogelia, N.J., LaVoie, G.K. and Glahn, J.F. 1976. Rodent biting pressure and chewing action and their effects on wire and cable sheath. Proceedings Wire and Cable Symposium, 25, 117–124.

Colvin, B.A. and Jackson, W.B. 1999. Urban rodent control programs for the 21st century. In: Singleton, G.R., Hinds, L.A., Liers, H. and Zhang, Z., ed., Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research, 243–257.

Davis, D.E. 1972. Rodent control strategy. In: Pest control strategies for the future. Washington, D.C., National Academy of Sciences, 157–171.

Davis, G.P. 2001. Man and wildlife in Arizona: the American exploration period 1824–1865, third edition. Pheonix, Arizona Game and Fish Department, 225 p.

Hoffmeister, D.F. 1986. The mammals of Arizona. Tucson and Phoenix, The University of Arizona Press and The Arizona Game and Fish Department, 602 p.

Hoffmeister, D.F. and Goodpaster, W.W. 1954. The mammals of the Huachuca Mountains, southeastern Arizona. Illinois Biological Monograph No. 24. University of Illinois Press, 152 p.

Jackson, W.B. 1982. Norway rat and allies. In: Chapman, J.A. and Feldhamer, G.A., ed., Wild mammals of North America. Baltimore, Maryland, The John Hopkins University Press, 1077–1088.

Jameson, E.W. and Peeters, J.J. 1988. California mammals. Berkeley, University of California Press, 403 p.

Lowery, G.H. 1974. The mammals of Louisiana and its adjacent waters. Baton Rouge, Louisiana State University Press, 565 p.

Marsh, R.E. 1994. Roof rats. In: Hyngstrom, S.E., Timm, R.M. and Larson, G.E., ed., Prevention and control of wildlife damage. Lincoln, University of Nebraska Cooperative Extension, B125–B133.

Rosen, P.C. and Schwalbe, C.R. 2002. Widespread effects of introduced species on reptiles and amphibians in the Sonoran Desert region. In: Tellman, B., ed., Invasive exotic species in the Sonoran region. Tucson, The University of Arizona Press and The Arizona–Sonoran Desert Museum, 221–240.

Tellman, B. 2002. Invasive exotic species in the Sonoran region. Tucson, The University of Arizona Press and The Arizona–Sonoran Desert Museum, 424 p.

United States Department of Agriculture, Arizona Agriculture Statistics Service. 2001. 2000 Arizona Agricultural Statistics. United States Department of Agriculture, Arizona Agricultural Statistics Service, Phoenix, Arizona, USA, 92 p.

Wilson, M.F., Leigh, L. and Felger, R.S. 2002. Invasive exotic plants in the Sonoran Desert. In: B. Tellman, ed., Invasive Exotic Species in the Sonoran Region. Tucson, The University of Arizona Press and The Arizona–Sonoran Desert Museum, 81–90.

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Evolutionary biology of the genus *Rattus*: profile of an archetypal rodent pest

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Abstract. *Rattus*, with at least 61 valid species, is the single largest genus of mammals. It belongs to a much larger assemblage of 'modern' murines, known informally as the 'new endemics', and distributed from South Asia to Indonesia. The first members of the genus *Rattus* probably evolved in the late Pliocene, around three million years ago. Early forms of *Rattus* underwent a rapid dispersal across the greater part of island Southeast Asia, despite the presence of a well-established rodent fauna in most areas. Today, the descendants of these early invaders survive on various islands and on scattered high mountain peaks. *Rattus* species probably colonised Australia only within the last 1–2 million years; nevertheless, they succeeded in colonising all major habitats including sandy desert. Within *Rattus*, the Norway rat (*R. norvegicus*) appears to have few, if any, immediate relatives. In contrast, the black rat (*R. rattus*) has numerous close relatives spread across mainland and island Southeast Asia. Three or more distinct species are probably included within the *R. rattus* complex. At least 15 species of *Rattus* are significant agricultural pests. Five of these are true commensals and three species now exist solely within the human environment. The role of these species in causing agricultural damage and in the dispersal and transmission of both human and wildlife pathogens is discussed.

Introduction

Species of the rodent genus *Rattus* have probably been responsible for more human suffering than any other group of vertebrates (with the exception of *Homo sapiens*!), not only through their destructive impact on food crops, but also through their role in the transmission of fatal or debilitating diseases such as plague, leptospirosis and typhus. However, the genus also contains species of immense scientific and clinical significance, such as the familiar Norway or laboratory rat (*R. norvegicus*), as well as a host of lesser-known but presumably beneficial species that inhabit a wide range of natural habitats from mangrove forests to sub-alpine grasslands. In matter of fact, the genus *Rattus*, with a total of 61 currently recognised species, is not only the single largest mammalian genus of all, but also arguably among the most complex and least well understood.

In this paper, we will give a brief summary of current thinking regarding the content and relationships of *Rattus*. We will also summarise the geographical distribution of *Rattus* and its closest allies, and examine the evidence for the geographical origin of the genus as a whole and of some of the economically more important species. Finally, some key biological attributes of the genus will be reviewed, including the role of various *Rattus* species as agricultural pests and as agents of disease transmission. All of these components will help us to frame one final question of profound evolutionary biological significance—why is *Rattus* so remarkably successful as a genus? We cannot promise any profound response to this question. However, we do believe that the act of framing the question is, in itself, worthwhile, and perhaps takes us one step closer to a better understanding of this most remarkable of mammalian genera.

Content and relationships of *Rattus*

Although *Rattus* was once considered to consist of more than 550 distinct forms (Ellerman 1941–1949), contemporary reviews list roughly one-tenth as many species in the genus (Corbett and Hill 1992; Musser and Carleton 1993). Many of the species formerly included within *Rattus* have been transferred to other genera such as *Maxomys*, *Berylmys*, *Leopoldamys*, and *Niviventer* (see references in Musser and Carleton 1993). However, even more have been grouped together to form fewer, widely distributed species (the *Rattus rattus* group alone has more than 150 synonyms, currently grouped under two species).

Despite these considerable advances, the boundaries of *Rattus* are by no means finally decided. The type species of *Rattus* is actually *Mus decumanus* Pallas 1778, a junior synonym of *R. norvegicus* (Berkenhout 1769), the familiar

Norway or laboratory rat. The other species often thought of as lying at the 'heart' of *Rattus* is the black or ship rat, *R. rattus*. The Norway rat is morphologically distinctive and appears to have few, if any, close relatives (Chan et al. 1979; Baverstock et al. 1986; Verneau et al. 1998). In contrast, the black rat is often confused with other Asian *Rattus* species and appears to have numerous close relatives. Musser and Carleton (1993, p. 649) listed 21 species in their *R. rattus* group, including the major agricultural pest species *R. argentiventer*, *R. nitidus*, *R. losea* and *R. tiomanicus*.

Several groups of species may still need to be excised from *Rattus*. These include members of the *R. xanthurus* group from Sulawesi; the '*Stenomys*' group from New Guinea and Seram; and the 'native Australian' group. Musser and Carleton (1993, p. 650) listed 10 individual species that they consider to be on the periphery of *Rattus*; many of these species are of special biogeographical interest (see below).

The evolutionary relationships of *Rattus* to other murid genera remain somewhat enigmatic. Musser and Heaney (1992) included *Rattus* among a group of essentially modern and progressive rodents that they termed the 'new endemics'. This group is widely distributed across mainland and island Southeast Asia, and includes the following genera: *Paulamys*, *Hooijeromys*, *Papagomys* and *Komodomys* of the Lesser Sunda Islands (Nusa Tenggara); *Bunomys*, *Paruromys* and *Taeromys* of Sulawesi; *Abditomys*, *Bullimus*, *Limnomys*, *Tarsomys* and *Tryphomys* of the Philippine Islands; and *Palawanomys*, *Sundamys* and *Kadarsanomys* of the Sunda Shelf Islands. Three mainland Asian genera (*Berylmys*, *Bandicota* and *Nesokia*) probably also belong to this group (Musser 1981; Musser and Brothers 1994).

The notion of a 'modern and progressive' 'new endemic' murid assemblage is supported by information from chromosomes (Yosida 1980 and refs; Baverstock et al. 1983a; Gadi and Sharma 1983), albumin immunology (Watts and Baverstock 1996 and refs), DNA/DNA hybridisation (Ruedas and Kirsch 1997), DNA sequencing (Suzuki et al. 2000) and analysis of LINE-1 retrotransposons (Verneau et al. 1998 and refs). Although none of these methods has yet been applied across the full range of relevant genera, the combined results strongly support the notion that *Rattus* evolved somewhere within the South to Southeast Asian region.

Just how recently this might have occurred is indicated by molecular estimates of divergence times between *Rattus* and other genera. These place the origin of *Rattus* at around 2–3 million years ago (Watts and Baverstock 1996; Verneau et al. 1998)—a remarkably young age for such a large and diverse genus. However, these dates are consistent with the fossil record of *Rattus*, which begins in Thailand with an extinct species of possible late Pliocene age (c. 3 million years ago; Chaimanee 1998) and includes Pleistocene records from India (Gaur 1986), Java (Musser 1982) and China (Zheng 1993; cited in Chaimanee 1998). *Rattus* is conspicuously absent from Pliocene and early Pleistocene fossil faunas of Europe (van de Weerd 1976) and Australia (Aplin 2002), and appears to have been confined to the Asian region through much of its early history.

Unresolved taxonomic problems within *Rattus*

Several species groups within *Rattus* are clearly still in need of taxonomic revision: notable examples are the *R. everetti* group in the Philippines; the *R. niobe* group in New Guinea; and the *R. sordidus* group in Australia. In each case, there are additional species that will be recognised following completion of more detailed morphological and genetic studies. However, in no group within *Rattus* is the need for taxonomic revision so glaringly and embarrassingly obvious as it is in the *Rattus rattus* complex.

Many authors have attempted to make sense of the morphological diversity among the black rats. Most attempts have been regionally based (e.g. Hinton 1918–1919 for the Indian subcontinent; Chasen 1933 for Malaysia) and the few broader-based attempts at revision have been defeated at the outset by a failure to distinguish *R. rattus* from other *Rattus* species, including *R. argentiventer*, *R. tiomanicus* and *R. sikkimensis* (e.g. Ellerman 1941–1949; Schwarz and Schwarz 1967). In addition, all but a very few attempts have placed too great an emphasis on belly fur colour, despite clear evidence dating back at least to Bonhote (1910) that this is highly polymorphic within populations and under relatively simple genetic control (see also Tomich and Kami 1968).

The first significant breakthrough in understanding the *R. rattus* complex came with Yosida's (1980 and refs) studies of chromosomal variation. Over a period of a decade, he documented 11 chromosomal variants that resolve into five major groups: (i) Asian black rats with $2n = 42$ chromosomes and high C-banding; (ii) Japanese black rats with $2n = 42$ chromosomes and low high C-banding; (iii) Ceylonese black rats with $2n = 40$ chromosomes; (iv) 'Oceanian' (also European) black rats with $2n = 38$ chromosomes; and (v) Mauritius black rats with $2n = 42$ (secondarily derived from the $2n = 38$ karyotype). Yosida found regional variation within the Asian black rat group in the frequency of minor Robertsonian rearrangements and in serum transferrin polymorphism. Laboratory F_1 hybrids were obtained between all major chromosomal variants but these invariably proved semi-sterile, with low yield of F_2 offspring. Natural hybrids were detected in four areas, either involving Asian and Oceanian types (Eniwetok Atoll, Marshall Islands; Chichijima Island, Japan; Karachi, India) or the Ceylonese and Oceanian types (Anaradhapura and Colombo, Sri Lanka).

Baverstock et al. (1983b) examined genetic differences between each of the chromosomally distinct populations, using isozyme electrophoresis and microcomplement fixation of albumin. The results show a major genetic division between the Asian and Ceylonese + Oceanian populations, with lesser differentiation between

each of the Japanese versus mainland Asian and between Ceylonese versus Oceanian types. As expected, the Mauritius black rats were genetically indistinguishable from the general Oceanian type. The level of genetic divergence between the two major groups within *R. rattus* was only slightly less than that separating *R. rattus* from other undisputed species of *Rattus* (e.g. *R. losea*) and this led Baverstock et al. (1983b) to conclude that the *R. rattus* complex could be validly divided into at least two species.

Musser and Carleton (1993) indeed listed two species of the *Rattus rattus* complex in their influential checklist, using the names *R. rattus* (Linnaeus 1758) for the 'Oceanian' group and *R. tanezumi* Temminck 1844 for the Asian group. This usage has gained some acceptance, however the lack of a comprehensive morphological review of the group has left many field workers uncertain as to whether they are catching *R. rattus*, *R. tanezumi* or possibly even both. An earlier morphological study by Schwabe (1979) had revealed some apparent differences in cranial proportions between European and Asian populations, but this finding requires broader-scale confirmation.

Our preliminary studies of the mitochondrial cytochrome b gene indicate that the taxonomy of the *R. rattus* group may be rather more complex than suggested by the chromosomal and electrophoretic data sets. In particular, we have found a fundamental genetic division *within* the Asian region between an endemic Southeast Asian taxon (recorded from Vietnam, Cambodia and southern Laos) and a northern and South Asian taxon (recorded thus far from Japan, Hong Kong, northern Vietnam, northern Laos, and Bangladesh). These taxa are probably regionally sympatric in parts of Vietnam and Laos. The Oceanian type *R. rattus* appears to be more closely related to (although probably specifically distinct from) this latter group than to the endemic Southeast Asian taxon. Until further analyses are completed, and the results fully published, it would be premature to speculate on the appropriate names for each of the two Asian taxa. However, the apparent extension of the northern Asian taxon (which probably includes Japanese *tanezumi*) through to the Indian subcontinent raises the possibility that *tanezumi* may not be the earliest available name for this group. Rapid resolution of these taxonomic and nomenclatorial problems is clearly of high priority given the agricultural and clinical significance of the *Rattus rattus* complex.

The geographical distribution of *Rattus*

The contemporary geographical distribution of *Rattus* is amongst the widest of any rodent genus, rivalled only by *Mus*. However, the greater part of this range is clearly due to commensalism on the part of a small number of species, namely, members of the *Rattus rattus* complex, *R. norvegicus* and *R. exulans*.

At a broad scale, the number of native *Rattus* species is highest on the island of New Guinea, followed by Australia, mainland Southeast Asia and Sulawesi. However, the true number of native *Rattus* species on mainland Southeast Asia and on the larger islands of the Sunda Shelf (e.g. Borneo, Sumatra and Java) is somewhat uncertain due to doubts over the original distribution of various commensal and agricultural pest species (see below).

Island endemics

Two groups of endemic species are of special interest. The first are the 'island' endemics (Table 1, Figure 1). As noted previously by Musser and Heaney (1985), the majority of these species are found on *oceanic* islands that are separated by deepwater straits from adjacent major islands or continental landmasses. The important feature of oceanic islands is that they remained isolated through the glacial periods when sea levels fell by as much as 140 m below the present level (Lambeck and Chappell 2001)—any *Rattus* species on these islands must have reached them by crossing water barriers at some time in the past. As shown in Figure 1, the majority of the island endemics are found in two geographical areas: (i) around the perimeter of the Southeast Asian continental shelf (the Sunda Shelf); and (ii) in the Moluccan and Nusa Tenggaran island groups, situated in the tectonically active zone between Sulawesi and New Guinea.

In phylogenetic terms, the island endemics can be divided into two broad categories, namely an *archaic* group and a *modern* group. Members of the 'archaic' group generally show no close relationship to other *Rattus* species in adjacent geographical areas; these may be descendants of early waves of dispersal through the region. Three of the archaic taxa are found on islands lying to the south of Sumatra: *R. enganus* of Pulau Enggano, and *R. macleari* and *R. nativitatus* of Christmas Island. Two are found in the Moluccan region: *R. morotaiensis* of the Halmahera Island group, and *R. ceramicus* of Seram; and two in the Nusa Tenggaran group—*R. hainaldi* of Flores and *R. timorensis* of Timor. One final member of this group, *R. jobiensis*, is found on the islands of Cenderawasih Bay of north coastal New Guinea.

Members of the 'modern' group are more obviously related to (and presumably immediately derived from) species found on nearby major islands or landmasses. For example, *R. pelurus*, found on Pulau Peleng, to the immediate east of Sulawesi, is a member of the otherwise endemic Sulawesian *R. xanthurus* group (Musser and Holden 1991). Similarly, *R. remotus* of Koh Samui and nearby islands in the South China Sea is very similar to (perhaps even conspecific with) *R. sikkimensis* of mainland Southeast Asia.

Eight members of the 'modern' group may be related specifically to *R. tiomanicus* of the Sunda Shelf, itself a close relative of the *R. rattus* complex (Musser and Newcomb 1983). One of these species is *R. mindorensis* from Mindoro Island in the central Philippines (Musser and Holden 1991). Another is *R. tawitawiensis* from the Sulu Archipelago, off the north-eastern corner of Borneo

(Musser and Heaney 1985). The remaining six species of this group are found on islands that lie to the south and west of Sumatra and the Malay Peninsula: *R. adustus* of Pulau Enggano; *R. lugens* of the Mentawi Islands; *R. simalurensis* of the Simalule Island Group; *R. burrus* and *R. palmarum* of the Nicobar Islands; and (less certainly) *R. stoicus* of the Andaman Islands (Musser and Heaney 1985). Several of these taxa are quite specialised in different ways, yet each shows a basic similarity in dental and cranial structure to *R. tiomanicus* and its close allies. Another possible member of this group is *R. hoffmani*, a widespread and common forest rat of Sulawesi (Musser and Holden 1991).

Three members of the 'modern' group are broadly clustered in the Moluccan region: *R. feliceus* from Seram; *R. koopmani* from Pulau Peleng; and *R. elaphinus* from the Sula Island group. The affinities of these species are not quite so obvious, however Musser and Holden (1991) suggest possible links to the native *Rattus* of New Guinea.

Table 1. Island (I) and montane (M) endemics within the genus *Rattus*. Species marked as 'I,M' are found in montane habitats on islands. Morphological groups are: A = archaic and M = modern.

Species	Habitat	Morphological group	Locality
adustus	I	M	Pulau Enggano, Indonesia
burrus	I	M	Nicobar Is group, India
elaphinus	I	M	Pulau Taliabu, Indonesia
enganus	I	A	Pulau Enggano, Indonesia
feliceus	I	M	Seram, Indonesia
jobiensis	I	A	Japen, Biak and Owi Is, Irian Jaya
koopmani	I	M	Pulau Peleng, Indonesia
lugens	I	M	Mentawi Is group, Indonesia
macleari	I	A	Christmas Is
mindorensis	I	M	Mindoro Is, Philippines
morotaiensis	I	A	Halmahera Is Group, Indonesia
nativitatus	I	A	Christmas Is
palmarum	I	M	Nicobar Is group, India
pelurus	I	A	Pulau Peleng, Indonesia
remotus	I	M	Koh Samui Is, Thailand
sanila	I	A	New Ireland, Papua New Guinea
simalurensis	I	M	Simalur Is group, Indonesia
stoicus	I	M	Andaman Is group
tawitawiensis	I	M	Tawitawi Is, Philippines
baluensis	I,M	M	Mt Kinabalu, Sabah
bontanus	I,M	A	Gunung Lamphobatang, Sulawesi
ceramicus	I,M	A	Seram, Indonesia
giluwensis	I,M	M	Mt Giluwe, Papua New Guinea
hainaldi	I,M	A	Flores, Indonesia
hoogerwerfi	I,M	A	Gunung Leuser, Sumatra, Indonesia
korinchi	I,M	A	Gunung Kerinci, G. Talakmau, Sumatra, Indonesia
marmosurus	I,M	A	Gunung Masarang, Sulawesi, Indonesia
mollicomulus	I,M	A	Gunung Lamphobatang, Sulawesi, Indonesia
montanus	I,M	A	Sri Lanka
omlichodes	I,M	A	Mt Jaya, Papua, Indonesia
richardsoni	I,M	A	Papua Province, Indonesia
timorensis	I,M	?	Gunung Mutis, Timor, Indonesia
vandeuseni	I,M	M	Mt Dayman, Papua New Guinea
osgoodi	M	M	Langbian Mts, Vietnam

Montane endemics

A second group of major interest are the 'montane' endemics. These are typically confined to forested or sub-alpine habitats on the highest peaks of the continental areas and larger islands (Table 1, Figure 1).

Somewhat surprisingly, there is only one montane endemic *Rattus* on mainland Asia. *R. osgoodi*, a rare species from the Langbian Mountains of southern Vietnam, is morphologically similar to *R. losea* and *R. argentiventer* (Musser and Newcomb 1985). The absence of other montane endemics on mainland Southeast Asia may reflect a lack of survey effort in appropriate habitats. However, recent surveys of montane habitats in northern Vietnam have produced specimens of the widespread taxa *R. sikkimensis* and *R. nitidus*, but no local endemics (Tam et al., this volume).

Three *Rattus* species are endemic to isolated upland areas on the Sunda Shelf: *R. hoogerwerfi* and *R. korinchi* from Sumatra; and *R. baluensis* from Mt Kinabalu on the island of Borneo. The Bornean endemic is probably a close relative of *R. tiomanicus* (Musser 1986). The two Sumatran taxa retain a suite of primitive characteristics (Musser 1986).

R. montanus from the highlands of Sri Lanka is said by Musser (1986, p. 22) to resemble *R. korinchi* but the molar pattern is overall more primitive. This poorly known taxon clearly lies at the periphery of *Rattus*.

The extensive mountain habitats of New Guinea support four endemic *Rattus* species (Flannery 1995a). *R. vandeuseni* is confined to the upper slope of Mt Dayman in south-eastern Papua New Guinea; it replaces the closely related but more widespread *R. verecundus* at around 1300 m elevation. *R. giluwensis* is confined to mossy forests and sub-alpine habitats above 2195 m on Mt Giluwe and the adjoining Lamende Range in Papua New Guinea. *R. richardsoni* and *R. omlichodes* are found in areas of sub-alpine to alpine habitat in the Indonesian province of West Papua. The higher altitude species are all small-bodied and the two West Papuan taxa retain many primitive dental features.

Interestingly enough, three of the island endemics would also qualify as montane endemics; these are currently confined to montane forests on Seram (*R. ceramicus*), Flores (*R. hainaldi*) and Timor (*R. timorensis*). These taxa are also similar to the majority of the other montane endemics in displaying numerous primitive morphological features (Kitchener et al. 1991a,b).

The survival of relatively archaic forms of *Rattus* on remote islands and in high mountain regions is not totally unexpected. What is perhaps surprising is the fact that the majority of these are found through the archipelagic portion of the range of *Rattus*, with few examples in what might be regarded as its core area of distribution on mainland Southeast Asia. As noted before, this might be a function of inadequate sampling of these areas. However, the presence of such taxa in the far-eastern Moluccan Islands and in New Guinea points to a wide and probably rapid dispersal of a small number of relatively archaic *Rattus* species through the region. The absence of any relictual species of *Rattus* in montane or rainforest habitats of Australia is consistent with the notion of a more recent invasion of this continental area.

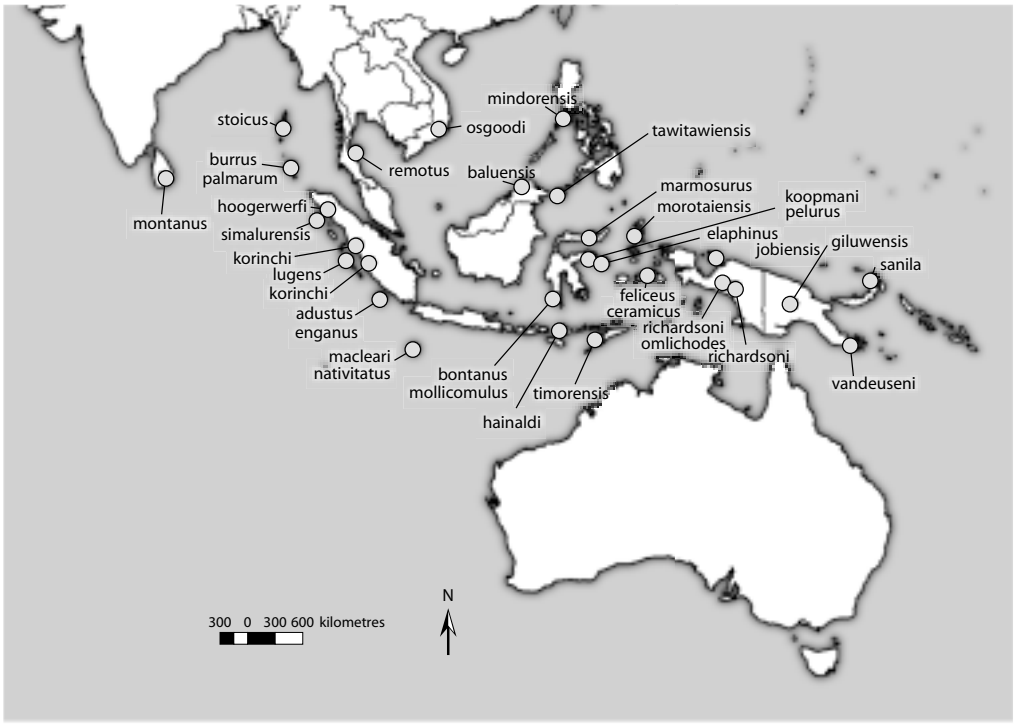

Figure 1. Distribution of island and montane endemic species within the genus *Rattus*.

Recent range expansions

Some species of *Rattus* have undergone huge recent expansions in geographical range. The best known examples are, of course, *R. norvegicus* and members of the *Rattus rattus* complex, both of which are now present on all continents except Antarctica, and on the great majority of the world's larger islands. As noted above, members of the *Rattus rattus* complex are widely distributed across Southeast and South Asia. A representative of this group (presumably the $2n = 38$ 'Oceanian' rat variety) is first recorded in the Middle East during the Upper Pleistocene (c. 20,000 years BP; Tchernov 1968), however it does not appear to have reached western Europe until much later, and did not enter the British Isles until shortly before the Roman Period (Somerville 1999). The later history of the species in Europe suggests that it was initially confined to the major commercial routes, and that its geographical coverage increased mainly through the 11^{th}–13^{th} centuries AD during the period of rapid urban growth (Audoin-Rouzeau and Vigne 1994).

The natural range of the Norway rat, *R. norvegicus*, is generally assumed to be south-eastern Siberia and northern China (Musser and Carleton 1993, p. 657). In northern Asia today, it is more typically associated with urban and agricultural landscapes (e.g. Won and Smith 1999). The Norway rat evidently spread out from Asia much later in time than the black rat—it does not appear in the European record until the Middle Ages. However, following the arrival of *R. norvegicus* in Britain, the black rat declined to a state of rarity. *R. rattus* is now largely confined to buildings, whereas the Norway rat occupies many different habitat types (Meehan 1984).

Other members of the *Rattus rattus* complex have expanded into the Pacific region, presumably through accidental transport with human traffic. This probably occurred during the prehistoric period to as far as the Philippines and Sulawesi. Later European activity in the Pacific probably led to the further dispersal of one or more Asian varieties of *R. rattus*, and to the introduction to many islands of the European black rat. On some Pacific islands (e.g. Eniwetok Atoll in the Marshall Islands) Asian and European forms of the black rat occur together, with some evidence for hybridisation and introgression (Yosida 1980).

The Pacific rat, *R. exulans*, has a huge geographical range that extends from Bangladesh and the Andaman Islands in the west, to New Zealand and Easter Island in the east. Throughout its range it is closely associated with human activities (Marshall 1977; Musser and Newcomb 1983, p. 523–524). *R. exulans* is absent in the fossil record of New Guinea (White 1972) and Nusa Tenggara (Glover 1986) until the last few thousand years, and it is presumed that it came from somewhere to the west. Musser and Newcomb (1983, p. 523–524) remarked on the morphological uniformity of *R. exulans* across its range and postulated a possible origin somewhere on mainland Southeast Asia.

The wide dispersal of *R. exulans* over the last few thousand years is clearly linked to the spread of Austronesian language speaking peoples; indeed it has been suggested that the rat may have been transported deliberately as a food item (Roberts 1991a). Matisoo-Smith et al. (1998) examined the pattern of mitochondrial DNA variation among Polynesian populations of the Pacific rat to document the course of its dispersal. Similar studies of Indonesian and Southeast Asian populations are now required to document its place of origin and pattern of spread in the western part of its range.

One final species that has evidently been carried by people into the Pacific region is *R. praetor*, a common species of lowland to mid-elevation habitats of northern New Guinea (Flannery 1995a). This species was probably introduced to the Bismarck Archipelago during late Pleistocene times and, more recently, to the Solomon Islands, Vanuatu and even to Fiji (White et al. 2000). In the Bismarck Archipelago, the introduction of *R. praetor* may have contributed to the extinction of an endemic species, *R. sanila* (Flannery and White 1991).

Several other species of *Rattus* have made somewhat less impressive inroads into island Indonesia and beyond. One of these is the Himalayan rat, *R. nitidus*, with a probable natural range somewhere in the belt of upland country that extends from north-eastern India through Myanmar, Thailand and Laos, to southern China and Vietnam (Musser and Holden 1991). In southern China, *R. nitidus* is a major agricultural pest (Yang et al. 1999), however in Southeast Asia it is variously recorded in forested habitat and as a house rat in upland villages (Marshall 1977, p. 463). Outside this area, *R. nitidus* occurs on Seram in the northern Moluccas; on northern Luzon in the Philippines; in the Palau Islands, south-east of the Philippines; and on the Bird's Head Peninsula of western New Guinea (Musser and Heaney 1985). The species is not present in sub-fossil faunas from either Sulawesi (Musser 1984) or the Bird's Head Peninsula (Aplin et al. 1999) of New Guinea; it is presumably introduced in these contexts. On mainland Asia, *R. nitidus* does not generally occur in lowland habitats or around ports, hence the circumstances of its accidental transport are somewhat mysterious.

R. tiomanicus may have also reached various island groups through human agency. This species occurs on many of the islands that ring the Sunda Shelf, often with endemic species derived from earlier invasions of a *tiomanicus*-like taxon (Musser and Califia 1982; Musser and Heaney 1985). Some of these populations appear to be subspecifically distinct, but others may have been introduced in recent times.

The two major pest species of lowland rice crops on mainland Southeast Asia are the rice-field rat, *R. argentiventer*, and the lesser rice-field rat, *R. losea*. Both species have probably undergone range expansions as a consequence of the widespread conversion of forest and swampland habitats to paddy over the last few thousand years or less (Khush 1997). Musser (1973) attributed

populations of *R. argentiventer* on Sulawesi, in the southern Philippines and in southern New Guinea to human-assisted dispersal and further commented on the morphological uniformity of this species throughout its range. In Malaysia, *R. argentiventer* is always encountered in one of two anthropogenic habitats, either rice fields or *Imperata* grassland (Harrison 1951). Marshall (1977, p. 468) also observed that "*Rattus argentiventer* is unknown in the wild state; that is all known populations are commensal with man, living in rice fields or adjacent lalang, oil palm plantations etc.". In rice fields, the onset of breeding in *R. argentiventer* appears to be cued to the maximum tillering stage of the crop (Leung et al. 1999). This apparent physiological link to grass phenology might suggest an original wetland or grassland habitat.

R. losea presents a somewhat different case. This species does show some geographical variation in its morphology (Marshall 1977; Musser and Newcomb 1985) and it is also known from upland habitats, as high as 900 m in China, Vietnam, Laos and Thailand. Marshall (1977, p. 466) reports the discovery of this species "in the wild state … in grass beneath pine forest at 850 m in Chaiyaphum Province (Thailand)". Nevertheless, within some parts of its range, *R. losea* is clearly associated with rice fields and there can be little doubt that it has benefited from the spread of rice-growing as a way of life. Breeding activity in *R. losea* is also clearly linked to rice cropping cycles (Brown et al. 1999) but little is known regarding the precise timing of events.

These examples illustrate some of the difficulties of delimiting the place or origin or natural range of the various *Rattus* species that are either strictly commensal or else have benefited from the widespread habitat changes associated with the spread of agriculture over the last few thousand years. As a final note of caution in this regard, we would also like to stress that simply encountering a species in 'natural' habitat, far from direct human activity, is no guarantee of 'native' status. By way of example, we can report the capture of both *R. exulans* and a member of the *R. rattus* complex in mossy *Eucalyptus urophylla* forest at c. 1500 m altitude on Gunung Mutis in Timor in 1991. Both species are clearly introduced to Timor, yet these species have been able to penetrate all habitat types, presumably assisted by episodic burning and perhaps by the lack of competition following extinction of the native Timorese rodent fauna (Glover 1986). Lehtonen et al. (2001) reported a similar penetration by *R. rattus* into relatively unmodified forest habitat in Madagascar—however, in this case, the invasion has occurred even in the presence of an extant native rodent fauna.

Rattus species as commensals and as agricultural pests

At least 14 of the 61 species of *Rattus* are significant agricultural pests (Table 2). Of these, five species also can be considered true commensals in the sense that they are regularly found inside human dwellings. The most widely distributed and best-known commensals are *R. rattus* and *R. norvegicus*, both of which are virtually global in distribution. However, in many parts of Asia and the Pacific, the most abundant village rat is the smaller and generally less-offensive Pacific rat, *R. exulans* (Williams 1973). *R. nitidus* and *R. turkestanicus* (often called *R. rattoides*) are recorded as commensals in upland regions of Central and Southeast Asia (e.g. Niethammer and Mardsen 1975). As noted above, two of the commensal species, the Norway rat and the Pacific rat, are now so firmly associated with the human landscape that they are no longer known for certain in the wild state.

The agricultural pest species can be divided into what may be termed *obligate* pests and *opportunistic* pests. 'Obligate' pests are those that seem to exist across all or part of their geographical range on the basis of human agricultural production. Included here are the rice-field rat, the Pacific rat, the Norway rat, the various members of the black rat complex, and *R. turkestanicus*. The Himalayan rat, *R. nitidus*, probably qualifies as such in the northern part of its range but appears to be more typically a forest rat in the uplands of Southeast Asia.

The scale of damage inflicted by each of these species varies in accordance with the scale of the agricultural systems that they exploit. Globally, members of the *R. rattus* complex may inflict the greatest total damage to crops. Black rats are ranked among the most important pests in India (Prakash and Ghosh 1992), Thailand (Boonsong et al. 1999) and the uplands of Laos (Khamphoukeo et al., this volume). In the uplands of northern India through to southern China, they are probably replaced by *R. nitidus* and *R. turkestanicus* as the dominant agricultural pests (Zhang et al. 1999), while through much of the Pacific region this title is held by *R. exulans* (Williams 1973). The dominant pests in the major lowland rice-producing areas of Southeast Asia are *R. argentiventer* and *R. losea*. Singleton and Petch (1994) estimated annual losses of around 5–20% in lowland rice systems, with occasional higher losses during 'outbreak' years. Chronic losses may be even higher in many rainfed and upland rice production areas, and these systems are also more prone to episodic irruptions (Douangboupha et al., this volume).

The 'opportunistic' pests are those that will take advantage of human agricultural production, but are not dependent on it to maintain their geographical distributions. One Southeast Asian species, *R. tiomanicus*, is included here (Boonsong et al. 1999), but others such as *R. sikkimensis* might also warrant inclusion. Similarly, only two New Guinean species are listed, but other species such as *R. leucopus*, *R. verecundus* and *R. novaeguineae* can be trapped in and around gardens and presumably also inflict some damage to crops (Taylor et al. 1982). Among the various Moluccan Island endemics, Flannery (1995b) mentioned that *R. morotaiensis* and *R. elaphinus* have been trapped in garden habitats. Of the four Australian species listed in Table 2, *R. sordidus* is by far the most important pest in economic terms (McDougall 1947 and refs). However, *R. colletti* and *R. villosissimus* are both, in a sense, 'emergent' pests that have

recently invaded new rice production areas in northern Australia. The undescribed *Rattus* sp. from central Queensland, a close relative of *R. villosissimus*, is reported to inflict local damage on wheat crops.

Rattus species as agents of disease

The role of *Rattus* as an agent of disease is most spectacularly illustrated through the example of the great plague pandemics. Black rats, or possibly just their fleas, harbouring in cloth and other trade goods, first carried the plague organism (*Yersinia pestis*) from Central Asia to the Middle East and Europe in the 5th century AD. In more recent times, shipping routes provided even more effective means of transporting plague-bearing rats around the world, leading to the infamous Black Death of the 14th century. The most recent pandemic, dating to around the turn of the 20th century, was combated to some extent by 'modern' medicine, but it still killed an estimated 10 million people, 535 of them in Australia (Curzon and McCracken 1989). Plague remains endemic in Central and Southeast Asia, many parts of Africa and South America, and across much of the United States of America (USA). In each area, rodents serve as the primary or enzootic hosts (Biggins and Kosoy 2001), with the pathogenic agent maintaining a sensitive balance between infection rate and death rate in order to persist indefinitely in the wild population.

Y. pestis has a remarkably broad host range (>200 species of mammals; Poland and Barnes 1979) and has pathogenic impacts on many species including most rodents. However, susceptibility may differ widely even between closely related taxa. Most Asian murids are highly susceptible to plague, but *R. norvegicus* and *R. rattus* both show moderate levels of resistance and may be significant enzootic hosts. The principal enzootic host of plague in Africa is the multimammate rat, *Mastomys natalensis* (Gratz 1997). However, in Madagascar, this role is taken over by *R. rattus*, which is evidently spreading as a consequence of forest destruction.

Rodents are known to serve as hosts for at least 60 zoonotic diseases (Hugh-Jones et al. 1995). Many of the clinically significant zoonoses are carried by commensal *Rattus* species (Gratz 1997). Examples include murine typhus (rickettsial disease), various spirochetal diseases (e.g. Lyme disease, leptospirosis) and some protozoal diseases (e.g. leishmaniasis, toxoplasmosis). Of these, leptospirosis is of special concern as an emergent infectious disease, with a recent upsurge in the rate of diagnosis of this previously 'hidden' disease (Singleton, Smythe et al., this volume). Commensal *Rattus* populations have been found to carry heavy leptospire infestations in widespread regions of Africa, Asia, Europe and North America (Gratz 1997).

Hantavirus infections are also of particular concern because of the high mortality rates (5–35%) associated with several of the 10 or so recorded viruses of this group (Hart and Bennett 1999). The Norway rat is a known reservoir for Seoul virus in the USA and a recent epidemiological study of this species in Baltimore showed a seroprevalence of nearly 50%; moreover, naturally infected rats did not show any reduction in reproductive capacity (Childs et al. 1989). Boonsong et al. (1999) summarised serological evidence of hantavirus infection in Thai

Table 2. Agricultural pest and commensal species of *Rattus*.

Region	Species	Primary affected crop	Economic significance	True commensal	Key references
Central + East Asia	*R. nitidus*	Cereals	++	+	Marshall 1977; Yang et al. 1999
	R. turkestanicus	Vegetables	+	+	Niethammer and Martens 1975; Hong 1989; Zhang et al. 1999
Southeast Asia	*R. argentiventer*	Rice	+++	–	Marshall 1977; Leung et al. 1999
	R. losea	Rice	++	–	Marshall 1977
	R. tiomanicus	Oil palm, vegetables	++	–	Wood and Liau 1984
Southeast Asia + Pacific	*R. exulans*	Vegetables, sugarcane	++	+	Williams 1973; Marshall 1977
Melanesia	*R. praetor*	Root crops, vegetables	+	–	Flannery 1995a,b
	R. steini	Root crops, vegetables	+	–	Flannery 1995a
Australia	*R. colletti*	Rice	+	–	Watts and Aslin 1981
	R. sordidus	Sugarcane	++	–	McDougall 1947; Whisson 1996
	R. villosissimus	Rice	+	–	Watts and Aslin 1981
	Rattus sp. (member of *sordidus* group)	Wheat	+	–	G. Gordon, Qld NPWS pers. comm.
Global	*R. norvegicus*	Various	+++	+	Meehan 1984
	R. rattus complex	Various, rice in Southeast Asia	+++	+	Meehan 1984

rodents including rural populations of *R. rattus* and *R. losea*. The likelihood of hantavirus infection is closely related to the intimacy and frequency of contact with rodents or their dried excreta—contamination of stored foods by faeces or urine poses an obvious risk in this regard. Hart and Bennett (1999) estimated a global infection rate for hantaviruses of 100,000–200,000 cases per year.

Much less is known about the potential for disease transmission between introduced *Rattus* species and native rodents. The Australian and Pacific region, where *Rattus* intruded late into an already well-established rodent fauna, provides an ideal model system in which to examine the nature of this interaction. Interestingly enough, a recent review of the helminth parasites of Australian rodents by Smales (1997) showed a marked contrast between the helminth communities of native *Rattus* species (dominated by nematodes) and native rodents belonging to other genera (dominated by trematodes). Only 13 helminth species are shared between these groups, compared with seven species shared exclusively between the recently introduced rodents (*Rattus* and *Mus* spp.) and native *Rattus*. Skerratt et al. (1995) made a strong case for an ancient transfer of trichostrongylid nematodes between native *Rattus* and other Australian rodent genera.

Another case study that documents the intensity of biotic interchange between invasive *Rattus* species and an established rodent fauna is Roberts' (1991b) study of endo- and ecto-parasites of the Pacific rat. Roberts contrasted populations of *R. exulans* that have either remained isolated from, or experienced contact with, the more recently introduced *R. rattus* and *R. norvegicus*. The evidence appears strong for cross-transfer of two nematodes, one cestode, four fleas and four mites. In a few populations, the 'new' parasites were found in isolated populations of *R. exulans*. Roberts interpreted these as reflections of unsuccessful invasion by the newly introduced *Rattus* species, where transfer of parasites had occurred quickly before the mammalian invader becoming locally extinct.

Some conclusions and some final questions

Many elements of the evolutionary history of *Rattus* are beginning to take shape as a consequence of recent morphological and molecular studies. The wider relationships of *Rattus* clearly lie among the suite of 'new endemic' murine genera, all of which are native to the Asian region. *Rattus* clearly evolved somewhere within this region, but exactly where remains uncertain. The available fossil evidence perhaps favours an origin on mainland Southeast Asia. However, two biogeographical observations point to an alternative origin in island Southeast Asia. The first is that the diversity of 'new endemic' genera is much higher in the insular region than it is on the mainland, especially on Sulawesi, in the Philippine Islands, and in Nusa Tenggara. Secondly, many of the more archaic *Rattus* species are found in these same areas, as well as in New Guinea and Australia. Archaic species are strikingly absent from mainland Asia, although they are present both on and off the margin of the Sunda Shelf.

Various biogeographical scenarios could be developed to account for these distributional patterns, however all would involve one or more early phases of dispersal by archaic forms of *Rattus*. These underwent modest to spectacular radiations in many areas. Archaic forms persisted on many smaller islands and in tropical forests, especially in montane refuges. *Rattus* may have entered New Guinea and Australia independently and perhaps at different times, leading to significant radiations in each area.

One of the most remarkable things about the dispersal and subsequent radiation of *Rattus* is that it occurred in most areas *in the presence of a pre-existing, diverse rodent fauna*. This is most striking in the case of Sulawesi, the Philippine Islands, New Guinea and Australia, each of which supports a rich and highly diversified murid rodent fauna with histories spanning 5–8 million years of local evolution (Aplin 2002). The presence of numerous, established competitors would normally represent a significant impediment to the establishment of an invasive species (Williamson and Fitter 1996). However, *Rattus* not only managed to gain a foothold in these areas, in most it was able to disperse and speciate in varied habitats from mangrove forest to sub-alpine heath; and, in Australia, extend into true deserts. Later in its history, *Rattus* was able to exploit another suite of newly created habitats—the gardens, rice fields and villages of early agricultural peoples—and then to travel with the descendants of these people to colonise many of the world's most remote islands.

To conclude this review, we should ask what it is about the genus *Rattus* that has made it so phenomenally successful? We do not pretend to know the answer to this question. However, some elements that might be included in a satisfactory answer are:

- the fact that most *Rattus* species are 'generalists'—in body size and form, in diet, in behaviour;
- the ability of at least some *Rattus* species to utilise stored abdominal fat during lean periods (e.g. Yabe 1994);
- the apparent propensity of *Rattus* species to undergo frequent chromosomal rearrangements, perhaps favouring rapid speciation in a widely dispersing group of animals (e.g. Bush et al. 1977); and
- the willingness of at least some *Rattus* species to enter water, thereby increasing their chances of dispersal and allowing them to utilise seasonally inundated habitats.

These few suggestions clearly fall well short of a satisfactory answer that should perhaps be framed in terms of physiological breadth, immunological capacity and reproductive potential. Unfortunately, knowledge of such things is too meagre at present among all but a few *Rattus* species to do more than flag these as potentially useful avenues for thought.

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References

Audoin-Rouzeau, F. and Vigne, J.-D. 1994. La colonisation de l'Europe par le Rat Noir (*Rattus rattus*). Revue de Paléobiologie, 13, 125–145.

Aplin, K.P. 2002. Ten million years of rodent evolution in the Australasian region. In: Merrick, J.R., Archer, M., Clayton, G. and Hand, S.J., ed., Vertebrate zoogeography and evolution in Australia. Chatswood, Reed Books (in press).

Aplin, K.P., Pasveer, J.M. and Boles, W.E. 1999. Late Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species. Records of the Western Australian Museum, Supplement No. 57, 351–387.

Baverstock, P.R., Adams, M. and Watts, C.H.S. 1986. Biochemical differentiation among karyotypic forms of Australian *Rattus*. Genetica, 71, 11–22.

Baverstock, P.R., Adams, M., Maxson, L.R. and Yosida, T.H. 1983b. Genetic differentiation among karyotypic forms of Australian *Rattus*. Genetics, 105, 969–983.

Baverstock, P.R., Gelder, M. and Jahnke, A. 1983a. Chromosome evolution in Australian *Rattus*—G-banding and hybrid meiosis. Genetica, 60, 93–103.

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.

Bonhote, J.L. 1910. On the varieties of *Mus rattus* in Egypt; with general notes on the species having reference to variation and heredity. Proceedings of the Zoological Society of London, 1910, 651–665.

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.

Brown, P.R., Hung, N.Q., Hung, N.M. and van Wensveen, M. 1999. Population ecology and management of rodent pests in the Mekong River Delta, Vietnam. 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, 319–337.

Bush, G.L., Case, S.M., Wilson, A.C. and Patton, J.L. 1977. Rapid speciation and chromosomal evolution in mammals. Proceedings of the National Academy of Sciences, USA, 74, 3942–3946.

Chaimanee, Y. 1998. Plio-Pleistocene rodents of Thailand. Thai Studies in Biodiversity, 3, 1–303.

Chan, K.L, Dhaliwal, S.S. and Yong, H.S. 1979. Protein variation and systematics of three subgenera of Malayan rats (Rodentia: Muridae, Genus *Rattus* Fischer). Comparative Biochemisty and Physiology, 64B, 329–337.

Chasen, F.N. 1933. On the forms of *Rattus rattus* occuring on the mainland of the Malay Peninsula. Bulletin of the Raffles Museum, 8, 5–24.

Childs, J.E., Glass, G.E., Korch, G.W. and Leduc, J.W. 1989. Effects of hantaviral infection on survival, growth and fertility in wild rat (*Rattus norvegicus*) populations in Baltimore, Maryland. Journal of Wildlife Diseases, 25, 469–476.

Corbett, G.B. and Hill, J.E. 1992. The mammals of the Indomalayan region: a systematic review. Oxford, Oxford University Press, 488 p.

Curzon, P. and McCracken, K. 1989. Plague in Sydney. The anatomy of an epidemic. Kensington, New South Wales University Press, 213 p.

Ellerman, J.R. 1941–1949. The families and genera of living rodents, volumes 2–3. London, British Museum (Natural History), 690 p.

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

Flannery, T.F. 1995b. Mammals of the south-west Pacific and Moluccan islands. Chatswood, Reed Books, 464 p.

Flannery, T.F. and White, J.P. 1991. Animal translocations. Zoogeography of New Ireland mammals. National Geographic Research and Exploration, 7, 96–113.

Gadi, I.K. and Sharma, T. 1983. Cytogenetic relationships in *Rattus*, *Cremnomys*, *Millardia*, *Nesokia* and *Bandicota* (Rodentia: Muridae). Genetica, 61, 21–40.

Gaur, R. 1986. First report of a fossil *Rattus* (Murinae, Rodentia) from the Pinjor Formation of Upper Siwalik of India. Current Science (India), 55, 542–544.

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.

Gratz, N.G. 1997. The burden of rodent-borne diseases in Africa south of the Sahara. Belgian Journal of Zoology, 127, 71–84.

Harrison, J.L. 1951. Reproduction in rats of the subgenus *Rattus*. Proceedings of the Zoological Society of London, 121, 673–694.

Hart, C.A. and Bennett, M. 1999. Hantavirus infections: epidemiology and pathogenesis. Microbes and Infection, 1, 1229–1237.

Hinton, M.A.C. 1918–1919. Scientific results from the mammal survey. No. XVIII. Report on the house rats of India, Burma, and Ceylon. Journal of the Bombay Natural History Society, 26, 59–88, 384–416, 716–725, 906–918.

Hong, C. 1989. The population dynamics and prediction to numbers of *Rattus rattoides*. Acta Theriologica Sinica, 9, 137–145 (in Chinese with English summary).

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

Khush, G.S. 1997. Origin, dispersal, cultivation and variation of rice. Plant Molecular Biology, 35, 25–34.

Kitchener, D.J., Aplin, K.P. and Boeadi 1991a. A new species of *Rattus* from Gunung Mutis, South West Timor Island, Indo-

nesia. Records of the Western Australian Museum, 15, 445–465.

Kitchener, D.J., How, R.A. and Maharadatunkamsi 1991b. A new species of *Rattus* from the mountains of West Flores, Indonesia. Records of the Western Australian Museum, 15, 555–570.

Lambeck, K. and Chappell, J. 2001. Sea level change through the last glacial cycle. Science, 292, 679–686.

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.

Leung, L.K.P., Singleton, G.R., Sudarmaji and Rahmini 1999. Ecologically-based population management of the Rice-Field Rat in Indonesia. 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, 305–318.

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

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.

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. East Grinstead, England, Rentokil, 383 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. 1981. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. Bulletin of the American Museum of Natural History, 168, 225–334.

Musser, G.G. 1982. The Trinil rats. Modern Quaternary Research in Southeast Asia, 7, 65–85.

Musser, G.G. 1984. Identities of subfossil rats from caves in southwestern Sulawesi. Modern Quaternary Research in Southeast Asia, 8, 61–94.

Musser, G.G. 1986. Sundaic *Rattus*: definitions of *Rattus baluensis* and *Rattus korinchi*. American Museum Novitates, 2862, 1–24.

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 Califia, D. 1982. Results of the Archbold Expeditions. No. 106. Identities of rats from Pulau Maratua and other islands off East Borneo. American Museum Novitates, 2726, 1–30.

Musser, G.G. and Carleton, M.D. 1993. Family Muridae. In: Wilson, D.M. and Reeder, D.M., ed., Mammal species of the world, 2nd edition. Washington DC, Smithsonian Institution Press, 501–755.

Musser, G.G. and Heaney, L.R. 1985. Philippine *Rattus*: a new species from the Sulu Archipelago. American Museum Novitates, 2818, 1–32.

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 the American Museum of Natural History, 211, 1–138.

Musser, G.G. and Holden, M.E. 1991. Sulawesi rodents (Muridae: Murinae): morphological and geographical boundaries of species in the *Rattus hoffmani* Group and a new species from Pulau Peleng. In: Griffiths, T.A. and Klingener, D., ed., Contributions to mammalogy in honor of Karl F. Koopman. Bulletin of the American Museum of Natural History, 206, 323–413.

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.

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

Niethammer, J. von and Martens, J. 1975. Die Gattungen *Rattus* und *Maxomys* in Afganistan und Nepal. Zeitscrift für Säugertierkunde, 40, 325–355.

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.

Prakash, I. and Ghosh, P.K. (ed.) 1992. Rodents in Indian agriculture, volume 1. State of the art. Jodhpur, Pawan Kumar Scientific Publishers. 692 p.

Roberts, M. 1991a. Origin, dispersal routes, and geographic distribution of *Rattus exulans*, with special reference to New Zealand. Pacific Science, 45, 123–130.

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

Ruedas, L.A. and Kirsch, J.A.W. 1997. Systematics of *Maxomys* Sodt, 1936 (Rodentia: Muridae: Murinae): DNA/DNA hyridization studies of some Borneao-Javan species and allied Sundaic and Australo-Papuan genera. Biological Journal of the Linnean Society, 61, 385–408.

Schwabe, H.W. von 1979. Vergleichend-allometrische Untersuchungen an den Schädeln europäischer und asiatischer Hausratten (*Rattus rattus* L.). Zeitscrift für Säugertierkunde, 44, 354–360.

Schwarz, E. and Schwarz, H.K. 1967. A monograph of the *Rattus rattus* group. Anales de la Escueal Nacional de Ciencias Biologicas, México, 14, 79–178.

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.

Skerratt, L.F., Beveridge, I. and Durette-Desset, M.-C. 1995. Distribution of species of trichostrongyloid nematode parasites in the small intestine of the bush rat *Rattus fuscipes*. Transactions of the Royal Society of South Australia, 115, 217–220.

Smales, L.R. 1997. A review of the helminth parasites of Australian rodents. Australian Journal of Zoology, 45, 505–521.

Somerville, E.M. 1999. Some aspects of the palaeoecology of commensals. Quaternary Proceedings, 7, 605–613.

Suzuki, H., Tsuchiya, K. and Takezaki, N. 2000. A molecular phylogenetic framework for the Ryuku endemic rodents *Tokudaia osimensis* and *Diplothrix legata*. Molecular Phylogenetics and Evolution, 15, 15–24.

Taylor, J.M., Calaby, J.H. and Van Deusen, H.M. 1982. A revision of the genus *Rattus* (Rodentia, Muridae) in the New Guinea region. Bulletin of the American Museum of Natural History, 173, 177–336.

Tchernov, E. 1968. Succession of rodent faunas during the Upper Pleistocene of Israel. Mammalia Depicta, X. Hamburg, Verlag.

Tomich, P.Q. and Kami, H.T. 1968. Coat color inheritance of the roof rat in Hawaii. Journal of Mammalogy, 47, 423–431.

Verneau, O., Catzeflis, F. and Furano, A.V. 1998. Determining and dating recent rodent speciation events by using L1 (LINE-1) retrotransposons. Proceedings of the National Academy of Science, USA, 95, 11284–11289.

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

Watts, C.H.S. and Baverstock, P.R. 1996. Phylogeny and biogeography of some Indo-Australian murid rodents. In: Kitchener, D.J. and Suyanto, A., ed., Proceedings of the first international conference on eastern Indonesian–Australian vertebrate fauna, Manado, Indonesia, November 22–26, 1994. Perth, Western Australian Museum, 47–50.

Weerd, van de A. 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. Utrecht Micropalaeontological Bulletin, 2, 1–216.

Whisson, D. 1996. The effect of two agricultural techniques on populations of the canefield rat (*Rattus sordidus*) in sugarcane crops in north Queensland. Wildlife Research, 25, 589–604.

White, J.P. 1972. Ol Tumbuna. Archaeological excavations in the eastern Central Highlands, Papua New Guinea. Terra Australis 2. Canberra, Department of Prehistory, Research School of Pacific Studies, The Australian National University.

White, J.P., Clark, G. and Bedford, S. 2000. Distribution, present and past, of *Rattus praetor* in the Pacific and its implications. Pacific Science, 54, 105–117.

Williams, J.G. 1973. The ecology of *Rattus exulans* (Peale) reviewed. Pacific Science, 27, 120–127.

Williamson, M. and Fitter, A. 1996. The varying success of invaders. Ecology, 77, 1661–1666.

Won, C. and Smith, K.G. 1999. History and current status of mammals of the Korean Peninsula. Mammal Review, 29, 3–33.

Wood, B.J. and Liau, S.S. 1984. A long term study of *Rattus tiomanicus* populations in an oil palm plantation in Johore, Malaysia. III. Bionomics and natural regulation. Journal of Applied Ecology, 21, 465–472.

Yabe, T. 1994. Fat deposits for wintering in the Norway rat, *Rattus norvegicus*. Journal of the Mammalogical Society, Japan, 19, 129–133.

Yang, Y., Zeng, Z., Deng, X., Luo, M., Liang, J. and Xie, R. 1999. Comparative population ecology of rodents in cropland of the western Sichuan Plain. I. Population dynamics and reproduction. Acta Theriologica Sinica, 19, 267–275.

Yosida, T.H. 1980. Cytogenetics of the black rat. Karyotype evolution and species differentiation. Tokyo, University of Tokyo Press, 256 p.

Zhang, Z., Chen, A., Ning, Z. and Huang, X. 1999. Rodent pest management in agricultural ecosystems in China. 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, 261–284.

Zheng, S. 1993. Quaternary rodents of Sichuan–Guizhou Area, China. Beijing, Science Press. 270 p. (in Chinese, with English summary).

Integrative systematics: the importance of combining techniques for increasing knowledge of African Murinae

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Abstract. The soft-furred rats of the *Praomys* group are of economic and health importance but represent one of the most difficult groups of the Murinae for systematics analyses due to a high degree of morphological similarity among species. Because neither morpho-anatomy nor morphometrics are 100% efficient, the use of cytotaxonomy and DNA sequencing is essential. We present together our recent results about taxonomy and biosystematics of the group. The distinction of two complexes, *P. jacksoni* and *P. tullbergi*, is here confirmed both by morpho-anatomy and geometric morphometrics, as well as by cytochrome b sequencing. It is also shown that the fronto-parietal crest disposition has a phyletic signal. However, these criteria cannot be applied to juvenile and very old specimens, which restricts its application. DNA sequencing of the mitochondrial cytochrome *b* gene also confirms the monophyly of the *Praomys* group. However, some incongruence is observed between molecules and morphology due to the paraphyly of the genus *Myomys*. This pattern points out the inaccuracy of external morphological characters taken as diagnostic criteria. In such a case, like in various other Murinae, the combination of different techniques appears necessary in order to better understand the taxonomy and biosystematics in the group. These results have important implications for epidemiological research.

Introduction

Systematics is the science devoted to discovery, identification, classification and interpretation of biological diversity. It is often divided into taxonomy (or description, naming and classification of taxa) and biosystematics (assessment of the evolutionary relationships between species, i.e. phylogeny). This distinction reflects different approaches and the frequent involvement of different groups of scientists. Nevertheless, the two disciplines share the phylogenetic approach and have the same fundamental aim: the production of stabilised classifications, allowing evolutionary inferences both for fundamental and applied biology. Systematics has recently benefited from a complete renewal, with the ongoing development of new methods and concepts, among them cladistics, morphometrics, molecular systematics and global genomics. The integrative application of all these tools to the same study models is now possible and this approach is developed in our research team. It provides a rich approach that leads to more complete and precise descriptions of biodiversity.

Tropical Africa supports very high micro-mammalian diversity, especially between African Murinae (Rodentia, Muridae). The soft-furred rats of the genus *Praomys* are widely distributed from West Africa (Senegal to Angola) to East Africa (Uganda to Malawi) and in both primary and secondary forest zones. The genus comprises 10 species whose geographical limits are still poorly known due to the low level of morphological differentiation among the species and a long history of confusion and misidentifications (Musser and Carleton 1993; Van der Straeten and Kerbis-Peterhans 1999). Until recently, the genus *Praomys* was broadly conceived and included members of such well recognised genera as *Mastomys*, *Hylomyscus* and *Myomys*. A revision of the genus *Praomys* also requires that we adopt a broader approach that includes these taxa, which together constitute the *Praomys* group. No phylogeny was formerly available, despite the fact that the entire group has economic and health importance (Lecompte et al., this volume). More specifically, *P. jacksoni* is a primary natural host of the arenavirus Mobala (Mills et al. 1997) and is probably a reservoir of Ebola virus (Morvan et al. 1999). Furthermore, some species of *Praomys* are almost unknown because they are restricted to some isolated montane forests. These species have special conservation importance.

Finally, the biodiversity of *Praomys* may be underestimated due to the probable existence of sibling species in various African Murinae, as suggested recently by Meester (1988) and Taylor (2000). A careful revision of

all members of the genus is required, but with special attention to *P. tullbergi*, the type species of the genus. In this paper, we have applied the integrative and comparative approach to the *Praomys* group, both at specific and generic levels, in order to solve some taxonomic problems. We will highlight the perspective brought by each technique, as well as the importance of comparing results and the implications of such an approach.

Material and methods

Voucher specimens from the collections of the Museum National d'Histoire Naturelle (MNHN; Paris, France), the Natural History Museum (London, England), and the Royal Museum for Central Africa (Tervuren, Belgium) have been used for morpho-anatomical, morphometric and phylogenetic analysis. Two taxonomic levels are considered in this study. First, the initial recognition of elementary taxonomic units (OTUs) is made both at genus and species level with the help of morphometric methods; and then, the analysis of relationships within *Praomys* is performed through phylogenetic methods and assessed for their consensus.

At the intraspecific level, 208 skulls of *P. tullbergi* from MNHN have been used for morphometric analyses (to be reported in detail elsewhere). Twenty skull and mandible measurements were taken using a caliper (0.01 mm precision). Principal component analysis (PCA) and canonical variable analysis (CVA) were done using log-transformed values. Outlines of dental rows were drawn using a binocular microscope with a camera lucida and digitised using a standard orientation after preliminary tests. A total of 194 dental-row outlines of *P. tullbergi* specimens from MNHN collections—86 females and 114 males, coming from Ivory Coast (N = 45), Cameroon (N = 2), Gabon (N = 94), Burkina Faso (N = 2), Central African Republic (N = 31), Senegal (N = 6) and Togo (N = 14)—were digitalised using TPSDig software (Rohlf 2001) and then analysed using specially devised MATLAB V.6. routines for Elliptic Fourier analysis (Kuhl and Giardina 1982). Coefficients of elliptic Fourier were calculated for normalised and orientated contours. Four landmarks at the junction of the teeth were taken in order to superimpose the outlines. Shape and size differences were analysed using PCA and CVA of Fourier coefficients.

Seven landmarks were taken on the left anterior half of the dorsal side of the skulls of different *Praomys* species (Figure 1). Landmarks were acquired using a charge coupled device (CCD) camera with a macrophotographic device and the Measurement TV software (version 1.92, Updegraff 1990). Thin-plate spline analyses were conducted using the thin-late splines relative warp (TPSRW) analysis software of Rohlf (2001) allowing superposition of landmarks and visualisation of shape deformations in function of variance.

On the basis of good taxonomical identifications, phylogenetic analysis can be performed. A preliminary morphological phylogeny (Lecompte et al. 2002a) was completed with new characters and increased samples within the *Praomys* group. The data matrix had 51 characters on 27 species, including 24 species of the *Praomys* group. Total genomic DNA was extracted from liver, heart or muscles preserved in 70% ethanol using a CTAB protocol (Winnepenninckx et al. 1993). Mitochondrial sequences containing the cytochrome b gene (1140 pb) were isolated via the polymerase chain reaction (PCR) and sequenced directly from purified PCR products with an automatic sequencer (CEQ2000; Beckman). The sequences were entered and manually aligned using the Bioedit software. Mutational saturation was studied for each codon position for transitions and transversions separately. Both for morpho-anatomical and molecular data, the phylogenetic relationships were analysed by the maximum parsimony (MP) method using PAUP 4.0 (Swofford 1998). Twenty species of the *Praomys* group, represented by one to six specimens, were treated with other Murinae species chosen as outgroups according to Lecompte et al. (2002b). The molecular and morphological trees were compared with Treemap 1.0 software (Page 1995).

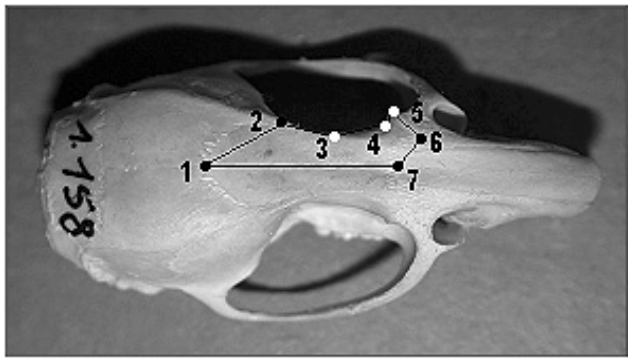

Figure 1. Dorsal view of a *Praomys* skull showing the landmarks used to analyse the shape of the frontal bone.

Results and discussion

OTU definition

Within the framework of the biological species concept of Mayr (1963), there is a need to define elementary taxonomic units (OTUs), especially when looking at 'non-natural' populations (issued from collections or systematic field inventories) where the critical tests of hybridisation cannot be made. It is also necessary in the case of sibling species (morphologically similar species but genetically structured and reproductively isolated; Mayr 1963). Classical morpho-anatomy or morphometric tools are well suited for morphospecies definition, however in the case of sibling species or a species complex, cytotaxonomic methods, especially using banding techniques, are better adapted.

Morpho-anatomy

The search for diagnostic characters is especially important for species identification. In the past, the diag-

nosis of species was based on external characters but this can lead to considerable confusion, especially in groups with high levels of morphological similarity and/or variability. In the *Praomys* group, most of the genera were long confused and even placed in the same genus (see Ellerman 1940–1941; Meester and Setzer 1971–1977). The first morphological revisions of the group grew out of Petter's (1965, 1975) and Rosevear's (1969) studies of skull and molar morphology, which provided some useful characters, both at the generic and specific levels. However, these authors each looked only at a few species of the genus. Around the same time, other authors reported some supplementary characters that allowed the discrimination of certain species, but comparisons were generally very limited. Our research group has, for the first time, examined all recognised species of *Praomys*, with samples of 15 to 100 specimens per species to accurately assess intraspecific variability. The selection of skull characters took into account the nature and extent of variability of the characters; all highly variable characters were rejected in devising the identification key.

The cranial characters selected for this identification key are illustrated in Figure 2. The only external character employed here is the mammary formula, because this was initially used by Thomas (1915) to separate the genera *Myomys*, *Mastomys* and *Praomys*. It is expressed as the total number of pectoral mammae and inguinal mammae. This character can be used only with adult females and consequently it is limited for purposes of species determination. We provide here an identification key for species of the genus *Praomys* (after Lecompte et al. 2001).

1. Supraorbital ridges absent or very weak (Figure 2, label a). 2.
   Supraorbital ridges present, more or less pronounced. 3.
2. Anterior limit of palatine bone extending to the level of the posterior part of M1 (Figure 2, h), nasal/frontal suture almost horizontal (Figure 2, f), zygomatic bone of the same breadth as malar process, mammary formula: 1 + 2 = 6. *P. morio*
   Anterior limit of the palatine bone extending to between M1 and M2 (Figure 2, i), nasal/frontal suture V-shaped (Figure 2, g), zygomatic bone very thin (half of the breadth of malar process), mammary formula: 2 + 2 = 8. *P. delectorum*
3. Supraorbital ridges beginning in the middle of frontals (Figure 2, b) 4.
   Supraorbital ridges very strong, straight, beginning in front of frontals (Figure 2, c) 7.
4. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M1 (Figure 2, j). 5.
   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M1 (Figure 2, k). *P. hartwigi*
5. Proportions of the teeth normal (ratio of molar row length/maximum length of skull >15%) *P. tullbergi*
   Microdonty (ratio of molar row length/maximum length of skull <15%) 6.
6. Interorbital constriction gradual and amphora-shaped (Figure 2, d) *P. misonnei*
   Interorbital constriction more sharply angular in the middle of frontal (Figure 2, e) *P. rostratus*
7. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M1 (Figure 2, j). *P. mutoni*
   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M1 (Figure 2, k). 8.
8. Four small accessory plantar pads, mammary formula: 1 + 2 = 6 *P. jacksoni*
   One or no small accessory pad, mammary formula: 2 + 2 = 8 *P. degraaffi*

Some characters must be handled carefully because of sex and/or age dependence. For instance, the 'supraorbital ridges' present some variation in relation to age—the ridges increasing in strength with the age of the animal. Thus, old *P. morio* can have similar ridges to young *P. tullbergi*, and the type of *P. morio*, a young adult, presents very weak ridges, which could be quite misleading. This illustrates the necessity of taking into account both sex

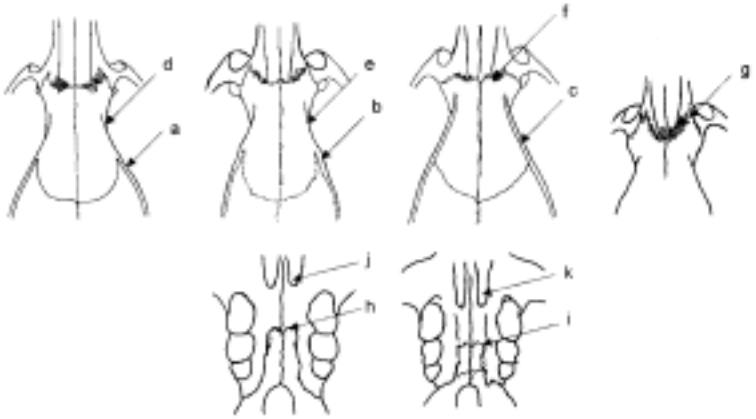

Figure 2. Morphological characters used in the identification key for *Praomys* species. See text for identification of morphological features.

and age influences on diagnostic morphological characters.

Molar teeth characters are useful for palaeontology and determination of remains in owl pellets (Denys 2002). *Praomys* teeth are characterised by an undifferentiated prelobe of the upper M1/, with t2 and t3 aligned and hardly distinguishable, low crowned teeth with well-fused cusps, a lack of deep valleys between cusps, and bunodonty of very narrow lower molars without developed cingula (Figure 3). In general, molar cusps are well united and there are few longitudinal crests.

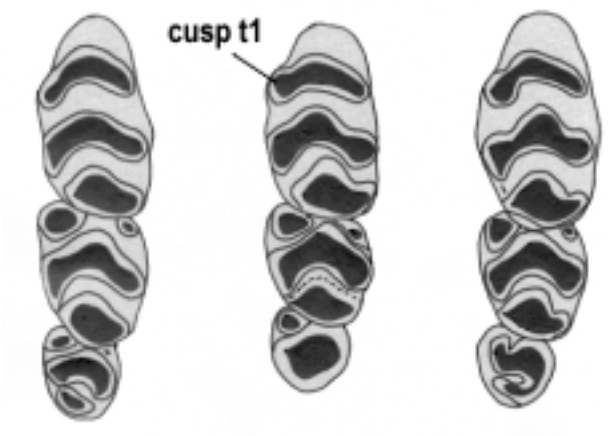

Figure 3. Variation in upper molar morphology among populations of *Praomys tullbergi*: left, Ivory Coast specimen; middle, Senegal specimen (notice the smaller size and that cusp t1 is better individualised); and right, Guinean specimen. All are left upper molar rows.

Cytotaxonomy

It has been shown recently that, in the case of African murids, cytogenetic variations provide some of the most reliable diagnostic criteria (karyospecies concept, Dobigny et al. 2002a,b). Unfortunately, cytogenetic information is lacking for some of the 10 recognised *Praomys* species. A preliminary survey of all published data indicates the existence of species complexes and of potential sibling species, especially in the *tullbergi* group, where two morphologies are known for the sexual chromosomes (Matthey 1958; Capanna 1996) (Table 1). No banding techniques have yet been applied to verify the taxonomic status of these forms. Molecular taxonomy, in this context, can also help to understand relationships within taxa and perhaps reveal cryptic species.

Morphometrics

Morphometrics is the quantitative description of size and shape of organisms (Rohlf and Marcus 1993). Initially based on distance measurements (classical morphometrics), it has been recently renewed with the use of thin-plate spline (TPS) and Fourier analysis methods which allow the analysis of shape of organisms (geometric morphometrics: Bookstein1991). Morphometric techniques are appropriate in taxonomy for species discrimination but can also help to find useful morphological characters for phylogenies or to analyse the evolution of shape by mapping onto cladograms. Classical morphometric techniques (canonical analyses) have been applied successfully to distinguish between *Praomys* taxa. For example, Van der Straeten and Verheyen (1981), Van der Straeten and Dieterlen (1987) and Van der Straeten and Dudu (1990) used these methods to define species complexes within *Praomys* and to justify the naming of new *Praomys* species. Discriminant analyses of distances have also been applied in studies of other African Murinae, both to investigate geographical patterns within species and to search for cryptic species (Taylor et al. 1993; Chimimba 1994). We present here the results of various morphometric analyses performed at different taxonomic levels, reflecting the fact that, in the case of *Praomys*, even the generic boundaries still need to be defined.

Table 1. Chromosomal data available to date for *Praomys* species (2N = diploid number of chromosomes; NFa = fundamental chromosome number; X = sex chromosome X; Y = sex chromosome Y; SM = submetacentric; M = metacentric; A = acrocentric).

Species	Chromosomal data	References
P. taitae	2N = 48, NFa = 54; X = SM	Matthey 1965
P. degraaffi	2N = 26, NFa = 24	Maddalena et al. 1989
P. jacksoni	2N = 28, NFa = 26; X = SM	Matthey 1959
P. misonnei	2N = 36, NFa = 46	Qumsiyeh et al. 1990
P. morio	2N = 34, NFa = 32; X = SM; Y = M	Matthey 1970
P. rostratus	2N = 34, NFa = 32	Gautun et al. 1986
P. tullbergi	2N = 34, NFa = 32; X = A; Y = A or X = M	Matthey 1958; Capanna 1996
Praomys sp.	2N = 42, NFa = 62; X = SM; Y = A	Matthey 1965

Morphometric methods were first applied at the population level in order to test whether the chromosomal variability observed by Matthey (1958) and Capanna et al. (1996) in *P. tullbergi* has any morphological basis (Figure 4) or if any geographical substructure occurs within the species. In Figure 4, the first canonical variate separates out *P. tullbergi* from Ivory Coast, while the second canonical variate sets Guinea and Senegal populations apart from the others. The major difference between the Ivory Coast and other populations is size—especially size of the molars. This geographical difference was also investigated by using geometrical techniques of outline reconstructions, specifically to see if changes in dental size were accompanied by any changes in their shape. Elliptical Fourier analysis shows effectively that, in addition to size, there are shape differences in upper molar outline between the Guinean and Senegal populations of *P. tullbergi* (Figure 5). These results indicate a possible taxonomic differentiation within the *tullbergi* species group for the

more western part of tropical Africa. Concerning the chromosomal difference between specimens from the Central African Republic and from the Ivory Coast, the morphometrics analyses confirm some differences but much more sampling is required to investigate this problem thoroughly.

At a higher taxonomic level, there is confusion in the literature with the type of *P. lukolelae* from Central Africa. This taxon was placed in synonymy with *Malacomys* (Musser and Carleton 1993). TPS analysis using landmarks on the dorsal part of the skull confirms the distinction between the two species complexes of *Praomys* and suggest placement of *M. lukolelae* among the *P. tullbergi* complex. Combined with traditional skull and dental analysis, this strongly suggests by a quantitative method that the taxon *lukolelae* does not belong in *Malacomys* (Figure 6). Fronto-parietal crest disposition, as well as shape of the frontal part of the skull, helped to firm up the qualitative characters of Petter (1975). However, in all cases presented here, morphometrics never provided full discrimination between species or populations, hence other techniques are now required for OTU determination.

In conclusion, objective identification of OTUs requires attentive observation of large series of specimens in order to see the variability and eliminate the age differences. Good skeletal preparations and knowledge of anatomy are necessary. The discrimination methods can be applied locally with some specific identification success or at the generic level. However, in the case of *Praomys*, other molecular and karyological techniques are now needed to solve the problem of OTU definition within this group.

Phylogeny and classification

Phylogeny retraces the sister relationships of a species or a group of species. The genealogy obtained is shown graphically as a tree where the topology represents an hypothesis corresponding to the inferred evolutionary relationships between taxa. Congruent phylogenetic trees produced from different types of characters can form the basis for stable classifications (build the tree of life). Robust monophyletic groups allow us to make hypotheses about the history of characters and distributions. Phylogenetic relationships within the *Praomys* group were inferred using both morphological (Lecompte et al. 2002a) and molecular data (Lecompte et al. 2002b). By comparing the results of these analyses (Figure 7), several points of incongruency are given emphasis.

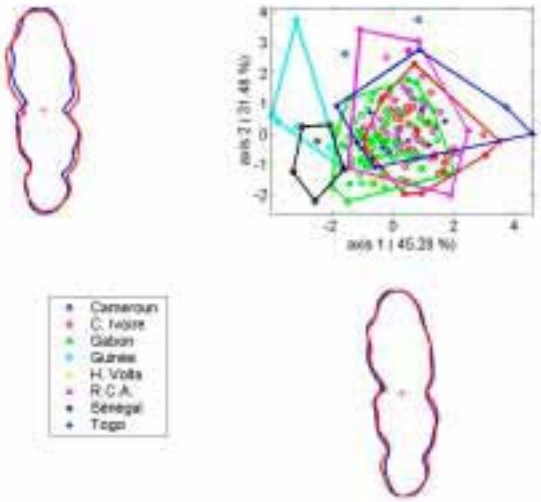

Figure 5. Canonical variable analysis (CVA) on upper molar row outlines and the representation of extreme shapes on each axis. The first canonical variable shows mainly a size difference and the second one a shape asymmetry especially on upper M1/.

A new maximum parsimony analysis is presented here for all members of the *Praomys* group. The morphology-based consensus tree displayed in Figure 7 (left), shows that the *Praomys* group is monophyletic and further confirms that the genus *Praomys* can be divided into two complexes, the *jacksoni* complex and the *tullbergi* complex. The crest character, first qualitatively identified by Petter (1975) and assessed quantitatively here (Figure 6), appears to have a robust phylogenetic value insofar as it provides an unambiguous synapomorphy for the *jacksoni* complex. The divergence between the *tullbergi* and *jacksoni* complexes is supported by a total of 13 synapomorphies. Species within

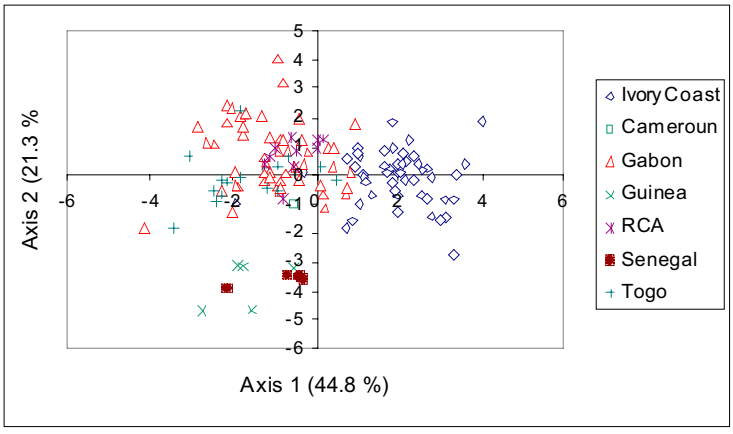

Figure 4. Results of the canonical variable analysis (CVA) based on 20 skull log-transformed measurements for 208 specimens of *P. tullbergi* from West Africa (axes 1 and 2) (RCA = Central African Republic).

the *tullbergi* group are distinguishable by up to six synapomorphies but there is no autapomorphy to define this entire group. Generally, some characters provide good local synapomorphies but they show convergence at the total *Praomys* group scale.

DNA sequencing is an important and objective source of characters usable in phylogeny (Figure 7, right). For the cytochrome b gene, the *Praomys* group is found to be monophyletic, as in the morphological tree. On the contrary, *Praomys*, *Myomys* and *Stenocephalemys* are this time paraphyletic. The cytochrome b sequences within the *P. tullbergi* group suggest the existence of a complex of species since *P. tullbergi* itself is divided into three paraphyletic units (E. Lecompte, unpublished). This pattern is consistent with previous geometric morphometrics and cytogenetic results.

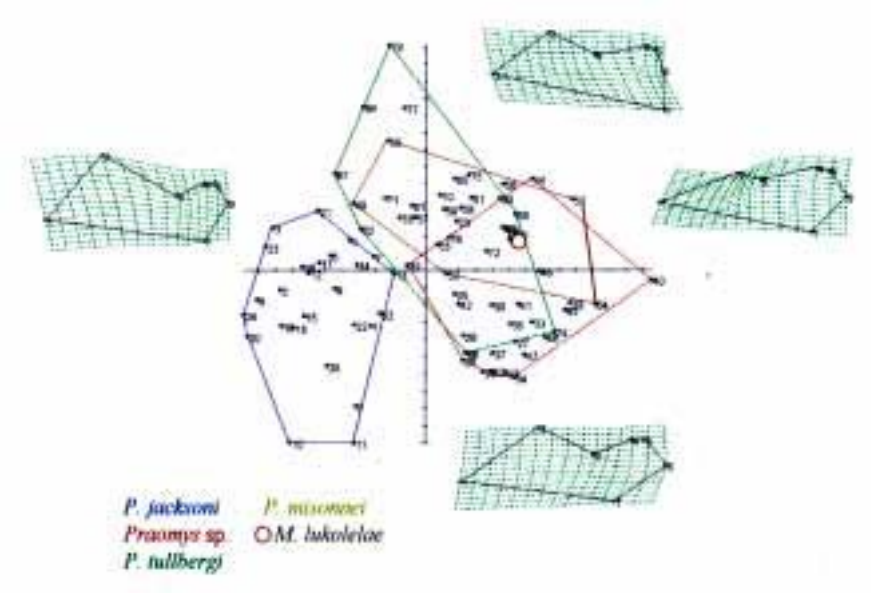

Figure 6. Thin-plate splines relative warp (TPSRW) analysis of variation in the dorsal outline of the frontal bone of different *Praomys* species. The results demonstrate the distinction of *P. jacksoni* on axis 1 and the similarity of the type of '*Malacomys*' *lukolelae* to members of the *P. tullbergi* complex.

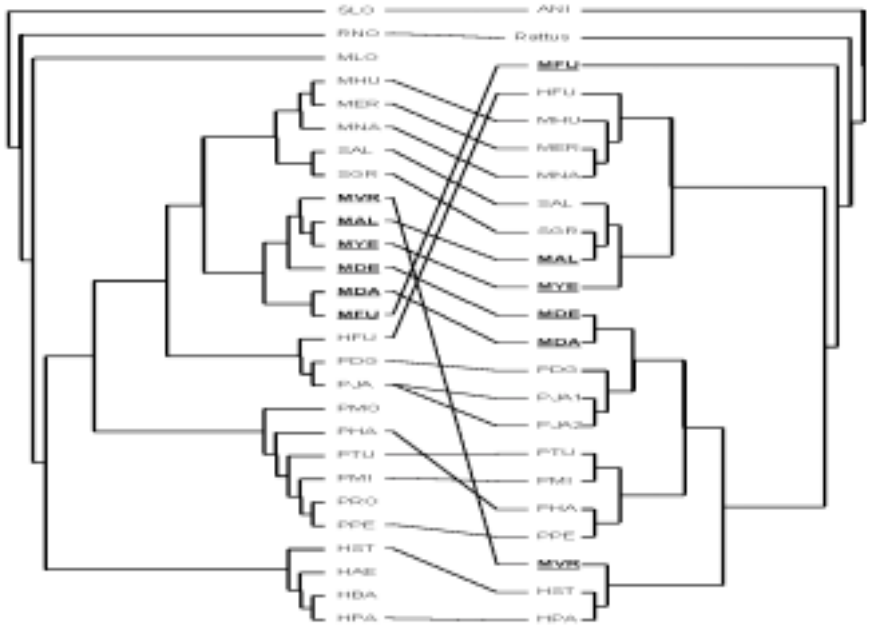

Figure 7. Morphological (left) and molecular (right) phylogenies of the *Praomys* group (after Lecompte et al. 2002a), showing the incongruence between these analyses. *Praomys* species are identified by acronyms beginning with P; *Hylomyscus* with H; *Stenocephalemys* with S; *Mastomys* are MER, MHU and MNA; *Heimyscus* is HFU; and the *Myomys* species are underlined.

In a recent article, Hillis and Wiens (1999) summarised the advantages and disadvantages of molecular versus morphological data for phylogenetic analysis. Both methods can provide useful information, especially when a range of different techniques is applied. Here, the comparison of the two trees with Treemap shows that the discrepant points are made by the *Myomys* species whose position in both the morphological and molecular trees is neither stable nor congruent. As a consequence, the morphological and molecular phylogenies are once again in conflict, especially in basal nodes and the monophyly/paraphyly of the genus *Myomys*. This conflict suggests that the genus *Myomys* is a possible cause of the wider confusion in the *Praomys* group. One classical criterion used to distinguish *Myomys* from *Praomys* or *Mastomys* species, is the number of mammae (10 in *Myomys* species), but the phylogenetic significance of this character is challenged by the molecular data that fail to support *Myomys* as a valid biological OTU. Similarly, the condition of a pure white belly may not be of phylogenetic value since this character is shared by *M. daltoni* and *M. fumatus*, which are highly divergent phylogenetically.

Similarly, morphologically divergent taxa like *Stenocephalemys* are found to be sister groups of certain *Myomys* species, and in this the new phylogeny confirms previous works by Lavrenchenko et al. (1999) and Fadda et al. (2001). The two phylogenies are congruent on the paraphyly of the genus *Praomys* (forest species): some *Myomys* (savannah species) are closer to *P. jacksoni* than to *P. tullbergi*. Interestingly, both *Praomys* species are hosts of arenaviruses (e.g. Mobala, Ippy, probably Ebola). The taxonomic results suggest that research on these viruses among related savannah taxa might prove of great interest from an epidemiological perspective.

Conclusion

In the *Praomys* group, it is now demonstrated that traditional diagnostic external morphological characters are far from effective in species identification. By combining cytogenetic, morphometric and molecular approaches in taxonomy, an accurate and stable classification can be achieved. Good species identification is still fundamental for applied research in agriculture and health. Furthermore, robust classifications that reflect the evolutionary history of the group may help in predicting the distributions of viruses and in discovering new species of potential hosts. The *Praomys* group has yielded numerous sibling species, especially in *Praomys* and *Mastomys* groups (Lecompte et al., this volume) and the biodiversity of the group is probably very much underestimated for these taxa. A similar conclusion can probably be inferred for most other genera of African Murinae. There is an urgent need to collect numerous specimens and tissues, spanning the entire geographical distributions of species within these genera. This is particularly pressing for some of the poorly known species that are under threat from drastic reduction of their primary and mountainous forest habitats.

References

Bookstein, F.L. 1991. Morphometric tools for landmark data: geometry and biology. New York, Cambridge University Press, 435 p.

Capanna, E., Codjia, J.T.C., Chrysostome, C. and Civitelli, M.V. 1996. Les chromosomes des Rongeurs du Bénin (Afrique de l'Ouest): 3 Murinae. Atti della Accademia dei lincei classe di scienze fisiche matematiche e naturali rendiconti lincei scienze fisiche e naturali, serie 9, 8, 25–37.

Chimimba, C. 1994. Non-geographic variation in *A. chrysophilus* (de Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa. South African Journal of Zoology, 29, 108–117.

Denys, C. 2002. The problem of species identification in palaeontology and biology: the case of *Mastomys* (Mammalia: Rodentia) and its dental variability. In: Baylac, M., Klingenberg, C.P., Fermon, Y. and Bailly, N., ed., Morphométrie multivariable, systématique et evolution: concepts, méthodes et applications. Paris, Muséum National d'Histoire Naturelle–Institut de Recherche pour le Développement (MNHN–IRD) Editions (in press).

Dobigny, G., Baylac, M. and Denys, C. 2002a. Geometric morphometrics and diagnosis of sibling species: the complex of west African *Taterillus* (Rodentia, Gerbillinae). Biological Journal of the Linnean Society (in press).

Dobigny, G., Granjon, L., Aniskine, V., Ba, K. and Volobouev, V. 2002b. A new sibling *Taterillus* species from West Africa. Mammalian Biology (in press).

Ellerman, J.R. 1940–1941. The families and genera of living rodents. London, British Museum (Natural History), 690 p.

Fadda, C., Corti, M. and Verheyen, E. 2001. Molecular phylogeny of *Myomys*/*Stenocephalemys* complex and its relationships with related African genera. Biochemical Systematics and Ecology, 29, 585–596.

Gautun, J.C., Sankhon, I. and Tranier, M. 1986. Nouvelle contribution à la connaissance des rongeurs du massif guinéen des monts Nimba (Afrique occidentale). Systématique et aperçu quantitatif. Mammalia, 50, 205–217.

Hillis, D.M. and Wiens, J.J. 1999. Molecules versus morphology in systematics. Conflicts, artefacts, and misconceptions. In: Wiens, J.J., ed., Phylogenetic analysis of morphological data. Washington D.C., Smithsonian Institution Press, 1–19.

Kuhl, F.P. and Giardina, G.R. 1982. Elliptic Fourier features of a closest contour. Computer Graphics and Image Processing, 18, 236–258.

Lavrenchenko, L.A., Milishnikov, A.N., Aniskin, V.M. and Warshavsky, A.A. 1999. Systematics and phylogeny of the genus *Stenocephalemys* Frick, 1914 (Rodentia, Muridae): a multidisciplinary approach. Mammalia, 63, 475–494.

Lecompte E., Denys, C. and Granjon, L. 2001. An identification key of the *Praomys* species (Rodentia: Muridae). In: Denys, C., Granjon, L. and Poulet, A., ed., African small mammals. Collection colloques et séminaires, Institut de Recherche pour le Développement (IRD) Editions, 127–140.

Lecompte, E., Granjon, L. and Denys, C. 2002a. The phylogeny of the *Praomys* complex (Rodentia: Muridae) and its phylogeographic implications. Journal of Zoological Systematics and Evolutionary Research, 40, 8–25.

Lecompte, E., Kerbis-Peterhans, J., Granjon, L. and Denys, C. 2002. Cytochrome-b based phylogeny of the *Praomys* group (Rodentia, Murinae): A new African radiation? Comptes Rendus de l'Académie des Sciences, Paris, Serie III (in press).

Maddalena, T., Van der Straeten, E., Ntahuga, L. and Sparti, A. 1989. Nouvelles données et caryotypes des rongeurs du Burundi. Revue Suisse de Zoologie, 96, 561–570.

Matthey, R. 1958. Les chromosomes et la position systématique de quelques Murinae africains (Mammalia–Rodentia). Acta Tropica, 15, 97–117.

Matthey, R., 1959. Formules chromosomiques de Muridae et de Spalacidae. La question du polymorphisme chromosomique chez les Mammifères. Revue Suisse de Zoologie, 66, 175–209.

Matthey, R. 1965. Etudes de cytogénétique sur les Murinae africains appartenant aux genres *Arvicanthis*, *Praomys*, *Acomys* et *Mastomys* (Rodentia). Mammalia, 29, 228–249.

Matthey, R. 1970. Caryotypes de Muridés et de Dendromuridés originaires de République Centrafricaine. Mammalia, 34, 459–466.

Mayr, E. 1963. Animal species and evolution. Cambridge, Harvard University Press.

Meester, J. 1988. Chromosomal speciation in southern African small mammals. South African Journal of Science, 84, 721–724.

Meester, J. and Setzer, H.W. 1971–1977. The mammals of Africa. An identification manual. Washington D.C., Smithsonian Institution Press.

Mills, J., Bowen, M. and Nichol, S. 1977 African arenaviruses—coevolution between virus and murid host. Belgian Journal of Zoology, 127, 19–38.

Morvan, J.M.M., Deubel, V., Gounon, P., Nakouné, E., Barrière, P., Murri, S., Volchov, V., Perpète, O., Selekon, B., Coudrier, D., Gautier-Hion, A. and Colyn, M. 1999. Identification of Ebola virus sequences present as RNA or DNA in organs of terrestrial small mammals of the Central African Republic. Microbes and Infection, 1, 1192–1201.

Musser, G.G. and Carleton, M.D. 1993. Family Muridae. In: Wilson, D.E. and Reeder, D.M., ed., Mammal species of the world: a taxonomic and geographic reference. Washington D.C., Smithsonian Institution Press, 501–755.

Page, R.D.M. 1995. Parallel phylogenies: reconstructing the history of host–parasite assemblage. Cladistics, 10, 155–173.

Petter F. 1965. Les *Praomys* d'afrique centrale. Zeitschrift für Säugetierkunde, 30, 54–60.

Petter F. 1975. Les *Praomys* de la République Centrafricaine (Rongeurs, Muridés). Mammalia, 39, 51–56.

Qumsiyeh, M.B., King, S.W., Arroyo-Cabrales, J., Aggundey, I.R., Schlitter, D.A., Baker, R.J. and Morrow, K.J. 1990. Chromosomes and protein in morphologically similar species of *Praomys* sensu lato (Rodentia, Muridae). Journal of Heredity, 81, 58–65.

Rohlf, F.J. 2001. TPSRW. Stony Brook, New York, Department of Ecology and Evolution, State University of New York.

Rohlf, F.J. and Marcus, L.F. 1993. A revolution in morphometrics, Trends in Ecology and Evolution, 8, 129–132.

Rosevear, D.R. 1969. The rodents of West Africa. London, Trustees of the British Museum (Natural History), 604 p.

Swofford D.L. 1998. PAUP: phylogenetic analysis using parsimony. Champaign, Illinois, Natural History Survey, 177 p.

Taylor, P.J. 2000. Patterns of chromosomal variation in southern African rodents. Journal of Mammalogy, 81, 317–331.

Taylor, P.J., Meester, J. and Kearney, T. 1993. The taxonomic status of Saunder's vlei rat, *Otomys saundersiae* Roberts (Rodentia : Muridae: Otomyinae). Journal of African Zoology, 107, 6, 571–596.

Thomas, O. 1915. List of mammals collected on the Upper Congo by Christy for the Congo Museum, Tervueren. Annals and Magazine of Natural History, Series 8, 16 , 465–481.

Updegraff, G. 1990. Measurement TV. Version 1.92. Data Crunch.

Van der Straeten, E. and Dieterlen, F. 1987. *Praomys misonnei*, a new species of Muridae from Eastern Zaïre (Mammalia). Stuttgarter Beiträge zur Naturkunde, serie A (Biologie), 402, 1–11.

Van der Straeten, E. and Dudu, A. M. 1990. Systematics and distribution of *Praomys* from the Masako Forest Reserve (Zaire), with the description of a new species, In: Peters, G. and Hutterer, R., ed., Vertebrates in the tropics. Bonn, Museum Alexander Koenig, 72–83.

Van der Straeten, E. and Kerbis-Peterhans, J.C. 1999. *Praomys degraaffi*, a new species of Muridae (Mammalia) from central Africa. South African Journal of Zoology, 34, 80–90.

Van der Straeten, E. and Verheyen, W. 1981. Etude biométrique du genre *Praomys* en Côte d'Ivoire. Bonner Zoologishe Beitrräge, 32, 249–264.

Winnepenninckx, B., Backeljau, T. and De Wachter, R. 1993. Extraction of high molecular weight DNA from molluscs. Trends in Genetics, 9, 407.

Landscape-dependent differentiation of deer mouse populations (*Peromyscus maniculatus*): a total-evidence approach using molecular and morphometric data

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Abstract. We employed random amplified polymorphic DNA (RAPD), microsatellite and morphometric measurements to study the microdifferentiation of five insular and four mainland populations of deer mice (*Peromyscus maniculatus)* from Lake Duparquet (Québec). Population divergence was assessed using distance comparisons and regressions were used to link the differentiation patterns to ecological and landscape variables. A significant fraction of among-population variance was detected, indicating a clear differentiation of the populations, in spite of the small size of the study area (50 km^2). Pairwise F_{st} values and Euclidean distances were computed to derive matrices of interpopulation differentiation. We found that barriers to dispersal were a key factor shaping the genetic structure of the insular populations. Indeed, three explanatory variables clearly emerged from our analyses, the *Area* of the islands, the *Remoteness* of an island from the shore, and the *Isolation index* combining the effect of *Remoteness* and *Mainland geometry*. The analysis of a total evidence matrix clarified the population differentiation pattern and allowed for a three-fold increase of the proportion of variance explained by the regression models. A multiple regression based on the ecological and landscape variables explained over 70% of the combined molecular and morphometric population divergence.

Introduction

Over the last decade, biologists have described and characterised the genetic structure of numerous rodent populations at various geographical scales (e.g. Jaarola and Tegelström 1996; Patton et al. 1996). The structure of the genetic variation can reflect historical factors related to the distribution of populations (phylogeography). However, the demography of populations and the landscape configuration can also alter the distribution of the genetic diversity within a species (Gilpin and Hanski 1991). Recently, the researches in molecular ecology and population genetics have focused on linking the genetic structure with landscape features that influence dispersal of individuals among populations and, consequently, gene flow (e.g. Mech and Hallett 2001). Investigation of the effects of these variables on population genetics will not only provide insights into microevolutionary processes operating at the ecological scale, but also extend our understanding of the effects of environmental modifications caused by human activity at the landscape level. Habitat fragmentation reduces the size of populations and increases their isolation, which accelerates genetic drift and decreases gene flow, respectively, inducing, in turn, a quick decline of the genetic variation. For these reasons, addressing the effects of landscape alteration on the spatial organisation and genetics of populations is of primary importance for management purposes and conservation biology (Berry 1986). Indeed, efficient management of the genetic diversity relies on the quantification of the population differentiation and a clear understanding of the relationship between genetic and landscape structures. From this perspective, the study of populations inhabiting insular landscapes is of great interest, since insular biotas can provide a simple yet accurate model of the long-term effects of extreme habitat fragmentation in a simplified habitat matrix (Vucetich et al. 2001).

In the present paper, we have addressed these issues by assessing the structure of the genetic variation of insular and mainland populations of deer mice (*Peromyscus maniculatus*) sampled from a single lake covering a limited geographical area (<50 km^2). Amounts of interpopulation differentiation were estimated using three classes of markers: random amplified polymorphic deoxyribonucleic acid (DNA) (RAPD), microsatellite and morphometric data. We tested whether the observed genetic structure could be explained by the landscape configuration and spatial structure of populations. The results obtained with the three data sets taken separately were compared and combined to clarify the effect of habitat fragmentation on the genetic differentiation of deer mouse populations.

Materials and methods

Sampling sites

Lake Duparquet is located at the southern edge of the Canadian boreal forest (48°30'N, 79°13'W). It covers approximately 50 km^2 and has more than 150 islands of various sizes. Deer mice were collected from five islands and four mainland sites in August 1995 and 1998 (Figure 1). Sites were selected to cover a wide range of geographical distances from each other or from the mainland (from 0.2 to 9.2 km). For the purposes of the present study, 64 specimens from nine populations were considered for both RAPD and microsatellite typing as well as for morphometric analysis (for sample sizes, see Table 1).

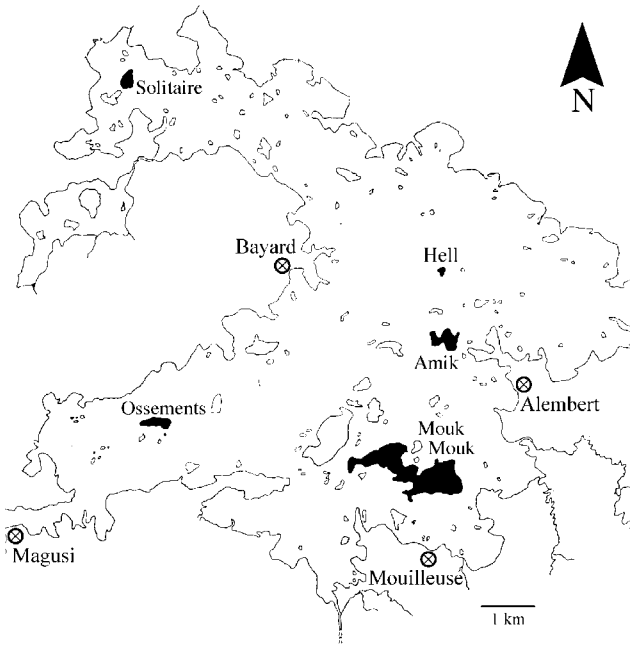

Figure 1. Map of Lake Duparquet (Abitibi, Québec) showing the five islands (in black) and the four mainland sites (crosses) analysed in this study.

Molecular data

DNA was extracted from fixed liver tissue, according to standard phenol/chloroform protocols. Three 10-mer primers were employed to derive the RAPD patterns, following the methods in Landry and Lapointe (1999), whereas microsatellite polymorphism was analysed at five loci using specific primers and polymerase chain reaction (PCR) profiles developed for *P. maniculatus* (Chirhart et al. 2000). Alleles were sized with an automated sequencer (ABI Prism 310) for microsatellites or using gel electrophoresis for RAPD typing.

Morphometric data

The morphological differentiation of populations was assessed by measuring 17 craniometric variables on each individual (see Landry and Lapointe 2001). These measurements were submitted to principal component analysis to correct for allometric growth. The first principal axis is assumed to represent a combination of the morphometric descriptors related to size, and the 16 subsequent orthogonal components were thus used to quantify morphometric differences between populations.

Population differentiation analyses

The amounts of population differentiation were calculated using an analysis of molecular variance (AMOVA; Excoffier et al. 1992). For both types of molecular data, pairwise interpopulation differentiation values were computed as linearised F_{st} values. In the case of morphometric measurements, Euclidean distances were computed between all pairs of individuals to measure population differentiation. Provided that the molecular and morphometric distances can be perfectly represented in a Euclidean space, this analytical framework applies to any type of data and was selected for the evaluation of all three distance matrices in a coherent fashion (see Landry and Lapointe 1999).

Ecological and landscape variables

The three population differentiation matrices were tested against six Euclidean distance matrices computed from the corresponding to each ecological and landscape variables (Table 1). The investigated variables were:

- *Population status*: coded 1 for island populations, and 0 for mainland populations.
- *Population abundance*: number of mice captured on each island (number of individuals/100 traps*night).
- *Island area*: for comparative purposes, the area (in ha) of all mainland sampling sites was set equal to the area of the largest island included in the analyses.
- *Remoteness*: distance (in km) separating each island from the mainland; for that matter, mainland populations have a remoteness of zero.
- *Mainland geometry*: angle of the shoreline (in degrees) at the closest distance from each island (see Landry and Lapointe 2001); small angles designate peninsulas whereas large angles indicate a flat-line shore; mainland populations are assigned a value of zero.
- *Isolation index*: combination of remoteness and mainland geometry (degrees*km); namely, an island situated close to a peninsula is considered to be less isolated than one located further away from a straight-line shore (Landry and Lapointe 2001).

Regression analyses

Contributions of the ecological and landscape variables to population differentiation matrices were assessed using a linear regression framework based on matrix comparison tests; the coefficients were tested using a permutation procedure (Mantel 1967). However, because all variables were strongly associated with population status, the effect of this descriptor was controlled with appropriate matrix treatment using a partial regression framework and population status as a covariate (Smouse et al. 1986). Ultimately, different combinations of distance matrices were evaluated in a multiple regression model.

Table 1. Details of the populations and ecological and landscape variables tested in this study.

Population	Sample size	Population status	Area (ha)	Population density (individuals/100 traps/night)	Remoteness (km)	Mainland geometry (degrees)	Isolation index (deg*km)
Amik	8	Island	13.0	35.6	0.20	60	12.0
Hell	8	Island	2.6	31.5	1.20	61	73.2
Mouk Mouk	8	Island	78.2	17.2	0.26	150	39.0
Ossements	8	Island	5.7	41.4	0.54	164	88.6
Solitaire	8	Island	6.7	9.4	0.34	90	30.6
Alembert	5	Mainland	78.2	3.1	0.00	–	–
Bayard	6	Mainland	78.2	3.8	0.00	–	–
Magusi	5	Mainland	78.2	1.6	0.00	–	–
Mouilleuse	8	Mainland	78.2	3.6	0.00	–	–

Only the matrices contributing significantly to the regression model were selected using a backward elimination procedure (Legendre et al. 1994). These analyses were computed independently from each of the three differentiation matrices as well as from a total evidence matrix averaging the morphometric and molecular interpopulation distance matrices to increase the amounts of information and maximise the explanatory power of the variables.

Split decomposition graphs

The structure of interpopulation differentiation was explored with a split decomposition graph (Huson 1998), in which the number of branches separating pairs of populations and the branch lengths are proportional to the differentiation among populations. This method allows visualisation of the multiple relationship patterns among populations by relaxing the constraints imposed by a tree representation. It also indicates alternative relationships supported by the data, combining information about historical factors and gene flow, the latter being represented by reticulated connections (parallel edges) in the graph. To evaluate the congruence among the three data sets, the topologies of the corresponding splitsgraphs were compared with a permutation test (Mantel 1967). A total evidence graph was then computed to represent the relationships among populations based on the combined data.

Results

RAPD data

Forty-eight polymorphic markers were scored from three RAPD primers and 64 individuals. No marker was unique to a particular population, and none could discriminate between insular and mainland populations. The AMOVA revealed that the sampled populations could be clearly discriminated despite the small spatial scale, with a large fraction of among-population variance (F_{st} = 21.8%, p = 0.0001). Interestingly, a significant fraction of intergroup variance was established between insular and mainland populations (6.3%, p = 0.0071). Pairwise interpopulation differences ranged from 5.56% to 29.12%, most of which exhibited significant differences at the 0.05 level (except for one pair: Bayard–Magusi).

Microsatellite data

The five loci analysed produced 72 alleles, with numbers of alleles per locus ranging from 11 to 18. The AMOVA analysis revealed a relatively large proportion of among-population variance (F_{st} = 11.5%, p = 0.0001). Contrary to RAPD findings, no significant differences were found among the mainland populations except for one (Bayard), which was significantly different from all the others. Similarly, no significant differences were detected between the island group and the mainland group (2.1%, p = 0.9805). On the other hand, all inter-island comparisons were significant at the 0.05 level, with pairwise interpopulation differences ranging from 1.1% to 40.2%.

Morphometric data

Euclidean distances among populations ranged from 0.051 to 0.617 and the analysis of variance computed from these morphometric distances indicated that populations were highly differentiated, with a substantial proportion of among-population variance (15.4%, p = 0.0001). The mainland populations were found to be morphometrically homogeneous, whereas the majority of insular populations were statistically different from one another at the 0.05 level. However, no significant difference was detected between mainland and insular populations (3.1%, p = 0.2742).

Regression analyses

Regression tests revealed that different ecological descriptors were related to the differentiation matrices. Whereas *Remoteness* (r = 0.409, p = 0.047) was significantly correlated with RAPD distances, the *Area* (r = 0.214, p = 0.028) was the only variable correlated with microsatellite differentiation. In the case of morphometric data, *Population abundance* (r = 0.432, p = 0.031), *Remoteness* (r = 0.573, p = 0.034) and the *Isolation index*

($r = 0.727$, $p = 0.003$) were all found to be significant in the simple regression models. When all distances were combined in a total evidence matrix, *Area* ($r = 0.265$, $p = 0.018$), *Remoteness* ($r = 0.816$, $p = 0.003$) and the *Isolation index* ($r = 0.547$, $p = 0.018$) were significantly correlated with the combined data. A multiple regression model including these variables revealed that 70% of the variance of the total evidence matrix can be explained by these ecological descriptors, which is more than three times the proportion of variance explained in the case of the separate data sets.

Splitsgraphs

Few features were congruent in the splitsgraphs obtained from the different data sets, as an important proportion of interpopulation distances was attributable to single population differentiation. The splitsgraphs computed from RAPD and microsatellite differentiation matrices exhibited somewhat different topologies, mainly regarding the position of the mainland populations (results not shown). Expectedly, no significant relationship was obtained when comparing the topological distances of these two graphs ($r = 0.191$, $p > 0.05$). However, restricting the analysis to inter-island comparisons revealed an exceptionally high level of congruence of the two splitsgraphs ($r = 0.740$, $p = 0.002$). Alternatively, the graph based on morphometric data was found to be remarkably congruent with the RAPD graph ($r = 0.733$, $p = 0.001$), but not with the microsatellite graph ($r = 0.112$, $p > 0.05$). Again, the incongruence was mainly caused by the mainland populations, and comparing only the islands revealed a much higher correlation ($r = 0.883$, $p = 0.049$). The splitsgraph of all populations based on the total evidence matrix combining the RAPD, microsatellite and morphometric distances is presented in Figure 2. This representation clarified and confirmed the relationships observed in the separate analyses. For one, the four mainland populations clearly formed a distinct group, separated from the five insular populations, and with shorter branches among them. Two pairs of populations (Hell–Amik and Ossements–Solitaire) also appeared to be strongly supported by the combined data. Interestingly, the same pairs were obtained in the separate analyses of the three data sets.

Discussion

Overall, the interpopulation values calculated with the three data sets consistently revealed a high proportion of among-population variance, indicative of strong population differentiation, considering the small geographical scale of the study area. The amounts of differentiation calculated from the microsatellite data were comparable to those observed from morphometric data, the main differences among data sets being attributable to mainland populations. In the case of RAPD data, our analyses underscored a clear division between islands and mainland populations, which is consistent with other results obtained for the same species using similar markers in a different insular landscape (Vucetich et al. 2001). Thus, it appears that such mainland–island disparities are likely to reflect the influence of habitat fragmentation on genetic processes. While island and mainland populations were sampled in different years, it is unlikely that variations in time could solely explain the directional changes implied by the difference observed. Indeed, the genetic structure in populations of *Peromyscus* has been shown to remain stable for six consecutive years (Baccus and Wolff 1989).

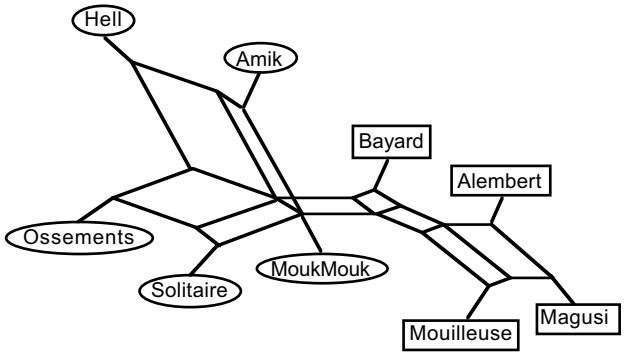

Figure 2. Split decomposition graph illustrating the relationships among nine populations of deer mice. The path-length distances are proportional to the amount of differentiation between pairs of populations from Lake Duparquet, Québec. Terminal branches are not drawn to scale to focus on the internal branches of the graph. Ellipses are used to represent insular populations, whereas rectangles designate mainland populations.

The absence of morphometric or microsatellite differentiation among mainland populations suggests extensive gene flow or large population size on the mainland. This also indicates that the interactions involving mainland populations are many times greater than those among insular populations; indeed, gene flow is expected to come mostly from the mainland. On the other hand, most insular populations were extremely divergent from one another, regardless of the data set analysed. Collectively, the substantial amounts of genetic differentiation documented here suggest that insular populations undergo reduced amounts of gene flow relative to the mainland populations. This observation is in agreement with other studies that also reported a reduction of genetic variability caused by increased genetic drift and reduced gene flow in insular populations (Vucetich et al. 2001).

Given the substantial gene flow among mainland populations, dispersal from the mainland to the islands was expected to be of primary importance in determining the amounts of island population differentiation. Three variables were related to this insular dispersal (*Remoteness*, *Area* and *Isolation*). *Isolation* is a composite index of two descriptors: *Remoteness* and *Mainland geometry.* When considered separately, these two variables contribute differentially to dispersal mechanisms. Whereas *Mainland geometry* measures the inclination of small mammals to

enter the water during dispersal (Landry and Lapointe 2001), *Remoteness* measures the length of the water barrier preventing a mouse from reaching an island. These two descriptors are not collinear and can be thus used in combination to quantify the similarities among populations. The *Isolation index* was found to be the strongest predictor of population morphometric divergence and was also highly significant with the total evidence data. *Remoteness*, on the other hand, was significant in the regression models based on RAPD, morphometric and total evidence distances. These results confirmed that population differentiation could not be explained without considering the habitat spatial structure and the biology of the species. *Peromyscus* mice are rather good dispersers on the mainland, and some mice are known to be able to swim across water barriers up to 200 m (Sheppe 1965). Despite their relatively poor ability to cross water barriers, one must bear in mind that deer mice are active all winter long and could disperse when the lake surface is frozen. Nevertheless, dispersal rarely occurs during the winter months when the activity is reduced (Fairbairn 1978). Therefore, limited over-water dispersal is expected to be an important factor preventing the gene flow from the mainland to the islands.

Relationships among populations arise both from historical factors and lateral transfer, even though pairwise F_{st} values cannot separate these factors. A split decomposition graph can be used, however, to visualise the relationships among populations, as it reconciles both conceptual interpretations of F_{st} values. The model underlying split decomposition is more flexible and desirable for population analysis than the commonly used dichotomous trees (Lapointe 2000). It allows for a larger fraction of the available information to be displayed while only retaining the strongest relationships among pairs of populations. Moreover, the residual fraction of the data is not represented in a splitsgraph, a desirable feature when working at small spatial scales and when random dispersal is very likely. Few compatible associations were recovered across the three data sets. Small sample sizes and the limited numbers of microsatellite loci analysed for the mainland populations can possibly explain these discrepancies. However, further examination of the splitsgraphs, ignoring the mainland populations, revealed that the three data sets were extremely congruent. Because of their very high variability, microsatellites require more extensive sampling than other genetic markers, and it is likely that only the strongest differences could be identified in the present case. Nevertheless, the splitsgraphs jointly showed that the relationships among populations were not reflected by the geographical location of the populations (see Figure 1).

Previous studies conducted at various spatial scales have reported a reduction of within-population genetic variability in island populations of rodents (oceanic islands: Berry and Jakobson 1975; Redfield 1976; Berry 1986; Ashley and Wills 1987; Lake islands: Loxterman et al. 1998; Vucetich et al. 2001). This depletion of genetic variability is caused by increased genetic drift and reduced gene flow related to isolation (Slatkin 1985), in turn inducing a strong genetic structure among populations. Our results corroborate these earlier findings using three different classes of genetic markers. Moreover, the RAPD results suggest the existence of a difference between mainland and island populations, which was also underscored by a very similar study involving RAPD markers in *P. maniculatus* populations (Vucetich et al. 2001). Still, this differentiation could not be observed either with microsatellites or morphometric data. Nevertheless, these findings stress the need for a closer scrutiny of insular population genetics, especially in the context of population insularisation caused by habitat fragmentation (Hanski 1998).

Finally, the use of a total-evidence approach proved to be fruitful to clarify the differentiation patterns among populations. The data combination clearly increased the amount of explained variance of the differentiation matrix in the multiple regression models. This result supports the hypothesis that adding molecular and morphological information maximises the content of evolutionary information. Moreover, the use of a distance approach based on fractions of interpopulation variance allowed us to compare and combine data from very different sources, providing a highly flexible analysis framework. The residual variance could be attributed to a series of random events altering the differentiation of insular populations, including random genetic drift.

Conclusion

We have shown that the amount of population genetic differentiation is associated with landscape configuration. We used a rigorous approach involving the statistical testing of all descriptors that allowed the evaluation of the relative effects of many variables. Our results clearly indicate that ‘ecological distances’ related to the dispersal abilities of a species are important to explain the population differentiation. The combination of different data sets in a total evidence matrix provided increased resolution to understand the factors influencing the genetic structure of insular populations. These results, along with the analytical approach presented in this paper, could be used to provide guidelines and a framework for the management of rodent populations or metapopulations inhabiting any fragmented landscape.

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References

Ashley, M. and Wills, C. 1987. Analysis of mitochondrial DNA polymorphisms among Channel island deer mice. Evolution, 41, 854–863.

Baccus, R. and Wolff, J.O. 1989. Genetic composition of fluctuating populations of *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy, 70, 592–602.

Berry, R.J. 1986. Genetics of insular populations of mammals, with special reference to differentiation and founder effects in British small mammals. Biological Journal of the Linnean Society, 28, 205–230.

Berry R.J. and Jakobson, M.E. 1975. Ecological genetics of an island population of the House mouse (*Mus musculus*). Journal of Zoology London, 175, 523–540.

Chirhart, S.E., Honeycutt, R.L. and Greenbaum, I.F. 2000. Microsatellite markers for the deer mouse *Peromyscus maniculatus*. Molecular Ecology, 9, 1669–1671.

Excoffier, L., Smouse, P.E. and Quattro, J.M. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics, 131, 479–491.

Fairbairn, D.J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*: proximal causes and effects on fitness. Oecologia, 32, 171–193.

Gilpin, M. and Hanski, I. (ed.) 1991. Metapopulation dynamics: empirical and theoretical investigations. San Diego, California, Academic Press.

Hanski, I. 1998. Metapopulation dynamics. Nature, 396, 41–49.

Huson, D.H. 1998. Splitstree: analyzing and visualizing evolutionary data. Bioinformatics, 14, 68–73.

Jaarola, M. and Tegelström, H. 1996. Mitochondrial DNA variation in the field vole (*Microtus agrestis*): regional population structure and colonization history. Evolution, 50, 2073–2085.

Landry, P.-A. and Lapointe, F.-J. 1999. The genetic heterogeneity of deer mouse populations (*Peromyscus maniculatus*) in an insular landscape. Researches on Population Ecology, 41, 263–268.

Landry, P.-A. and Lapointe, F.-J. 2001. Within-population craniometric variability of insular populations of deer mice, *Peromyscus maniculatus*, elucidated by landscape configuration. Oikos, 95, 136–146.

Lapointe, F.-J. 2000. How to account for reticulation events in phylogenetic analysis: a comparison of distance-based methods. Journal of Classification, 17, 175–184.

Legendre, P., Lapointe, F.-J. and Casgrain, P. 1994. Modeling brain evolution from behavior: a permutational regression approach. Evolution, 48, 1487–1499.

Loxterman, J.L., Moncrief, N.D., Dueser, R.D., Carlson, C.R. and Pagels, J.F. 1998. Dispersal abilities and genetic population structure of insular and mainland *Oryzomys palustris* and *Peromyscus leucopus*. Journal of Mammalogy, 79, 66–77.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research, 27, 209–220.

Mech, S.G. and Hallett, J.G. 2001. Evaluating the effectiveness of corridors: a genetic approach. Conservation Biology, 15, 467–474.

Patton, J.L., Da Silva, M.N.F. and Malcolm, J.R. 1996. Hierarchical genetic structure and gene flow in three sympatric species of Amazonian rodents. Molecular Ecology, 5, 229–238.

Redfield, J.A. 1976. Distribution, abundance, size and genetic variation of *Peromyscus maniculatus* on the Gulf islands of British Columbia. Canadian Journal of Zoology, 54, 463–474.

Sheppe, W. 1965. Dispersal by swimming in *Peromyscus leucopus*. Journal of Mammalogy, 46, 336–337.

Slatkin, M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics, 16, 393–430.

Smouse, P.E., Long, J.C. and Sokal, R.R. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Systematic Biology, 35, 627–632.

Vucetich, L.M., Vucetich, J.A., Joshi, C.P., Waite, T.A. and Peterson, R.O. 2001. Genetic (RAPD) diversity in *Peromyscus maniculatus* populations in a naturally fragmented landscape. Molecular Ecology, 10, 35–40.

Systematics and distribution of the house mice of Russia and neigbouring countries, with special regard to zones of high genetic polymorphism

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Abstract. The taxonomy of house mice (genus *Mus*) of Russia and neigbouring countries is reviewed. Two free-living species (*Mus spicilegus*, *M. macedonicus*—both monotypic) and one commensal species (*M. musculus*—polytypic) are found in the former Union of Soviet Socialist Republics. The distribution of these species is described and the origin of zones of high genetic polymorphism in Transcaucasia and Asia is discussed. The Transcaucasian populations are interpreted as early-differentiated forms of *M. musculus* that preserve the ancestral gene pool. In Adjaria, secondary contact occurs between these forms and differentiated *M. domesticus* from Turkey. Analysis of hybrid populations of house mice in Russia demonstrates the particular significance of hybridisation in the evolution of commensal taxa.

Introduction

Karl Linnaeus described *Mus musculus* in 1758 from Uppsala. Since that time, a total of 151 morphologically defined taxa of house mice have been described (Marshall 1998). In the territory of the former Union of Soviet Socialist Republics (USSR) authors described 25 different taxa of house mice (5 species and 20 subspecies).

The systematics of the genus *Mus* have advanced during the last three decades, largely owing to the application of biochemical and molecular genetic methods. Two large, divergent groups have been identified in the *Mus musculus* species group. The first group includes the commensal speces: *Mus musculus*, *M. domesticus*, and *M. castaneus* [after Sage et al. (1993) we consider these as distinct species]. The second group includes the indigenous free-living species *M. spretus*, *M. macedonicus* and *M. spicilegus*.

The aims of this work are: (i) to review the available data concerned with the taxonomy of house mice in Russia and neighbouring countries, with emphasis on the distribution of each species; and (ii) to discuss the origin of Transcaucasian and Asian populations possessing high levels of genetic variability.

Taxonomy and distribution of house mice in Russia and neighbouring countries

Intensive systematic studies, involving the investigation of allozyme variation among more than 600 individuals, and morphological analysis of both genetically marked individuals and other museum specimens (collections of zoological museums of Moscow, St Petersburg, Kiev and others), have revealed three species of the genus *Mus* in the former USSR. One is commensal (*Mus musculus*), while two are free-living (*M. spicilegus* and *M. macedonicus*) (Mezhzherin and Kotenkova 1989, 1992; Frisman et al. 1990). Some populations of house mice had high levels of genetic polymorphism, sometimes extending across large zones (e.g. Transcaucasia and Asia) (Mezhzherin et al. 1998; Yakimenko et al. 2000).

Mus spicilegus, the mound-building mouse, is a small mouse with a grey homogeneous or contrasting two-coloured coat. The tail of *M. spicilegus* is always shorter in length than its body and it is thinner than the tails of other species. *M. spicilegus* occurs in Ukraine, Moldova and some regions of Romania, Hungary, Serbia, Macedonia, Bulgaria, and Austria (Sokolov et al. 1998; Figure 1). An isolated population was described at Ulcinj, close to the border between Montenegro and Albania (Krystufek and Macholan 1998). Attention should be paid to the easternmost as well as the northern edges of the distribution of this species. Available data do not support the occurrence of *M. spicilegus* in northern Caucasus. Across its range, *M. spicilegus* occurs sympatrically with *M. musculus*.

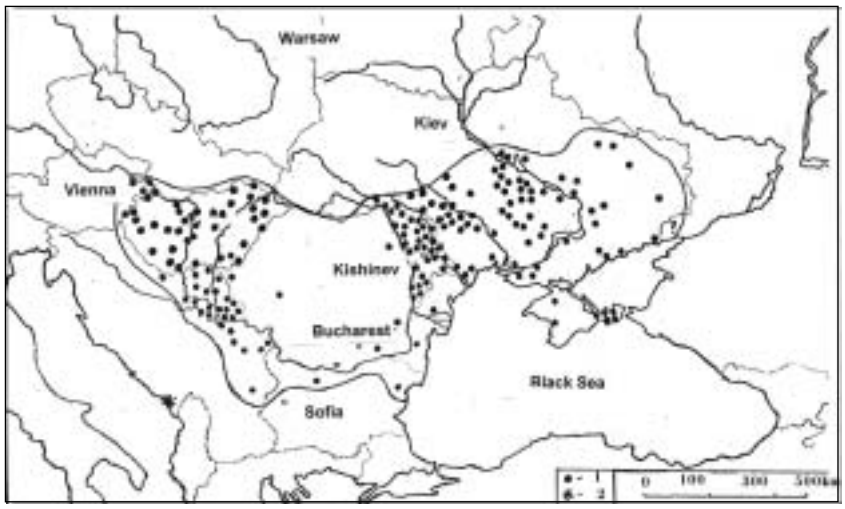

Figure 1. Distribution of *Mus spicilegus* (Krystufek and Macholan, 1998; Sokolov et al. 1998). Dots represent documented *M. spicilegus* captures or mounds; star represents an isolated population of *M. spicilegus*.

Mound-building mice inhabit a variety of agro-ecosystems and, as a rule, are locally abundant throughout their range. A distinctive characteristic of *M. spicilegus* is its grain-hoarding activity. In autumn, groups of 4–14 mice construct special mounds (kurgans) in which to store food and spend the winter. Seeds of 84 species of plants belonging to 29 families have been found within these mounds; 28 of these are major forage plants (Sokolov et al. 1998).

The mound-building mouse was supposedly first described by Nordmann (1840) as *Mus hortulanus* from a specimen collected at the Botanical Garden of Odessa, Ukraine. Nordmann did not mention mounds, which are typical of *M. spicilegus*, and indicated that the colour of *M. hortulanus* was brown. In the Zoological Museum of the Russian Academy of Science, St Petersburg, we located one skull of a mouse from Odessa (No. 4460) identified by Nordmann as *M. hortulanus*. The skull is badly damaged, but the breadth of the zygomatic process of the maxillary (>0.8 mm) suggests that the skull belongs to *M. musculus*. Gerasimov et al. (1990) used discriminant function analysis to show that this specimen can be referred to as *M. m. musculus*. Evidently, what Nordmann described was the wild form of *M. musculus*, which is widespread throughout the steppes of southern Ukraine and Moldova. In 1882, J.S. Petenyi (Chyzer 1982) described the mound-building mouse as *Mus spicilegus*. The type series is still preserved in good condition in the Hungarian Natural History Museum, Budapest; the lectotype is an adult male, mounted, No. 161.7 from Felsobesnyo, collected on 15 April 1852 (Csorba and Demeter 1991).

Mus macedonicus, the eastern Mediterranean mouse, is a comparatively large mouse with a contrasting two-coloured coat. Mice from Transcaucasia have light sandy backs and white bellies. Transcaucasia is situated between the Black and Caspian Seas to the south-east of the large Caucasus mountain ridge and includes the territories of Georgia, Armenia and Azerbaijan. The tail of *M. macedonicus* is always shorter than the length of its body. In Transcaucasia, this species occurs sympatrically with populations of commensal mice that are genetically intermediate between *M. musculus* and *M. domesticus* (Figure 2), and is found in both agro-ecosystems and natural habitats.

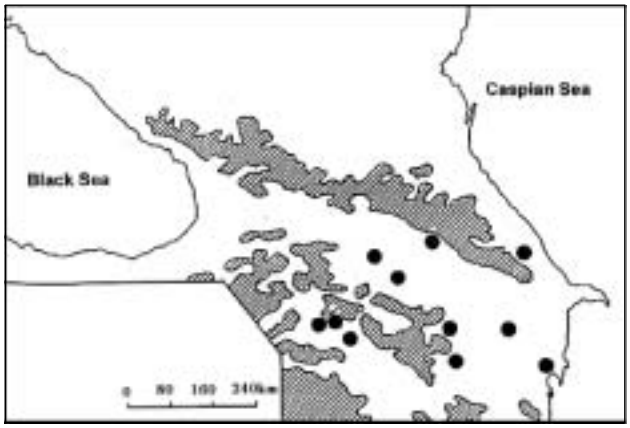

Figure 2. Distribution *of Mus macedonicus* in Transcaucasia. Dots represent documented *M. macedonicus* captures.

Mus musculus is a widespread and polytypic commensal found in eastern Europe and Asia. Considerable variation exists in coat colour and tail length. Coat colour varies from a homogeneous grey to contrasting two-coloured. The dorsal colour can be grey, reddish-grey, reddish, brownish, light-reddish, sandy and so on. Fur colour of the belly varies from grey to pure white. In some commensal populations, especially in large cities, the level of coat colour polymorphism is very high. The tail can be shorter or longer than the body. *M. musculus* occurs throughout practically all of the former USSR. The range of *M. musculus* can be divided into four ecological zones based on the level of commensalism (Prilutskaya 1984; Figure 3). In the northern zone, house mice live year-round in human dwellings. In the two intermediate

zones, these rodents leave the houses in spring and spend the summer in natural habitats (in the second zone, never far from houses). In autumn, they return to human dwellings. In the southern zone, house mice are free-living but sometimes inhabit dwellings.

The former USSR supports a minimum of three subspecies, which differ in external morphology and, according to Lavrenchenko (1994), are readily distinguished on multifactorial analysis of 18 skull measurements. These can be characterised thus:

- *Mus musculus musculus* Linnaeus, 1758 (syn. *funereus*, *borealis*, *hortulanus*). Colour of back is grey, reddish-grey, reddish, brownish or light-reddish; colour of belly is light grey to whitish. The tail is usually longer than body, however in some regions, e.g. Ukraine steppe, the tail is shorter than the body. This subspecies occurs in Pribaltica, Ukraine, Byelorussia, the European part of Russia, southern Siberia, northern Pribaikalie and in some parts of Far East Russia.
- *M. m. wagneri* Eversmann, 1848 (syn. *bicolor*, *decolor*, *sareptanicus*, *severtzovi*, *oxyrrhinus*, *pachycercus*). Short-tailed; colour of back is pale straw; colour of belly is pure white or whitish. This subspecies is found in the Pricaspian lowland, Kazakhstan (except some northern and eastern regions) and Middle Asia.
- *M. m. raddei* Kastschenko, 1910 (syn. *variabilis*). Short-tailed; colour of back is brownish or reddish; colour of belly is whitish. The 17th chromosome has increased in size through addition of pericentromeric heterochromatin blocks. It is not clear how this subspecies relates to the more easterly forms *M. m. manchu* and *M. m. mongolium*. *M. m. raddei* occurs in eastern Kazakhstan, Altai and eastern Zabaikalie.

Yakimenko et al. (2000) investigated pericentromeric heterochromatin in the karyotypes of about 1000 commensal and indigenous individuals from the former USSR and divided the short-tailed house mice into four subspecies: *wagneri*, *gansuensis*, '*molossinus*-like' and *musculus*. Although this division based on chromosome morphology requires confirmation, the data nevertheless support the viewpoint that *Mus musculus* is a highly polytypic species that requires additional investigation.

Zones of high levels of genetic polymorphism and the role of hybridisation in the evolution of commensal house mice

The significance of introgressive hybridisation in the evolution and diversification of mammals (including *Mus musculus* sensu lato) is an important problem of evolutionary theory. There is a narrow (16–50 km wide) zone of introgressive hybridisation between *M. musculus* and *M. domesticus* in Central Europe, and a well-studied zone of secondary contact (Sage et al. 1993) that traverses different habitats along its course through the Alpine and Balkan mountains and across the plains of Central Europe. Allozyme analysis has shown that Transcaucasian populations of commensal house mice possess an admixture of *musculus* and *domesticus* genes (Mezhzherin and Kotenkova 1989, 1998; Milishnikov et al. 1990). This region is either a zone of secondary contact between *musculus* and *domesticus*, with very wide introgression of *domesticus* genes into the genome of *musculus* (Mezhzherin and Kotenkova 1989; Frisman et al. 1990; Mezhzherin et al. 1998), or these are relict populations descended from non-differentiated forms with ancestral

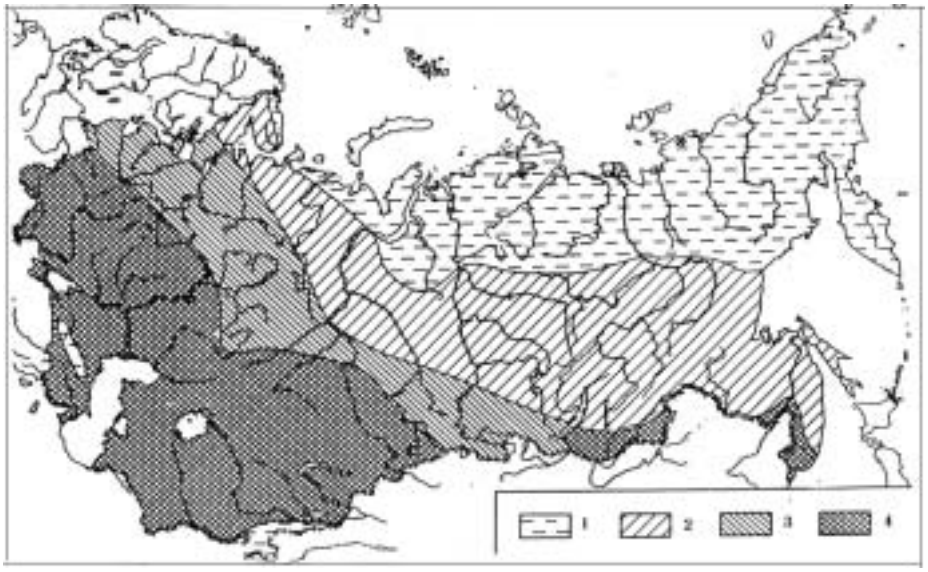

Figure 3. Distribution of *Mus musculus* in Russia and neighbouring countries. There are four ecological zones: 1 = house mice inhabit houses during all year; 2 = house mice leave houses during summer, but stay not far from houses; 3 = house mice leave houses during spring and summer; and 4 = house mice can be free-living all year round.

polymorphism (Milishnikov et al. 1990). The main feature of this zone is the unusually large extent of *domesticus* gene which occurs throughout the entire Transcaucasia region (about 300 km^2).

Within the last decade, much progress has been made in the study of populations of the *M. musculus* species group in India and Pakistan (Din et al. 1996). Populations of house mice from the northern part of the Indian subcontinent are more heterozygous than samples from any other region. They also contain the majority of the alleles that exist in the various differentiated species at the periphery of the wider geographic range of the group. According to a neighbour-joining analysis using Nei's genetic distances, and a factorial correspondence analysis of allelic composition, the Pakistani and Indian populations occupy a genetically central position with respect to the peripheral species. Din et al. (1996) interpreted these results as a retention of ancestral genetic polymorphism and identified northern India as the probable cradle of this commensal species. *M. musculus* and *M. domesticus* lineages probably started to differentiate a few hundred thousand years ago in isolated mountain areas, and they may have colonised the peripheral parts of their ranges only recently. In a related publication, Orth et al. (1996) reiterated the view that the Transcaucasian region is a zone of secondary contact between *M. musculus* and *M. domesticus*. However, a hybrid origin of Transcaucasian populations of house mice is doubtful in the light of the following facts:

1. There are no genetic gradients suggesting introgression of domesticus genes from west to east Transcaucasia.
2. Populations of Transcaucasian house mice contain some alleles that are not found in peripheral populations of *M. musculus* and M. *domesticus*. These genes are all found in northern Indian populations (Din et al. 1996), and some of them occur in populations from Turkmenistan and Tadjikistan (Milishnikov et al. 1994).
3. Populations of house mice in south-western Georgia (Adjaria, Kobuletty) possess a predominantly *domesticus* genotype but have a *musculus* morphotype according to multifactorial analysis of cranial morphology (Lavrenchenko 1994).
4. In a comparative analysis of exploratory behaviour in eight populations of different species and subspecies of house mice, the Adjarian population was similar to populations of *M. m. musculus* (Kotenkova et al., this volume).

These observations favour the view that Transcaucasian house mouse populations are relicts of an early-differentiated form of *M. musculus*, preserving much of the ancestral gene pool. The Adjarian population would then be a product of secondary contact between these forms and fully differentiated *M. domesticus* from Turkey.

Large zones of hybridisation are present also in Asia. According to Yakimenko et al. (2000) there is a minimum of three large hybrid zones in Primorie, Priamurie and Sakhalin. The taxa involved in the formation of these hybrid zones are *M. castaneus*, *M. domesticus* and various subspecies of *M. musculus*. The hybrid zone of Primorie is very young, dating to the last 30–40 years of the 19^{th} century at a time when the territory of Primorie was settled by people from Priamurie—the European part of Russia, Siberia and China.

Analysis of hybrid populations of house mice in Russia demonstrates the particular significance of hybridisation in the evolution of commensal taxa. This enhanced role in commensals is linked to their unique ability to expand their geographical ranges through human agency and even survive as commensals in areas that are beyond their physiological tolerance. Subjects that warrant further investigation include the mechanisms of precopulatory isolation in commensal taxa and the fitness of mice from hybrid populations.

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References

Chyzer, C. 1982. Reliquiae Petenyianae. Termeszetrajzi Fuzetek, 5, 113–128 (in Russian).

Csorba, G. and Demeter, A. 1991. Annotated list of type specimens of recent mammals in the Hungarian Natural History Museum. Miscellanea Zoologica Hungarica, 6, 77–85.

Din, W., Anand, R., Boursot, P., Darviche, D., Dod, B., Jouvin-Marche, E., Orth, A., Talwar, G.P., Cazenave, P.-A. and Bonhomme, F. 1996. Origin and radiation of the house mouse: clues from nuclear genes. Journal of Evolutionary Biology, 9, 391–415.

Frisman, L.V., Korobitsina, K.V. and Yakimenko, L.V. 1990. Genetic differentiation of U.S.S.R. house mice: electrophoretic study of proteins. Biological Journal of the Linnean Society, 41, 65–72.

Gerasimov, S., Nikolov, N. and Michailova V. 1990. Morphometric stepwise discriminant analysis of the five genetically determined European taxa of the genus *Mus*. Biological Journal of the Linnean Society, 41, 47–64.

Krystufek, B. and Macholan, M. 1998. Morphological differentiation in *Mus spicilegus* and the taxonomic status of mound-building mice from the Adriatic coast of Yugoslavia. Journal of Zoology, 245, 185–196.

Lavrenchenko, L.A. 1994. Craniometric analysis of house mice *Mus musculus* sensu lato (Rodentia: Muridae): multifactorial approach. Zoological Zhurnal, 73, 1889–1678 (in Russian).

Marshall, J.T. 1998. Identification and scientific names of Eurasian house mice and their European allies, subgenus *Mus* (Rodentia: Muridae). Virginia, Springfield, 80 p.

Mezhzherin, S.V. and Kotenkova, E.V. 1989. Genetic marking of subspecies of house mice of the USSR. Doklady AN SSSR, 34, 1272–1275 (in Russian).

Mezhzherin, S.V. and Kotenkova, E.V. 1992. Biochemical systematics of house mice from the Central palearctic region. Zeitschrift für Zoologische Systematik und Evolutionsforschung, 30, 180–188.

Mezhzherin, S.V., Kotenkova, E.V. and Mikhailenko, A.G. 1998. The house mice, *Mus musculus* s.l., hybrid zone of Transcaucasus. Zeitschrift für Saugetierkunde, 63, 154–168.

Milishnikov, A.N., Lavrenchenko, L. A., Rafiev, A.N. and Orlov, V.N. 1990. High level of introgression of *Mus domesticus* genes into populations of *M. musculus* s. str. in Transcaucasus. Doklady AN SSSR, 311, 764–768 (in Russian).

Milishnikov, A.N., Rafiev, A.N. and Orlov, V.N. 1994. Genetic variation in populations of the house mouse *Mus musculus* L. 1758 s. stricto from western, central, and southeastern parts of species range. Genetica, 30, 906–912 (in Russian with English summary).

Nordman, A. 1840. Observations sur la faune pontiqui. In: Voyage dans la Russie Meridionale et la Crimee, par la Hongrie, la Valachie et la Moldavie. Paris, Demidoff, 3, 43–47.

Orth, A., Lyapunova, E., Kandaurov, A., Boissinot, S., Boursot, P., Vorontsov, N. and Bonhomme, P. 1996. L'espece polytypigue *Mus musculus* in Transcaucasie. Comptes Rendus de l'Academie des Sciences, Paris, Sciences de la vie, 319, 435–441.

Priluztskaya, l.D. 1984. Range of the house mouse in the USSR. Avtoreferat disertatzii kandidata biologicheskih nauk. PhD thesis. Moscow, Vsesouiznyi Nauchno-Issledovatelskyi Insititut Jhrani Pripodi i Zapovednogo Dela (All-union Scientific Institute of Nature Conservation and Reserve Territories), 1–26.

Sage, R.D., Atchley, W.R. and Capanna, E. 1993. House mice as a model in systematic biology. Systematic Biology, 42, 523–561.

Sokolov, V.E., Kotenkova, E.V. and Mikhailenko, A.G. 1998. *Mus spicilegus*. Mammalian Species, 592, 1–6.

Yakimenko, L.V., Korobitsyna, K.L., Frisman, L.V., Moriwaki, K. and Yonekawa, H. 2000. Genetic studies on house mice from the hybrid area of the Primorskii Krai. Genetica, 36, 77–86 (in Russian with English summary).

Rodents and other small mammal diversity in Lore Lindu National Park, central Sulawesi, Indonesia

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Abstract. A terrestrial small mammal survey of Lore Lindu National Park was carried out from March 2000 to July 2001, sampling 11 major vegetation types on eight land systems and at altitudes ranging from 400 to >2100 m above sea level (asl). The survey used a standardised arrangement of trap type, trap spacing and two types of bait, roasted coconut and dried fish. Forty locations were surveyed, using 200 traps at each location for a total of four nights (800 trap-nights/survey site). In all, 309 individuals of 22 species of rodents were trapped using snap-traps and cage-traps. Seven species constituted 75% of captures as follows: *Rattus hoffmani* (17.1%), *R. marmosurus* (15.2%), *Bunomys chrysocomus* (12.3%), *B. prolatus* (11.6%), *B. penitus* (9.7%), *Paruromys dominator* (9.7%) and *Taeromys celebensis* (8.1%). Significantly more rats were captured in cage-traps (171 individuals) than snap-traps (138 individuals) and dried coconut was preferred (196 individuals) to fish as bait (113 individuals).

Rodent diversity as measured by Fisher's α peaked in the altitude range 1200–1500 m asl and generally declined at higher elevations. However, a secondary peak above 2100 m in diversity reflected the very low and even abundance of upper montane species. Simpson's and Shannon–Weiner indices were relatively constant across all altitude categories. Among the surveyed vegetation types, rodent diversity was highest in cloud forest, upper montane forest, montane forest, lower montane moist forest, swamp forest and marsh habitats, and lowest diversity in lower montane forest, lowland forest and monsoon forest. Fisher's α and Simpson's diversity indices attained highest values in the Kototinggi land system and for Shannon–Weiner index in the Telawi land system.

Introduction

Lore Lindu National Park is located just south of the equator in Central Sulawesi. It lies within the intertropical convergence zone and contains high mountains rising to above 2100 m above sea level (asl) and formed during late Miocene to Pliocene times. A geographical information system (GIS) (RePPProT 1989), developed in the context of a Department of Transmigration initiative and with assistance from the United Kingdom's Overseas Development Administration (ODA), identified 10 major land systems in the park (Lore Lindu National Park 2001). The island of Sulawesi has a unique mammalian fauna that is not particularly rich in species, but features a very high level of endemism. This has resulted from its long period of isolation from other landmasses and its location in the biological region of Wallacea, situated between the rich source areas of Sahul and Sunda. Before the current survey, several important mammal populations were known to occur in this park, including: dwarf mountain anoa, *Anoa quarlesi*; babyrousa, *Babyroussa babyrusa*; tarsiers, *Tarsius pumilus*, *T. dianae*, and *T. spectrum*; giant Sulawesi civet, *Macrogalidia musschenbroecki*; and Sulawesi cuscus, *Strigocuscus celebensis*. Three species of murid rodents, *Margaretamys elegans*, *Melasmothrix naso* and *M. rhinogradoides*, are recorded only from Lore Lindu National Park (Musser and Dagosto 1987).

Despite the publications of Musser (1969a,b,c, 1971, 1991), Musser and Dagosto (1987), van Strien (1986) and Suyanto et al. (1998) on the murid rodents of Sulawesi, little is known regarding the distribution of species in relation to vegetation, habitat, altitude and land systems. This study was designed to provide detailed information on the micro-distribution of rats in Lore Lindu National Park to be used in the design of management strategies. In particular, information was sought on: habitats or areas particularly rich in numbers of species or numbers of individuals of a particular species; on habitat preferences of individual species and their location along altitudinal gradients; and on seasonal shifts in habitat requirements of particular species. The survey represents the most extensive field study of rats yet carried out in Lore Lindu National Park, and indeed anywhere in Sulawesi.

Methods

Sampling areas

The survey was carried out from March 2000 to July 2001. All 11 major vegetation types were surveyed: cloud forest, upper montane forest, montane forest, lower montane forest, lower montane moist forest, marsh, mixed garden, monsoon forest, swamp forest, lowland forest, and degraded lowland forest. These vegetation types lay on eight land systems over an altitudinal range of 400 to >2100 m asl. Geological and geomorphic characteristics of the eight major land systems are given in Table 1.

Forty sites were selected to represent the varied geography, climate and habitat of the park (Figure 1). Each trap line was geo-located using a Garmin 12 global positioning system (GPS), and the elevation of each site recorded using an altimeter.

Seven altitudinal groupings were recognised as follows: 300–599 m, 600–899 m, 900–1199 m, 1200–1499 m, 1500–1799, 1800–2099 m and above 2100 m.

Table 1. Land system types in Lore Lindu National Park sampled in this study.

Land system type	Land and rock types
Telawi	Precipitously oriented mountain ridges on acid igneous rocks, granite, granodiorite, rhyolite
Bukit Balang	Irregular mountain ridges on intermediate basaltic, volcanics, andesite, basalt breccia
Kototinggi	Moderately sloping, non-volcanic alluvial fans
Bukit Baringin	Very steep, ordered hills on acid igneous rocks, rhyolite, granite
Bukit Pandan	Precipitously oriented metamorphic ridges, quartzite, schist, gabbro, granite, serpentinite
Pendreh	Asymmetric, broadly dissected ridges on sandstone and mudstone
Batang Anai	Long, very steep ridges over metamorphic rocks
Lindu	Lacustrine plains

Capture techniques

Mammals were trapped using a standardised trapping arrangement of trap type, trap spacing and bait. Two types of traps were used: small Kasmin cage-traps made of wire with dimensions of 28 × 12 × 12 cm; and standard snap-traps of sufficient size to capture the largest rat species.

Ten transect lines were set at each survey site. Each line was comprised of 20 traps—a cage-trap alternated with a snap-trap placed every 5 m. Traps were set for four nights, giving a standard trapping effort of 800 trap nights per site. Two types of bait were used: a lightly roasted coconut and dried fish; these were placed alternately in each trap type.

Small mammal trapping results from elsewhere in Indonesia suggest a substantial reduction in rate of captures of additional species of mammal over a weekly period (Kitchener et al. 1997; Maryanto and Kitchener 1999; I. Maryanto, unpublished). Accordingly, a trapping period of 4 days was considered adequate.

Data analysis

Diversity measures variably reflect both the number and relative abundance of species in a community. Three indices of species diversity were used: Simpson's, Shannon–Weiner and Fisher's α (Krebs 1989). The results of the survey were entered into a Microsoft Access database linked to an Arcview 3.2 GIS. Diversity indices were calculated using an Ecological Methodology computer package. Chi-square tests were used to analyse patterns of habitat association, and to compare the effectiveness of different trap and bait types.

Observations and results

Species captured

Twenty-two species of rodents was trapped in the park, including 21 Muridae and one Sciuridae (*Prosciurus murinus*; two individuals). The murid rodents were: *Bunomys chrysocomus* (Hoffmann 1887), *B. penitus* (Miller and Hollister 1921), *B. prolatus* Musser 1991, *Lenomys meyeri* (Jentink 1879), *Margaretamys elegans* Musser 1981, *Maxomys hellwaldii* (Jentink 1879), *M. musschenbroecki* (Jentink 1879), *M. wattsi* Musser 1991, *Melasmothrix naso* Miller and Hollister 1921, *M. rhinogradoides* Musser 1969, *Paruromys dominator* (Thomas 1921), *Rattus exulans* (Peale 1848), *R. hoffmani* (Matschie 1901), *R. marmosurus* Thomas 1921, *R. rattus* (Linnaeus 1758), *R. xanthurus* (Gray 1867), *Rattus* sp. (undescribed?), *Taeromys celebensis* (Gray 1867), *T. hamatus* (Miller and Hollister 1921), *T. punicans* (Miller and Hollister 1921) and *Taeromys* sp. (undescribed?). One individual of the widespread insectivore *Suncus murinus* was also captured.

Trapping success

In all, 309 small mammals were caught in 32,000 trap-nights during the survey. Overall trap success was one animal captured on average for each 104 trap-nights or <1%. Seven species of murid rodents accounted for 75% of captures, as follows: *Rattus hoffmani* (17.1%), *R. marmosurus* (15.2%), *Bunomys chrysocomus* 12.3%, *B. prolatus* (11.6%), *B. penitus* (9.7%), *Paruromys dominator* (9. 7%) and *Taeromys celebensis* (8.1%). Significantly more rats were captured in cage-traps (171 individuals) than snap-traps (138 individuals) ($p > 0.05$, $\chi^2 = 3.524$, df = 1).

Trap and bait effectiveness

Dried coconut was preferred (196 individuals) to fish baits (113 individuals) ($p < 0.001$, $\chi^2 = 22.29$, df = 1). The combination of trap and bait type significantly influence

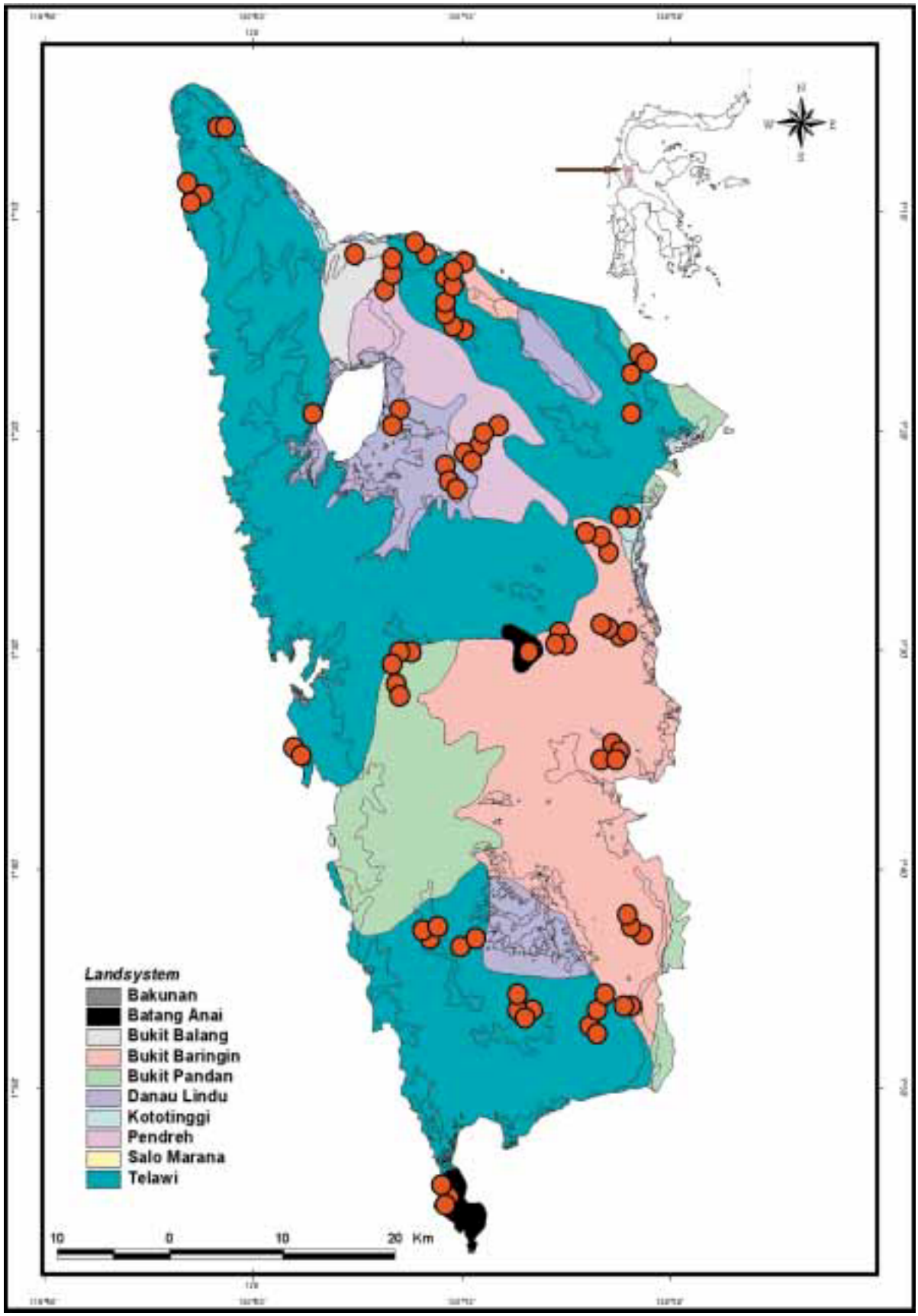

Figure 1. Map of the small mammal survey locations.

capture rates of *Maxomys hellwaldii* ($p < 0.05$, $\chi^2 = 7.149$, df = 1), *Paruromys dominator* ($p < 0.001$, $\chi^2 = 29.119$, df = 1), *Rattus marmosurus* ($p < 0.05$, $\chi^2 = 3.848$, df = 1), *Taeromys celebensis* ($p < 0.001$, $\chi^2 = 25.781$, df = 1) and *T. hamatus* ($p < 0.05$, $\chi^2 = 4$, df = 1). Among the vegetation/land system types, only captures in lower montane forest on the Pendreh land system were significantly influenced ($p < 0.05$, $\chi^2 = 5.04$, df = 1) by a combination of trap type and bait, with rodents preferring cage-traps baited with dried coconut. There were no significant associations of capture rate, trap type and bait type with either altitude or vegetation type. Only on Bukit Pandan and Bukit Balang land systems were capture rates not significantly associated ($p > 0.05$) with trap and bait type.

Species diversity

Trends in each of the three diversity indices are shown in Figure 2 (elevational zone), Figure 3 (vegetation type) and Figure 4 (land system type). All three indices show a peak in murid diversity in either the 990–1199 m or the 1200–1500 m zones, with a secondary peak above 2100 m. However, an examination of the raw data (Table 2) shows that the actual species number above 2100 m is not particularly high (8 species compared with 14 at 900–1199 m). Rather, the return to higher index values reflects the even representation of species, all of which were caught in very low numbers (total of 16 individuals). The Shannon–Weiner values remain more constant across all altitude groups but with a low point at 1500–1799 m.

Low capture rates make it difficult to recognise clear trends in diversity among vegetation types (Table 3). However, all three indices indicated that the highest murid diversity occurred in cloud forest, upper montane forest, montane forest, lower montane moist forest, swamp forest, and marsh habitats, and the lowest murid diversity occurred in lower montane forest, lowland forest and monsoon forest. Fisher's α and Simpson's diversity indices were highest in the Kototinggi land system, while the Shannon–Weiner index was highest in the Telawi land system (Table 4). Among habitat types, Fisher's α diversity was highest in Kototinggi lower montane forest and lowest in Bukit Balang lower montane forest (Table 5).

Discussion

In this study, cage-traps proved more effective than snap-traps and dried coconut better than dried fish at capturing small mammals. A similar result was obtained by Kitchener et al. (1997) in the Freeport area of West Papua province (formerly Irian Jaya) and on Gag Island, West Papua province, by Maryanto and Kitchener (1999).

Twenty-one species of murid rodents were recorded in Lore Lindu National Park. Of the 51 murids known in total from Sulawesi, the following species are recorded only in Central Sulawesi: *Melasmothrix rhinogradoides, M. naso, Lenomys meyeri, Bunomys penitus, B. prolatus, Margaretamys elegans, Taeromys hamatus, Maxomys wattsi*, and the unidentified *Rattus* sp. and *Taeromys* sp.

Table 2. Comparison of diversity indices based on elevation zones (m above sea level) (*N* = number of species captured, Sum = total captures).

	300–599	600–899	900–1199	1200–1499	1500–1799	1800–2099	>2100
N	1	12	14	11	7	10	8
Sum	1	83	111	33	18	46	16
Simpson		0.852	0.899	0.905	0.817	0.844	0.908
Shannon–Weiner		2.978	3.4	3.204	2.399	2.806	2.858
Fisher's α		3.851	4.238	5.773	4.205	3.934	6.365
Fisher's α se		0.622	0.756	2.691	3.762	1.132	26.845

Table 3. Comparison of diversity indices based on vegetation types (*N* = number of species captured, Sum = total captures).

	Cloud forest	Degraded lowland forest	Lower montane forest	Lower montane moist forest	Lowland forest	Marsh	Mixed garden	Monsoon forest	Montane forest	Swamp forest	Upper montane forest
N	13	1	13	4	7	6	1	4	11	8	8
Sum	54	3	131	6	20	11	5	8	35	17	17
Simpson's	0.861		0.863	0.8	0.863	0.891		0.786	0.892	0.882	0.772
Shannon–Weiner	3.058		3.76	1.792	2.633	2.482		1.811	3.128	2.749	2.396
Fisher's α	5.432		3.585	5.244	3.827	5.408		3.183	5.514	5.896	5.896
Fisher's α se	1.497		0.607	2.203	2.491	6.703		18.982	2.305	34.261	34.261

Table 4. Comparison of diversity indices based on land system types (*N* = number of species captured, Sum = total captures).

	Batang Anai	Bukit Balang	Bukit Baringin	Bukit Pandan	Lindu	Kototinggi	Pendreh	Telawi
N	4	5	12	6	9	10	7	18
Sum	4	19	49	15	28	19	27	148
Simpson's	1	0.708	0.894	0.829	0.878	0.924	0.86	0.893
Shannon–Weiner	2	1.845	3.244	2.333	2.901	3.156	2.652	3.523
Fisher's α	4	2.21	5.066	3.706	4.592	8.54	3.064	5.37
Fisher's α se	1.665	1.075	1.476	4.024	2.209	12.144	1.238	0.833

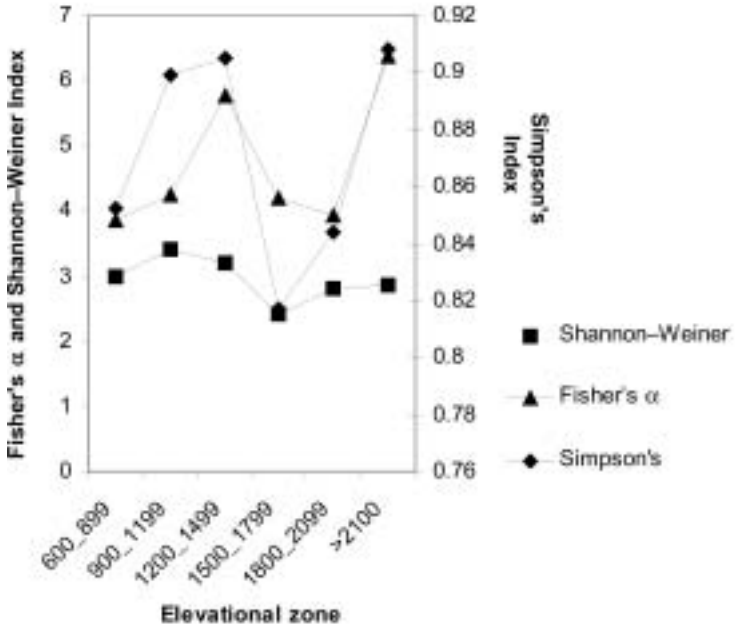

Figure 2. Comparison of trends in three diversity indices across elevational zones.

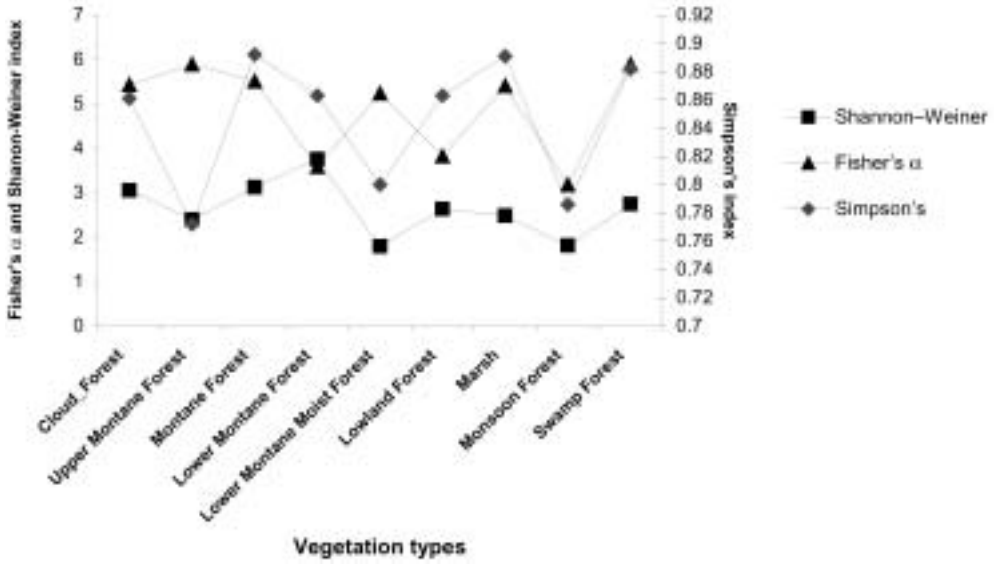

Figure 3. Comparison of trends in three diversity indices across vegetation types.

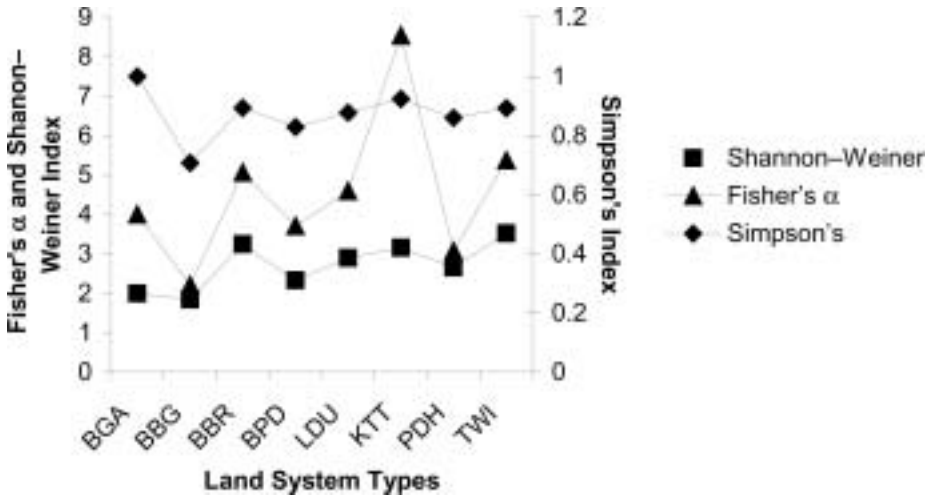

Figure 4. Comparison of trends in three diversity indices across land system types (BGA = Balang Anai, BBG = Bukit Balang, BBR = Bukit Baringin, BPD = Bukit Pandan, LDU = Lindu, KTT = Kototinggi, PDH = Pendreh, TWI = Telawi).

The three diversity indices used in this study (Fisher's α, Simpson's and Shannon–Weiner indices) did not always indicate the same trends in diversity. Indeed, correlation coefficients calculated between pairs of indices for each of the four data sets generally show weak association; R^2 values are typically below 0.3 and never exceed 0.6. The strongest association was found between the Simpson's and Shannon–Weiner indices for the elevational data set (R^2 = 0.591). Peet (1974) noted that the Shannon–Weiner index was particularly sensitive to changes in the abundance of rare species. Because rare species are probably poorly sampled by the trapping approach used in this study, the Shannon–Weiner index was perhaps the least appropriate method to apply to our data. Fisher's α method of estimating diversity is perhaps the most appropriate index for data of this kind, but in reality it may be concordance between the various methods used in this study that gives the most reliable indication of biological meaning (Krebs 1989). Whitmore (1984) observed that plant diversity in tropical rain forests generally falls with increasing elevation. Heaney et al. (1989) and Medway (1972) showed that diversity of pteropodid fruit bats also typically decreased at higher elevations. Little is known in Indonesia of changes in either species richness or species diversity of mammals with increasing altitude.

The highest estimate of rat diversity using Fisher's α was recorded at altitudes above 2100m (Fisher's α = 6.36). However, this value has a very high standard error (se = 26.845) and we have little faith in this result. Similarly, all of the highest values of Fisher's α based on vegetation, land system and habitat categories have high standard errors. Maryanto and Yani (2001) reported much lower standard errors in the estimates of species diversity of bats from Lore Lindu National Park and this undoubtedly relates to the fact that many more individuals of each species of bat were collected compared with rodents in this study.

The very low capture rates for rodents and other small terrestrial mammals pose considerable difficulties for documenting patterns of habitat association in small mammals of the park. Overall trap success was less than 1%, with one capture on average per 104 trap nights. This capture rate is comparable with the trapping figures reported by Kitchener and Yani (1998) from Gunung Ranaka, Flores, where, on average, 117 trap-nights were required to collect each small mammal (total 37,604 trap-nights). These Indonesian capture rates appear very low when compared to other tropical Asian studies. Medway (1972) reported that at 300–2400 m asl on Gunung Benom, West Malaysia, 50 trap-nights were required to capture each small mammal (total 5777 trap-nights). Heaney et al. (1989) reported that at 300–900 m asl on Leyte Island, Philippines, 30 trap-nights were required (total 3485 trap-nights), and at 0–1500 m asl, on Guisayawan, Negros Island, Philippines, 11 trap-nights were required (total 3231 trap-nights).

In summary, this study showed that species diversity of murid rodents in Lore Lindu National Park varies with altitude, vegetation, land system and habitat. It is important that future management practice in the park protects the full variety of animal habitats. In particular, the environs around Lake Lindu contain marsh habitat that is here identified as having high murid species diversity. This area also produced what may be a new murid species; hence, it is important that the marsh habitat is represented within the core zone of the park. Human encroachment onto this marshy country and its progressive conversion to paddy is of major concern. Finally, the monsoon forest vegetation/habitat type is also identified in this study as being distinctive; this habitat should also be included in the core zone of the park.

Table 5. Comparison of diversity indices based on habitat types (*N* = number of species captured, Sum = total captures).

	Cloud forest–Bukit Pandan	Cloud forest–Telawi	Degraded lowland forest–Telawi	Lower montane moist forest–Bukit Baringin	Lower montane forest–Bukit Balang	Lower montane forest–Bukit Baringin	Lower montane forest–Kototinggi	Lower montane forest–Pendreh	Lower montane forest–Telawi	Lower montane forest–Batang Anai	Lowland forest–Kototinggi	Lowland forest–Telawi	Lowland forest–Batang Anai
N	2	13	2	4	5	10	7	7	12	2	5	5	
Sum	3	51	4	6	19	21	9	27	58	2	10	10	
Simpson's	0.667	0.865	0.5	0.8	0.708	0.905	0.944	0.86	0.844	1	0.844	0.867	
Shannon–Weiner	0.918	3.092	0.811	1.792	1.845	3.065	2.725	2.652	2.916	1	2.171	2.246	
Fisher's α		5.629		5.244	2.21	7.478	9	3.064	4.594		3.978	3.978	
Fisher's α se		1.641		2.203	1.075	70.057	2.497	1.239	1.162		21.233	21.233	

Table 5. Continued

	Marsh–Lindu	Mixed garden–Lindu	Mixed garden–Telawi	Monsoon forest–Telawi	Montane forest–Batang Anai	Montane forest–Bukit Baringin	Montane forest–Bukit Pandan	Montane forest–Telawi	Swamp forest–Lindu	Upper montane forest–Pendreh	Upper montane forest–Telawi	Upper montane forest–Bukit Baringin	Upper montane forest–Bukit Pandan
N	6		2	4	2	9	4	3	8		5	1	2
Sum	11		6	8	2	19	10	4	17		10	3	2
Simpson's	0.891		0.333	0.786	1	0.912	0.733	0.8333	0.882		0.905		1
Shannon–Weiner	2.482		0.666	1.811	1	3.011	1.761	1.5	2.749		2.236		1
Fisher's α	5.401			3.183		6.686	2.47	4	5.896		3.978		
Fisher's α se	6.703			18.982		48.475	3.286	1.665	34.261		21.223		

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References

Heaney, L.R., Heideman, P.D., Rickart, E.A., Utzurrum, R.B. and Klompen, J.S.H. 1989. Elevation zonation of mammals in the Central Philippines. Journal of Tropical Zoology, 5, 259–280.

Kitchener, D.J., Boeadi, and Sinaga, M.H. 1997. The mammals of the Freeport Contract of Work Region, Irian Jaya: results from the survey of 14 February–6 March 1997. Unpublished report to Freeport, Jakarta, 54 + 12 p.

Kitchener, D.J. and Yani, M. 1998. Small non-volant terrestrial mammal diversity along an altitudinal gradient at Gunung Ranaka, Flores Island, Indonesia. Tropical Biodiversity, 5, 155–159.

Krebs, J.C. 1989. Ecology methodology. New York, Harper and Row, 654 p.

Lore Lindu National Park 2001. Draft management plan 2002–2027. Vol. I. Data and analysis. Taman Nasional Lore Lindu, Dirjen Perlindungan Hutan dan Konservasi Alam (PHKA) and The Nature Conservancy, 205 p.

Maryanto, I. and Kitchener, D.J. 1999. Mammals of Gag Island. Treubia, 31, 177–217.

Maryanto, I. and Yani, M. 2001. Small mammal survey from Lore Lindu National Park Central Sulawesi, Indonesia. Unpublished report to The Nature Conservancy, 93 p.

Medway, Lord 1972. The Gunung Benom Expedition 1967. 6. The distribution and altitudinal zonation of birds and mammals on Gunung Benom. Bulletin of the British Museum (Natural History), 23, 103–154.

Musser, G.G. 1969a. Notes on the taxonomic status of *Rattus aspinatus* Tate and Archbold and *Mus callitrichus* Jentink. Results of the Archbold Expeditions No. 89. American Museum Novitates, 2365, 1–9.

Musser, G.G. 1969b. A new genus and species of murid rodents from Celebes, with a discussion of its relationships. Results of the Archbold Expeditions No. 91. American Museum Novitates, 2384, 1–41.

Musser, G.G. 1969c. Taxonomic notes on *Rattus dolmanni* and *Rattus hellwaldii* (Rodentia, Muridae) of Celebes. Results of the Archbold Expeditions No. 92. American Museum Novitates, 2386, 1–24.

Musser, G.G. 1971. Taxonomic association of *Mus feberi* Jentink and *Rattus xanturus* (Gray), as species know only from Celebes. Zool. Meded Leiden, 45(9), 107–118.

Musser, G.G. 1991. Sulawesian rodents: description of new species of *Bunomys* and *Maxomys* (Muridae, Murinae). American Museum Novitates, 3001, 1–41.

Musser, G.G. and Dagosto, M. 1987. The identity of *Tarsius pumilus*, a pigmy species endemic to montane mossy forest of Central Sulawesi. American Museum Novitates, 2867, 1–53.

Peet, R.K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics, 5, 285–307.

RePPProT 1989. Review of phase I results. Java and Bali, Regional Physical Planning Programme for Transmigration, Department Transmigrasi Jakarta, 507 p.

Suyanto A., Yoneda, K., Maryanto, I., Maharadatunkamsi and Sugaarjito, J. 1998. Checklist of the mammals of Indonesia: scientific name and distribution areas table in Indonesia including CITES, IUCN and Indonesian category for conservation. Lembaga Ilmu Pengetahuan Indonesia–Japan International Cooperation Agency (LIPI–JICA), 34 p.

Van Strien, N.J. 1986. Abbreviated checklist of the mammals of the Australasian archipelago. Bogor, Indonesia, School of Environmental Conservation Management, 91 p.

Whitmore, T.C. 1984. Tropical rain forest of the Far East, 2nd edition. Oxford, Clarendon Press, 282 p.

Modelling rodent pest distributions in Mexico

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Abstract. Ecological niche models based on museum specimen data were generated to provide predictions of geographical distributions of native rodents known to be agricultural pests in Mexico. By overlapping rodent pest distributions, we found significant correlation between predicted presence of rodent species and crop damage in four main crops widely distributed nationwide. This study provides a first step for generating risk maps for crop damage due to rodent pests in agricultural regions. Museum collections may thus provide essential information for expanding these analyses to other pests.

Introduction

Mexico is an extremely varied country with a rich crop diversity. Historically, Mexico has mainly focused on agriculture, which presently occupies almost half of its area, producing corn, beans, sorghum, and sugarcane, among other crops. Mexico has a diverse rodent fauna, which has been reported as pests in crops (de Ita 1992). Most of these rodent species share the life-history traits of frequent litters, short gestation periods, post-partum oestrous, and aseasonal reproduction (Nowack 1991). In a previous study, we used novel techniques for modelling ecological niches of 17 rodent pests to determine potential species distributions, and showed that crop damage was related significantly to the predicted presence of rodent pests in the Mexican state of Veracruz (Sánchez-Cordero and Martínez-Meyer 2000). Here, we expand these analyses at a national level in four main and widely distributed crops. This approach can be used as a first approximation for generating risk maps in crop damage due to rodent pests, as well as other pests, in agricultural regions in the country.

Material and methods

Distribution data for each species were obtained from the mammal collections of the University of Kansas Natural History Museum (KU), The Field Museum of Natural History (FMNH) and the Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México (CNMA). Species names and taxonomic arrangements followed accepted authorities. Locality data were geo-referenced to the nearest 10^{-3} degree by direct consultation of maps, and reduced to unique latitude–longitude combinations. The four thematic geographical coverages used (annual mean temperature, annual mean precipitation, elevation, potential vegetation) consisted of raster grids (5×5 km pixels), obtained from Conabio (2002).

Rodent pest distributions

Ecological niches and potential geographical distributions were modelled using the genetic algorithm for rule-set prediction (GARP) (Stockwell and Peters 1999; see BIODI 2002). Specifically, GARP relates ecological characteristics of known occurrence points to those of points randomly sampled from the rest of the study region, seeking to develop a series of decision rules that best summarise those factors that are associated with the species' presence (Stockwell and Peters 1999). GARP includes several distinct algorithms for niche modelling in an artificial-intelligence-based approach. Occurrence points are divided evenly into training and test data sets. It works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection, choosing a method from a set of possibilities (e.g. logistic regression, bioclimatic rules) applied to the training data. Then a rule is developed or evolved. Predictive accuracy is then evaluated based on 1250 points resampled from the test data and 1250 points sampled randomly from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model—the algorithm runs 1000 iterations or until convergence. These component 'rules' are then incorporated into a broader

rule-set, defining portions of the landscape as within or without the ecological niche. GARP models thus provide a heterogeneous rule-set that delimits a polygon or set of polygons within which the species is expected to be able to maintain populations, and outside of which it should not. This model of the ecological requirements of a species is the key to the inferential portion of the method (Stockwell and Peters 1999). GARP has demonstrated ability to predict small mammal species' distributions in the Neotropics (Peterson et al. 1999; Sánchez-Cordero and Martínez-Meyer 2000).

Rodent pest species previously identified to be related to crop damage (see Sánchez-Cordero and Martínez-Meyer 2000), and included in the present analyses, were (G = granivore, H = herbivore, O = omnivore): one squirrel (*Sciurus aureogaster*, O), thirteen rats and mice (*Microtus mexicanus*, H; *Oligoryzomys fulvescens*, O; *Oryzomys couesi*, O; *O. melanotis*, O; *Peromyscus aztecus*, G; *P. leucopus*, G; *P. levipes*, G; *P. maniculatus*, G; *Reithrodontomys fulvescens*, G; *R. megalotis*, G; *R. mexicanus*, G; *R. sumichrasti*, G; *Sigmodon hispidus*, H), and three pocket gophers (*Orthogeomys hispidus*, H; *Pappogeomys merriami*, H; and *Thomomys umbrinus*, H).

Crop loss and statistical analyses

We used the 1999 agricultural census data that provide reliable information on planted and harvested areas for seasonal crops of corn, sugarcane, beans, and sorghum for each of the 193 crop districts nationwide (SAGARPA 2002). We included only non-irrigated agricultural areas. Crop loss was calculated as the difference between planted and harvested area, assuming that non-harvested areas were partially related to damage by rodent pests (Table 1, Figure 1). These estimates are biased since biotic (other pests), abiotic (climatic conditions), and economic (lack of funding for harvesting) factors are also related to crop losses. We overlapped the distribution hypotheses of rodent pests with the crop districts using a geographical information system (GIS) (Arc View 3.2) (Figure 1). Forward stepwise multiple regression analyses were performed using Statistica 4.3.

Table 1. Total area cultivated and area lost (cultivated – harvested), as well as statistical significance (*P*), of stepwise multiple regression models relating areas with crop damage reported for the 1999 agricultural census data nationwide (n_1), and rodent species' presence (n_2), and numbers of granivore (G), herbivore (H), and omnivore (O) species included in the statistical analyses. In parentheses are parts of plant crops damaged by rodents.

Crop	Total area (ha)	Area lost (ha)	R^2	$F_{n2,\ n1}$ (*P*)	G	H	O
Corn (seeds, stems)	157,269,099	16,278	0.08	$F_{14,\ 184}$ (0.05)	4	3	2
Sugarcane (stems)	2,708,207	165,445	0.12	$F_{3,\ 89}$ (0.01)	4	3	2
Beans (seeds)	4,775,180	415,323	0.38	$F_{5,\ 132}$ (0.005)	6	1	3
Sorghum (seeds, stems)	155,706	16,278	0.05	$F_{3,\ 23}$ (0.094)	6	1	3

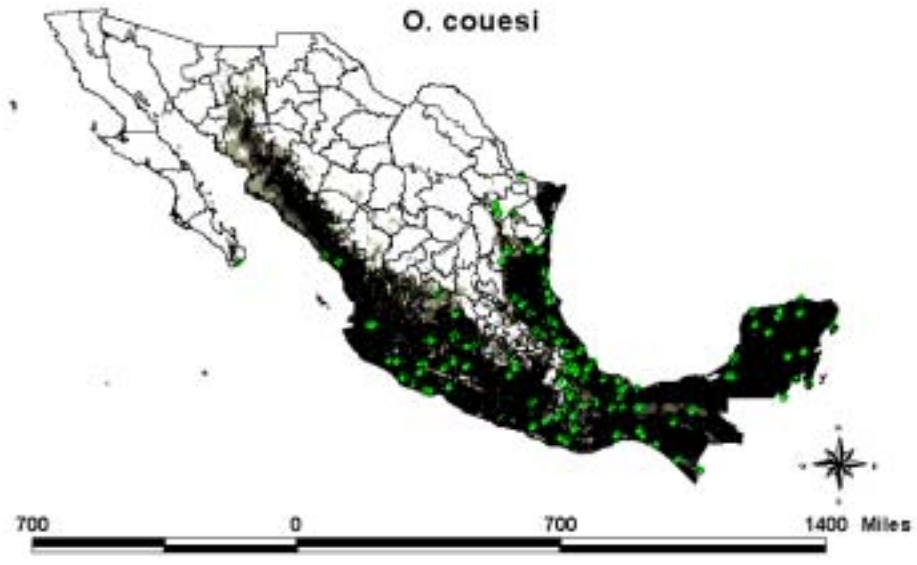

Figure 1. Map depicting the predicted distribution (in black) of the rice rat, *Oryzomys couesi*, a major rodent pest in Mexico. Green dots are known collecting localities of rice rats, and polygons represent all crop districts, where the 1999 agricultural census data for corn, sugarcane, beans, and sorghum are available nationwide.

Results and discussion

We generated ecological niche models for each of the 17 rodent species, using these models as the potential species distributions in the country (Figure 1). These rodent species identified as agricultural pests include a high taxonomic diversity, belonging to the families Muridae (rats and mice), Sciuridae (squirrels) and Geomyidae (pocket gophers). Such high rodent diversity results in a high diversity of food habits, such as granivores, herbivores and omnivores, with the potential for causing damage to a wide range of crops (de Ita 1992). In a previous study, Sánchez-Cordero and Martínez-Meyer (2000) developed a similar modelling approach for these rodent pests in the state of Veracruz, along the Gulf of Mexico in Mexico, and provided preliminary evidence of a causal relationship between predicted presence of rodent pests and crop damage. Stepwise multiple regression models predicted crop damage in each crop in the 193 crop districts nationwide (dependent variable) related to the proportional predicted coverage of that crop district by each of the 17 rodent species (independent variables). Models for all crops were statistically significant, explaining 5–38% of variation in crop damage, and rodent food habits matched food items supplied by these crops (Table 1). Interestingly, these statistical relationships were previously documented for these crops and rodent pests when analyses were conducted in the Mexican state of Veracruz (Sánchez-Cordero and Martinez-Meyer 2000). We interpret these findings to strengthen our modelling approach for identifying risk areas in other agricultural regions.

Considering the scale (the whole country) of cultivated areas used in the present study, the predicted distribution of rodent pests suggests significant economic impacts of rodent pests on large agricultural regions in Mexico; crop loss estimates were 0.1% for corn, 6.0% for sugarcane, 8.6% for beans, and 10.0% for sorghum (Table 1). These results are supported by recent studies documenting crop damage caused by the cotton rat, *Sigmodon hispidus*, and the rice rat, *Oryzomys couesi*, on sugarcane and sorghum fields in several states, such as Veracruz, Morelos, Michoacán, Tamaulipas, Sinaloa, and Sonora (de Ita 1992; Sánchez-Cordero and Martínez-Meyer 2000; SAGARPA 2002).

Conclusions

Integrated pest control programs require robust distributional hypotheses of pest species across agricultural landscapes (Prakash 1988; Buckle and Smith 1994; Singleton and Petch 1994). Our approach provides a solid baseline to launch such programs at a national level, and can serve as a useful tool with applicability to other pest taxa and agricultural regions worldwide.

Acknowledgments

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References

BIODI 2002. Biodiversity species workshop. In: Advanced computational approaches to environmental and biodiversity information. La Jolla, San Diego Supercomputer Center. On the Internet: <http://biodi.sdsc.edu/>.

Buckle, A.P. and Smith, R.H. (ed.) 1994. Rodent pests and their control. Wallingford, UK, CAB International, 405 p.

Conabio 2002. Comisión Nacional para el Uso y Conocimiento de la Biodiversidad. On the Internet: <http://www.conabio.gob.mx>.

de Ita, R. 1992. Distribución y Descripción de Roedores de Importancia Agrícola en México. Mexico, D.F., Maxico, Secretaría de Recursos Hidráulicos y Ganadería.

Nowak, R.M. 1991. Walker's mammals of the world, volume II. Baltimore, Maryland, Johns Hopkins University Press.

Peterson, A.T., Soberón, J. and Sánchez-Cordero, V. 1999. Conservatism of ecological niches over evolutionary time. Science, 285, 1265–1267.

Prakash, I. (ed.) 1988. Rodent pest management. Baton Rouge, Florida, CRC Press, 480 p.

SAGARPA (Secretaría de Agucultura, Ganadería, Desarrollo Rural, Pesca y Alimentación) 2002. 1999 agricultural census data. On the Internet: <http://www.sagarpa.gob.mx>.

Sánchez-Cordero, V. and Martínez-Meyer, E. 2000. Museum specimen data predict crop damage by tropical rodents. Proceedings of the National Academy of Sciences USA, 97, 7074–7077.

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.

Stockwell, D. and Peters, D. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographic Information Science, 13, 143–158.

The distribution of *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae) in South Africa

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Abstract. Although *Mastomys natalensis* and *M. coucha* are widely distributed in South Africa, the respective distributions of these medically and agriculturally important cryptic species of rodents are still uncertain. Karyotyped and/or electrophoretically identified specimens were used to clarify the geographical distributions and predict the most likely areas of occurrence of the two sibling species; and the derived distributions were compared with reported incidence of plague in South Africa. Both verified and predicted distributions show a geographical separation along the eastern escarpment of South Africa that appears to be influenced by altitude and rainfall. *M. natalensis* occurs in the low altitude/high rainfall area of the eastern coastal region, extending to north-eastern South Africa, while *M. coucha* occurs in the high altitude/moderate rainfall area of central and north-eastern South Africa. The two species were found to be either sympatric or to occur in close proximity at four localities. Statistical analyses showed significant differences between eco-geographical characteristics of localities associated with each of the two sibling species. The reported cases of plague in South Africa to some extent coincide with the distributional range of *M. coucha* rather than that of *M. natalensis*.

Introduction

Mastomys natalensis (*sensu lato*) was considered a single species until it was found to include two electrophoretically distinct cytotypes (2*n* = 32, 'slow' haemoglobin electromorph; and 2*n* = 36, 'fast' haemoglobin electromorph) (Gordon and Watson 1986). This, together with the absence of hybrids in areas of sympatry, led to the recognition of two cryptic species referred to as the nominate species, *M. natalensis* (2*n* = 32) and *M. coucha* (2*n* = 36).

Although the combined geographical range of the two sibling species in South Africa is extensive, their respective geographical distributions remain uncertain. There is a critical need for more reliable delimitations of geographical ranges of these two species as they cause extensive damage to agricultural products and have been implicated in epidemiological problems.

The present investigation represents the first attempt to delimit the geographical distributions of *M. natalensis* and *M. coucha* in South Africa, based on specimens positively identified by karyotype and/or electrophoretic data. The distributions so derived are in turn used to predict the most likely areas of occurrence of the two cryptic species, and for assessment with reference to previously reported incidence of plague in South Africa.

Materials and methods

Locality data were gathered from karyotyped and/or electrophorectically identified specimens in the collections of the Transvaal (TM) and Durban (DM) Museums, South Africa, as well as from the literature (Hallett 1977; Smit et al. 2001). The prediction of the most likely areas of occurrence of the two sibling species was based on spatial analysis (Eastman 2001) using the following eco-geographical variables (EGVs): altitude; mean annual precipitation; mean annual temperature; mean daily minimum temperature for July; coefficient of variation of precipitation; mean primary production; and potential evaporation.

Analysis of variance (ANOVA), unweighted pair-group arithmetic average (UPGMA) cluster analysis, principal components analysis (PCA), and canonical variable (discriminant) analysis (CVA), in combination with multivariate analysis of variance (MANOVA), were used to test for statistical differences in EGVs between localities associated with each of the sibling species. EGV loadings derived from the PCA were used to weight each EGV's relative contribution for the spatial analysis.

The geographical ranges derived from both verified locality data and predicted distributions were used to assess historical incidence of plague in South Africa as reported by Davis (1964).

Results and discussion

Positively identified records were located from 77 localities in South Africa, of which 31 were for *M. natalensis* and 46 were for *M. coucha*. The geographical distributions of *M. natalensis* and *M. coucha* show a distinct pattern of segregation along the eastern escarpment of South Africa. Their distributions thus appear to be largely influenced by altitude and rainfall. *M. natalensis* occurs along the low altitude/high rainfall eastern coastal region, extending up to the north-eastern corner of South Africa. In contrast, *M. coucha* occurs in the high altitude/moderate rainfall central and north-eastern parts of South Africa.

The two species were recorded either in sympatry or else in close proximity to each other at four localities, namely Pretoria and Satara (Kruger National Park) in the north-eastern part of South Africa, and Grahamstown and Addo Elephant Park in the Eastern Cape province. Interestingly, predictions of the most likely areas of occurrence for the two species also suggest a zone of overlap along the eastern escarpment. However, additional field survey is needed to determine the specific zone of parapatry between the two species in South Africa.

The ANOVA showed highly statistically significant differences ($P < 0.001$) for all EGVs associated with collecting localities of *M. natalensis* and *M. coucha* in South Africa. UPGMA cluster analysis and PCA of the EGV data showed two discrete clusters of localities which coincided in large part with the collecting localities associated with each of the two species in South Africa. Where overlap occurs, the localities in question fall in areas of potential sympatry or parapatry between the two species. A CVA and a MANOVA indicated a highly statistically significant difference between group centroids ($F_{7,69} = 20.21$, $P < 0.001$) of the species-linked collecting localities.

PCA loadings from the first two axes suggest that all of the EGVs are important in determining the species' distributions. The inverse relationship between the coefficient of variation of precipitation and the mean annual precipitation is of particular interest as it suggests that *M. natalensis* prefers relatively wet areas with a stable rainfall pattern, whereas *M. coucha* prefers relatively dry areas with a more erratic rainfall pattern. The particular importance of mean annual temperature on PCA axis 2 may further imply that *M. coucha* is more able to withstand a drier environment than *M. natalensis*—this can be tested through controlled laboratory investigations.

Geographical distributions based on both the verified locality data and the predicted distributions show that previously reported cases of plague in South Africa coincide to some extent with the distributional range of *M. coucha* rather than *M. natalensis*. Exceptional areas include the north-eastern parts of South Africa that have records of *M. coucha* but no historical records of plague, and the western parts that have no records of *M. coucha* but have reported incidence of plague. Since the discovery of the two sibling species, it has been demonstrated that *M. coucha* is susceptible, while *M. natalensis* is resistant, to *Yersinia pestis* infection. However, the imperfect match of plague incidence with the geographical range of *M. coucha* may suggest that either a complex of taxa is involved in the epidemiology of the disease, and/or that population eruptions of *M. coucha* in these areas do not attain infectious levels.

Conclusion

Geographical distributions of two medically and agriculturally important rodent species, *Mastomys natalensis* and *M. coucha* in South Africa, derived from karyotyped and/or electrophoretically identified specimens, show a geographical separation along the eastern escarpment. This pattern of distribution seems to be influenced by altitude and rainfall whereby *M. natalensis* prefers low altitude/high rainfall regions, while *M. coucha* has a preference for higher altitude/relatively drier parts of South Africa. The two species appear to have a zone of parapatry along the eastern escarpment but are locally sympatric. The geographical distribution of previously reported human cases of plague in South Africa seems to coincide more with the distributional range of *M. coucha*, a species that is susceptible to plague infection, than with the more plague-resistant *M. natalensis*. However, there are significant exceptions that caution against any simplistic interpretation of the epidemiology of plague in South Africa.

References

Davis, D.H.S. 1964. Ecology of wild rodent plague. In: Davis, D.H.S., ed., Ecological studies in southern Africa. The Hague, W. Junk Publishers, p. 301.

Eastman, J.R. 2001. Guide to GIS and image processing, IDRISI32 Release 2 Guide 2, 7–21.

Gordon, D.H. and Watson, C.R.B. 1986. Identification of cryptic rodents (*Mastomys*, *Aethomys*, *Saccostomus*) in the Kruger National Park. South African Journal of Zoology, 21, 95–99.

Hallett, J.M. 1977. Cytological and cytogenetical studies on the multimammate mouse *Praomys* (*Mastomys*) *natalensis*. MSc thesis. University of the Witwatersrand, South Africa.

Smit, A., van der Bank, H., Falk, T. and De Castro, A. 2001. Biochemical genetic markers to identify morphologically similar South African *Mastomys* (Rodentia: Muridae). Biochemical Systematics and Ecology, 29, 21–30.

Identification of rodents of the genus *Bandicota* in Vietnam and Cambodia

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Abstract. *Bandicota indica* and *B. savilei* are broadly sympatric across Southeast Asia and both species can be locally abundant. *B. savilei* is not often reported in ecological or rodent management literature and is presumably misidentified either as immature *B. indica* or as other rodent species. New material from Vietnam and Cambodia helps to clarify the morphological distinction between these species. Special care is needed to distinguish adult *B. savilei* from juvenile or immature *B. indica*. The Cambodian specimens of *B. indica* and *B. savilei* represent the first records for either species in this country where so little collecting has occurred.

Introduction

Burrow systems dug by bandicoot rats of the genus *Bandicota* are one of the most conspicuous signs of rodent activity in the agricultural landscapes of South and Southeast Asia. However, with the exception of one species found chiefly on the Indian subcontinent, comparatively little is reported in the scientific literature about either their basic biology or their role as pest species in agricultural systems. Accurate field identification represents the first step towards improving ecological knowledge, but for *Bandicota* this has proven elusive.

Across most of its geographical range, the genus *Bandicota* is represented by co-occurring large and small species. The larger form is generally called *B. indica*. The smaller forms were previously treated as a single species under the name *B. bengalensis*, but are now generally divided into true *B. bengalensis* of the Indian subcontinent and *B. savilei* of Southeast Asia (Musser and Carleton 1993). Whereas *B. bengalensis* and *B. indica* differ in obvious morphological features (Musser and Brothers 1994), *B. indica* and *B. savilei* differ primarily in adult size. In this paper, we report on new material of *B. indica* and *B. savilei* from Vietnam and Cambodia that helps to clarify the morphological distinction between these species.

Materials and methods

We variously trapped and purchased *B. indica* and *B. savilei* at various localities in the north and south of Vietnam and in two provinces in Cambodia. All specimens were weighed and an external assessment made of sexual maturity and reproductive status. The following standard external measurements were taken: head+body length; tail length; pes length (without claw); and ear length. Selected specimens were prepared as voucher specimens (either whole bodies, skins, or heads). The majority of the voucher material is registered in the Australian National Wildlife Collection, the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Canberra.

K. Aplin and N.P. Tuan examined specimens of *Bandicota* in the zoological collection of the University of Hanoi (previously reported by Tien 1985).

Results and discussion

Geographical distributions of *Bandicota* species

The probable natural geographical range of *Bandicota indica* includes all or part of India, Sri Lanka, Nepal, Bangladesh, Myanmar, Thailand, Laos, Cambodia, Vietnam and southern China (Musser and Brothers 1994). This taxon was introduced historically to Taiwan and to the Kedah and Perlis regions of the Malay Peninsula, and possibly pre-historically to Sumatra and Java (Musser and Newcomb 1983). We have recorded this species in numerous localities in both the south and north of Vietnam (Brown, Tuan et al., this volume; La Pham Lan et al., this volume) and in the vicinity of Phnom Penh and in Kampong Cham province in Cambodia. It is sympatric with *B. savilei* in southern Vietnam and in both study areas in Cambodia. Musser and Brothers (1994) noted other instances of sympatry in Vietnam and Thailand.

B. savilei is recorded from scattered localities in Central Myanmar, Thailand and Vietnam (Musser and Brothers 1994). In southern Vietnam, K. Aplin, L.P. Lan and N.M. Hung collected specimens of *B. savilei* in Ho Chi Minh City province and in Binh Thuan province—no specimens were obtained within the Mekong Delta proper, despite intensive sampling (La Pham Lan et al., this volume). A. Frost collected specimens of *B. savilei* from two localities in Cambodia (Somrong commune, Kampong Cham province and near Phnom Penh). K. Aplin and N.P. Tuan recorded specimens of *B. savilei* from several northern provinces (see Table 1) in the zoological collection of the University of Hanoi. These include specimens previously reported by Tien (1985) as *B. bengalensis*. *B. savilei* is also tentatively recorded from southern Laos (Khamphoukeo et al., this volume) based on a photographic record.

The natural range of *B. bengalensis* probably includes all or part of Pakistan, India, Sri Lanka, Nepal, Bhutan, Bangladesh and Myanmar (Musser and Brothers 1994). It has been introduced to Penang Island off the west coast of Malaysia, to the Aceh region of Sumatra and eastern Java in Indonesia, to Saudi Arabia, and possibly to Kenya in East Africa. In central Myanmar, this species and *B. savilei* have been collected within 30 km of each other and they may yet be found in sympatry.

Figure 1. Adult individuals of *Bandicota indica* (top) and *B. savilei* (bottom) from the Cambodian Institute of Agricultural and Rural Development field station near Phnom Penh, Cambodia. Photographs by A. Wildman and A. Frost.

The Cambodian specimens of *B. indica* and *B. savilei* represent the first records for either species in this country where so little collecting has occurred (see Figure 1 for illustrations of live animals).

Identification of Southeast Asian *Bandicota*

Bandicota species can be distinguished from other Southeast Asian murid rodents, including members of the genus *Rattus*, by their relatively broader, heavier incisors (which exceed 3 mm in combined width, even in juveniles) and by the nature of their claws, which are straighter and more forward projecting than in typical murids. Adult *Bandicota* tend to have coarser pelage than most other rodents, with conspicuous guard hairs, but the difference between an adult *B. savilei* and a *Rattus rattus* in this regard is subtle. The tail is relatively shorter in *Bandicota* species than it is in many *Rattus* species, however there are exceptions in the latter genus (e.g. *R. argentiventer*) that negate the diagnostic value of this feature.

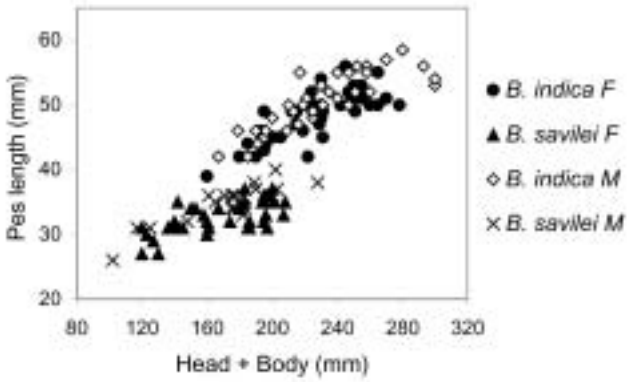

Figure 2. External measurements (head+body length, pes length) of *Bandicota indica* and *B. savilei* from Bin Thuan province, Vietnam, showing a complete bivariate separation of the two species. Slight overlap in pes length occurs between young female *B. indica* and fully adult male *B. savilei.*

Our largest regional *Bandicota* sample, comprising 82 individuals of *B. indica* and 59 of *B. savilei*, comes from Binh Thuan province in the south of Vietnam. In this area, adult *B. indica* are readily distinguished from *B. savilei* by their much larger size, overall darker colouration and more prominent guard hairs. However, immature *B. indica* closely resemble *B. savilei* in colouration and fur texture, and considerable care is needed to reliably distinguish the two species. Adult *B. savilei* often have a rust-coloured patch on the chest and throat that is rarely, if ever, seen in *B. indica*.

For both species in the Binh Thuan sample, males average slightly larger than females for all measurements (Table 1). There is considerable overlap between the species in head+body, tail and ear lengths, and in body weight. The ratio of tail to head+body does not distinguish the species or the sexes within each species. In contrast, pes length shows little overlap between the two species and no overlap when used in bivariate combination with

Table 1. External measurements of *Bandicota* spp. summarised by locality, species and sex (SVN = southern provinces, Vietnam; CVN = central provinces Vietnam; NVN = northern provinces, Vietnam). Measurements of specimens from Bac Thai, Hai Phong, Hoa Binh and Hung Yen provinces are taken from specimen labels in the Zoology Museum, University of Hanoi. Measurements for Gai Lai province are from Tien and Sung (1990; type series of *B. bengalensis giaraiensis*). All other measurements were taken by the authors on live or freshly dead specimens. Details given are mean ± standard deviation, range (where relevant) and number in sample.

Locality/Species	Sex	Head+body (HB) length (mm)	Tail length (mm)	Tail/HB%	Pes length (mm)	Ear length (mm)	Body weight (g)
Binh Thuan, SVN							
B. savilei	M	171 ± 30.6 102–228 (*n* = 21)	141 ± 23.4 90–183 (*n* = 20)	84 ± 4.6% 75–92% (*n* = 20)	35 ± 3.2 26–40 (*n* = 21)	23 ± 2.0 19–25 (*n* = 21	157 ± 65.0 45–290 (*n* = 21)
B. savilei	F	169 ± 28.5 120–228 (*n* = 37)	139 ± 20.6 95–176 (*n* = 36)	83 ± 6.5% 74–98% (*n* = 36	33 ± 2.5 27–37 (*n* = 37)	23 ± 1.4 20–26 (*n* = 37)	147 ± 58.1 55–292 (*n* = 38)
B. indica	M	231 ± 34.9 167–300 (*n* = 38)	196 ± 28.6 147–248 (*n* = 34)	85 ± 4.1% 73–91% (*n* = 34)	51 ± 4.2 42–58.5 (*n* = 38)	25.5 ± 2.1 19–29 (*n* = 34)	370.5 ± 191.0 125–870 (*n* = 37)
B. indica	F	229 ± 28.2 160–278 (*n* = 44)	190 ± 26.6 135–235 (*n* = 37)	84 ± 6.3% 73–99% (*n* = 37)	49 ± 3.9 39–56 (*n* = 41)	25 ± 1.8 21–29 (*n* = 37)	364.5 ± 130.4 110–640 (*n* = 43)
Vinh Phuc, NVN							
B. indica/savilei	M	213 ± 19.4 180–285 (*n* = 35)	197 ± 17.1 150–234 (*n* = 31)	93 ± 6.1% 82–111% (*n* = 31)	41 ± 4.6 35–54 (*n* = 35)	22 ± 3.3 18–34 (*n* = 35)	239 ± 106.3 115–600 (*n* = 35)
B. indica/savilei	F	233 ± 25.6 200–280 (*n* = 14)	212 ± 26.4 164–255 (*n* = 13)	84 ± 2.5% 95–105% (*n* = 13)	44 ± 4.2 37–50 (*n* = 14)	26 ± 4.0 19–31 (*n* = 14)	277 ± 97.9 154–473 (*n* = 14)
Hai Phong, NVN							
B.indica	M	275	270	98%	48	31	600
B.indica	F	255.0	216.0	85%	47.0	28.0	483.0
Hoa Binh, NVN							
B.savilei	M	235	195	83%	38	22	235
B.indica	M	185–205 (*n* = 2)	170–175 (*n* = 2)	83–95% (*n* = 2)	40–41 (*n* = 2)	27–28 (*n* = 2)	170–235 (*n* = 2)
B.indica	F	207	185	89%	40	28	246
Bac Thai, NVN							
B.savilei	F	220	182	83%	38	22	235
B.indica	M	258	250	97%	46	30	550
B.indica	F	240	182	76%	43	26	235
Hung Yen, NVN							
B.indica	M	285.0	260.0	91%	50.0	35.0	616.0
Gia Lai, CVN							
B. savilei	F	164–205 (*n* = 2)	136	83%	33–36 (*n* = 2)	21–25 (*n* = 2)	–
B. savilei	M	193	183	95%	33	25	–
Ho Chi Minh, SVN							
B. savilei	F	190	–	–	35	24	190
Cambodia							
B. savilei	M	120–125 (*n* = 2)	110–115 (*n* = 2)	92% (*n* = 2)	35–36 (*n* = 2)	22–23 (*n* = 2)	78–88 (*n* = 2)
B. savilei	F	120–175 (*n* = 3)	110–159 (*n* = 3)	80–95% (*n* = 3)	32.5–36.5 (*n* = 3)	19.5–25 (*n* = 3)	78–157 (*n* = 3)
B. indica	M	232 ± 32.9 175–285 (*n* = 19)	196 ± 28.6 147–248 (*n* = 18)	93 ± 6.4 84–107 (*n* = 18)	49 ± 3.0 43–54 (*n* = 19)	26 ± 1.1 24–29 (*n* = 19)	402 ± 203.2 78–830 (*n* = 18)
B. indica	F	229 ± 25.8 175–285 (*n* = 14)	218 ± 35.2 140–270 (*n* = 14)	95 ± 7.6 78–108 (*n* = 14)	48 ± 3.3 40.5–52 (*n* = 14)	27 ± 1.3 25–29 (*n* = 14)	370 ± 121.4 115–540 (*n* = 14)

head+body length (Figure 2). The very slight interspecific overlap in pes length occurs between young female *B. indica* and fully adult male *B. savilei*. The hind foot of *B. savilei* is more slender than that of juvenile *B. indica* (Figure 3) but is similar in colouration and the configuration of plantar pads.

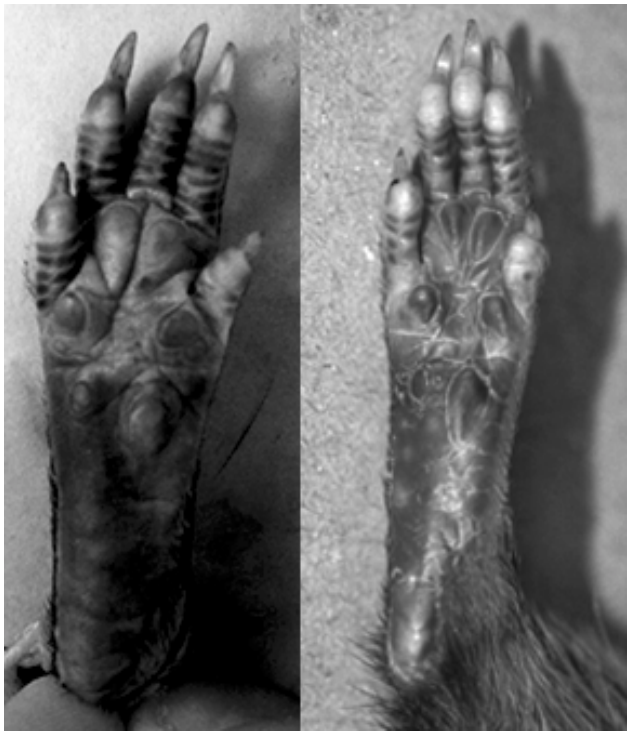

Figure 3. Sole of the right hind foot of a juvenile *Bandicota indica* (on left) and an adult *B. savilei* (on right). Both individuals are from Binh Thuan province, Vietnam. Note the more robust nature of the hind foot of *B. indica*.

The smaller Cambodian sample also includes two clearly distinct taxa that compare favourably with the Binh Thuan samples (Figure 4). However, Cambodian *B. indica* appear to have slightly larger hind feet and a proportionally longer tail that sometimes exceeds head+body Length (Table 1). Male *B. savilei* from Cambodia also appear to have slightly larger feet than their counterparts in Binh Thuan province of Vietnam (Figure 5).

The *Bandicota* sample from Vinh Phuc province in northern Vietnam was measured over the course of an extended period of fieldwork (Brown, Tuan et al., this volume) and few voucher specimens were taken. In both sexes, the hind feet are shorter relative to head+body length than in the Binh Thuan and Cambodian samples (Figures 4 and 5). There is also a strong suggestion that two species are included within the sample, especially among the males. Without voucher material of the smaller taxon, the identity of this population cannot be resolved. However, specimens from Hoa Binh and Bac Thai provinces leave us in no doubt that *B. savilei* is present regionally in the north of Vietnam and this species may well be present in Vinh Phuc. We have not examined the type series of *B. bengalensis giaraiensis* Tien and Sung 1990 from Gia Lai province, but published measurements (repeated in Table 1) are consistent with the other material referred here to *B. savilei*.

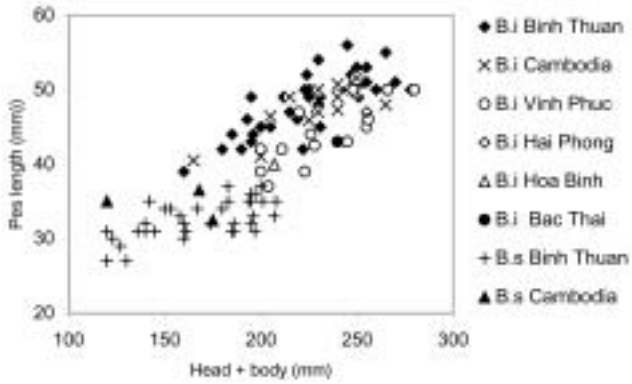

Figure 4. External measurements (head+body length, pes length) of female *Bandicota indica* and *B. savilei* (B.i and B.s in legend) from various localities in Vietnam and Cambodia. The sample of *B. indica* from Vinh Phuc in northern Vietnam probably includes some individuals of *B. savilei*.

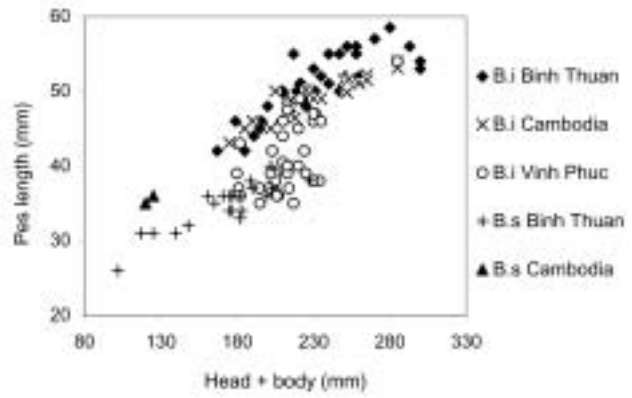

Figure 5. External measurements (head+body length, pes length) of male *Bandicota indica* and *B. savilei* (B.i and B.s in legend) from various localities in Vietnam and Cambodia. The sample of *'B. indica'* from Vinh Phuc in northern Vietnam probably includes some individuals of *B. savilei*.

Conclusion

B. indica and *B. savilei* are broadly sympatric across Southeast Asia and both species may be locally abundant. However, *B. savilei* is not often reported in ecological or rodent management literature and is presumably misidentified either as immature *B. indica* or as other rodent species. Close attention to the incisors and nature of the claws on the hind feet will distinguish *Bandicota* species from other rodents such as species of *Rattus*. Southeast Asian *Bandicota indica* and *B. savilei* are readily distinguished by the size and morphology of the hind feet, which are proportionally larger and heavier in *B. indica*. Special care is required to distinguish adult *B. savilei* from juvenile or immature *B. indica*.

References

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 Carleton, M.D. 1993. Family Muridae. In: Wilson, D.M. and Reeder, D.M., ed., Mammal species of the world, 2nd edition. Washington DC, Smithsonian Institution Press, 501–755.

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.

Tien, D.V. 1985. Scientific results of some mammals surveys in North Vietnam (1957–1971). Hanoi, Scientific and Technical Publishing House, 330 p.

Tien, D.V. and Sung, C.V. 1990. Six new Vietnamese rodents. Mammalia, 54, 233–238.

Integrative systematics: contributions to *Mastomys* phylogeny and evolution

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Abstract. The multimammate rats (genus *Mastomys*) are widely distributed throughout Africa and their interactions with human populations can have important consequences in regard to agriculture and human health. The latest results in the systematics and phylogeny of four *Mastomys* species, namely *M. coucha*, *M. huberti*, *M. erythroleucus* and *M. huberti* are presented here, combining results from morphology, morphometrics, cytogenetics and molecular analysis. In general, *Mastomys* species are morphologically similar, some of them being sibling species, thus no simple method of discrimination between the four studied species is successful. The use of morphometric analysis on skull and dental measurements does not allow complete discrimination, despite the fact that *Mastomys* species are strongly molecularly and chromosomally divergent, which allows reconstructions of their phylogenetic relationships. By comparing the different data sets, we are able to detect evolutionary patterns within *Mastomys* and to raise some new perspectives for further analyses. The use of a variety of different techniques will be necessary to resolve the systematics of the group.

Introduction

The method of integrative systematics combines results from numerous methods to improve the taxonomy and phylogenetic resolution of a group under study. This is even more important in the case of sibling species for which classical identification techniques are not efficient, and where a good attribution is fundamental for any phylogenetic work.

The African multimammate rats (*Mastomys* species) are found in all savannah areas in sub-Saharan Africa. Different populations can be morphologically very similar but chromosomally highly divergent (reviewed by Granjon et al. 1997). Some of these species are commensal, with very wide areas of distribution, and they are often found in sympatry, but not always in the same biotopes (Duplantier and Granjon 1988) since there is strong ecological structuring among *Mastomys* species. A recent review by Granjon et al. (1997) recognised seven species in the genus but indicated that the status of some forms was still to be resolved.

The interaction of certain *Mastomys* species with human populations can have important consequences, especially in regards to agriculture and human health. Several species can achieve high local population densities and outbreaks of *Mastomys natalensis* have been reported in East Africa (Leirs et al. 1996; Mwanjabe et al. 2002). The highest population density observed in Tanzania was more than 1400 rats/ha (Mwanjabe et al. 2002). At such densities, these rodents can cause seed depletion and losses in field crops, which have strong economical consequences (Mwanjabe et al. 2002). In the health domain, some *Mastomys* species are reservoir hosts and/or vectors of viruses and parasites responsible for human diseases such as bubonic plague (Green et al. 1978), Lassa fever (Wulff et al. 1975; McCormick et al. 1987), Rift Valley fever (Diop et al. 2000) and schistosomiasis (Imbert-Establet et al. 1997; Duplantier and Sène 2000). Each *Mastomys* species has its own biological properties in contact with the virus or parasites (Diop et al. 2000).

A good knowledge of the systematics of these rodents is clearly necessary and the integrative approach could be appropriate. The results obtained by the simultaneous use of morphological, morphometric, cytogenetic and molecular studies on the same individuals are presented here in order to give an overview of the systematics and evolution of one *Mastomys* sibling species complex.

Materials and methods

The *Mastomys* sibling species complex studied here comprises four species, namely *M. coucha*, *M. huberti*, *M. erythroleucus* and *M. huberti*, identifiable unambiguously only by their karyotypes (Table 1). The morphological,

morphometric and molecular studies were all carried out on karyotyped specimens.

Table 1. Chromosomal characteristics and geographical distribution of *Mastomys* species (2N = diploid number of chromosomes; NFa = fundamental autosome number).

	Chromosomal data	Distribution
M. coucha	2N = 36; NFa = 54	South Africa
M. huberti	2N = 32; NFa = 44	West Africa
M. erythroleucus	2N = 38; NFa = 52–56	West Africa to southern Ethiopia
M. natalensis	2N = 32; NFa = 52–54	Sub-Saharan Africa

The skulls of all specimens were examined under a microscope, with close attention paid to the tympanic bullae, the foramina and the teeth. The characteristics of the fur were not considered because of their high intraspecific variability. The specimens were sorted by age according to their stage of dental wear (Verheyen and Bracke 1966) so that age-related variation could be ascertained. Due to the wear of their molar crown surface, older specimens of stages 5–6 were not incorporated into the analyses.

A total of 208 specimens belonging to *M. natalensis*, *M. huberti*, *M. coucha* and *M. erythroleucus* were used and 12 dental measurements taken from each (lengths and widths of the crown for the three upper and three lower molars). Log-transformed data were analysed using principal components analysis (PCA) and discriminant function analysis (DFA).

Mastomys species are cytogenetically divergent and the chromosomal characteristics can be used to infer phylogenetic relationships. Chromosome analyses were performed on preparations obtained from fibroblast cultures. Each identified structural rearrangement was considered as a character and its presence or absence scored in the various taxa (see details in Volobouev et al. 2002). The matrix of chromosomal characters was analysed by maximum parsimony (MP) using the exhaustive search option in PAUP 4.0 (Swofford 1998) for 5 taxa and 41 characters.

Total genomic deoxyribonucleic acid (DNA) was extracted from liver, heart or muscles preserved in 70% ethanol using a CTAB protocol (Winnepenninckx et al. 1993). Mitochondrial sequences containing the complete cytochrome b gene were isolated via polymerase chain reaction (PCR) and sequenced directly from purified PCR products with an automatic sequencer CEQ2000 (Beckman). The sequences were entered and manually aligned using Bioedit software. Mutational saturation was studied for each codon position, with transitions and transversions treated separately. Phylogenetic relationships were analysed by MP. The phylogenetic analyses were conducted using PAUP 4.0. The MP analysis was done with a heuristic search using stepwise addition. Robustness of trees was assessed by the bootstrap method performed by PAUP 4.0. (1000 replicates) and by the decay index (DI) using Autodecay software. The divergence dates were calculated based on transversion in the 3rd codon position. The molecular clock hypothesis was tested by relative-rate tests using RRTree and Mega programs.

Results and discussion

Results

The four *Mastomys* species considered show very similar morphology and high intraspecific variability. Thus, no qualitative characters have yet been found to discriminate between them.

The DFA of dental measurements of karyotyped specimens (Figure 1) shows that *M. erythroleucus* and *M. natalensis* are rather well discriminated both by size and shape. This is not the case for *M. huberti* and *M. coucha*, which are not very different from each other. The percentage of misclassified specimens for all species is high (between 45.86 and 57.74%) and all *M. coucha* specimens are misclassified. *M. natalensis* and *M. erythroleucus* have the best reclassification results. Axis 1 discriminates *M. natalensis* and *M. erythroleucus* on both size and shape, while *M. huberti* and *M. coucha* are indistinguishable. Overall, no complete discrimination has been found between any two of the four *Mastomys* species and wide intra-specific variability has been observed for *M. natalensis* (Denys 2002).

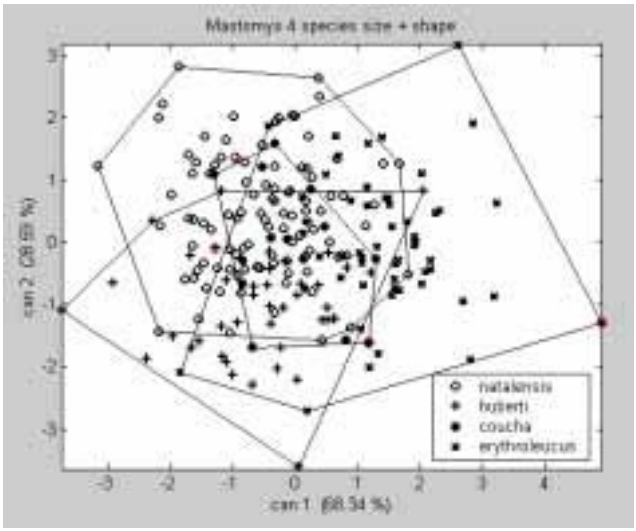

Figure 1. Discriminant analysis on 12 molar measurements for karyotyped specimens of four species of *Mastomys*. The sample consists of 101 *M. natalensis* from Senegal, Tanzania and South Africa, 43 *M. huberti* from Senegal, 14 *M. coucha* from South Africa and 54 *M. erythroleucus* from Senegal. Where possible, the type of each species has also been measured.

Phylogenetic relationships within *Mastomys* species have been inferred by chromosomal and molecular data (Lecompte et al. 2002; Volobouev et al. 2002). Figure 2 compares the results obtained from the two data sets. The cytogenetic and molecular trees are incongruent in regard

to the phylogenetic position of *M. erythroleucus* and *M. natalensis*, which are sister taxa according to the molecular data set, while *M. natalensis* is closest to *M. huberti* in the chromosomal phylogeny.

With respect to the molecular data, the highest genetic distance between the four species is approximately 10%. The monophyly of this clade is strongly supported (100% of bootstrap replicates). The basal position of *M. coucha* versus *M. huberti* is less supported at 77% bootstrap support. *M. erythroleucus* and *M. natalensis* are sister species in this analysis, with high support (88%). The relative rate tests do not reject the molecular clock hypothesis for this data set, hence we are able to estimate the dates of the divergence between *Mastomys* species. The initial divergence of the four species is estimated about 3 million years which is congruent with discriminate analysis (DA) of *Mastomys* fossil at 3.7 million years (Denys and Jaeger 1986). The two first species within this terminal clade appear almost at the same time, then *M. erythroleucus* and *M. natalensis* diverge 1 million years later.

Discussion

Our analysis suggests that traditional morpho-anatomical and classical morphometric techniques do not seem very efficient at discriminating between sibling species of *Mastomys.* This confirms previous work on skulls by Duplantier (1988) and Dippenaar et al. (1993). The use of geometrical morphometrics is now required. This technique has proven successful for discriminating *Mus* species (Auffray et al. 1996) and *Praomys* species (Denys et al., this volume) but less effective in the case of sibling *Taterillus* species (Dobigny et al. 2002). When standard karyotypes fail to discriminate between taxa, cytogenetic banding analysis is required. Moreover, this banding information allows phylogenetic reconstruction, and can be integrated in a global analysis and compared with other data sets, such as morphology or molecular data. Previous phylogenetic relationships within *Mastomys* were inferred from chromosomal data (Britton-Davidian et al. 1995) and from DNA/DNA hybridisation (Chevret et al. 1994). These studies gave incongruent results and an absence of clear (robust) resolution at the interspecific level. In the case of the cytogenetic studies, *M. natalensis* and *M. huberti* were identified as sister groups, while *M. erythroleucus* was found to be most divergent (Britton-Davidian et al. 1995). In the DNA/DNA hybridisation tree, *M. coucha* was found to be the more divergent species (Chevret et al. 1994), a result that is supported by the new molecular data. The chromosomal and molecular trees are clearly incongruent in regard to the positions of *M. coucha* and *M. erythroleucus*. The DNA sequencing data allows us to solve in part the irresolution of the DNA/DNA tree, however both new analyses confirm the instability of *Mastomys* classification.

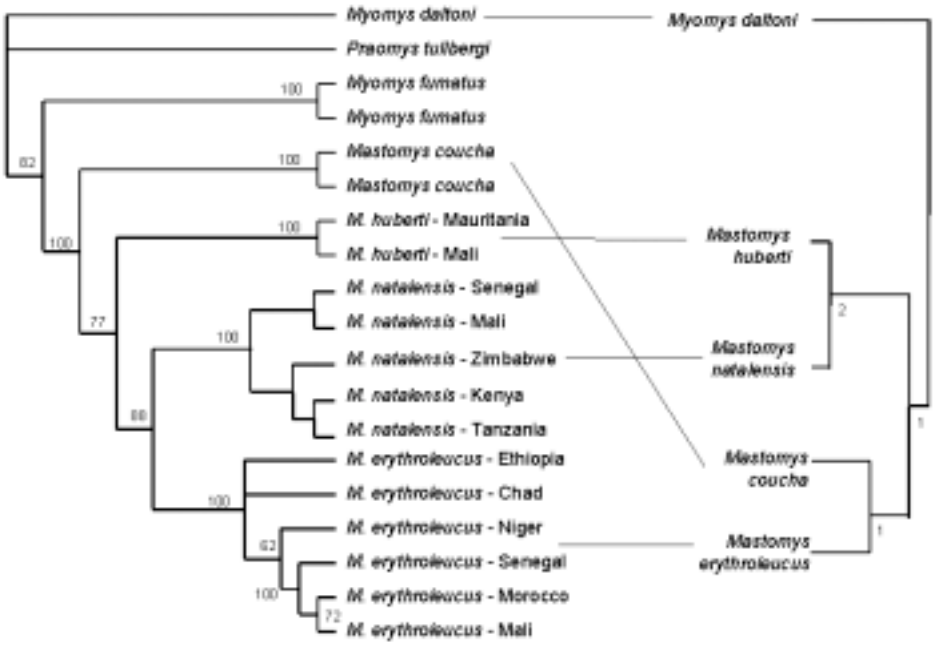

Figure 2. Phylogenetic relationships within *Mastomys* species reconstructed using molecular data (left) and chromosomal data (right) (after Volobouev et al. 2002 and Lecompte et al. 2002). The molecular phylogeny is the strict consensus of two trees (consistency index (CI) = 0.695; retention index (RI) = 0.766). The chromosomal tree is the most parsimonious tree (CI = 0.941; RI = 0.900). The values above the nodes (molecular tree) are bootstrap values; the values under the nodes (cytogenetic tree) are decay index values.

The degree of morphological stasis in the group, together with the incongruence between phylogenies, suggests that this lineage is the product of radiation that involved formation of numerous sibling species. The almost simultaneous divergence of the *M. coucha* and *M. huberti* is consistent with this hypothesis, whereas the mitochondrial phylogeny provides evidence of divergence between *M. erythroleucus* and *M. natalensis* 1 million years later. The seemingly late divergence of these taxa might result from the introgression of mitochondrial DNA between the two forms during hybridisation, as hypothesised by Volobouev et al. (2002). This introgression could explain the incongruity between the molecular (mitochondrial) and the cytogenetical (nuclear) phylogenies, and the later divergence of these species. Hybridisation between *Mastomys* species may occur during the early stage of their diversification, thus explaining the incongruities among the data sets. The chromosomally distinct forms within *M. erythroleucus* also suggest a possible species complex (Volobouev et al. 2002). It will be necessary to test these hypotheses with new data for more systems including nuclear markers, and to add supplementary specimens of the rarer *Mastomys* species.

Conclusion

The various *Mastomys* species are morphologically very similar, and complete discrimination cannot be achieved using only qualitative morphology or classical morphometrics. In all cases, cytogenetic analysis is needed for identification. Sibling species within *Mastomys* are strongly genetically divergent based on both molecular and chromosomal data. Phylogenetic relationships reconstructed using cytogenetic and molecular data are partially incongruent. However, the contrasts between the two data sets have generated new hypotheses on *Mastomys* origins and evolution. The results of this study suggest that, for further progress in *Mastomys* systematics, we will need to explore new fields of investigation, such as geometrical morphometrics or nuclear molecular analyses.

This example demonstrates the importance of the integration of different methods to make correct taxonomic determinations and to accurately infer relationships between species. Incongruence between data sets highlights areas that are testable by other data sets. The combination of these different methods is essential to the development of a precise and reliable method of determination of *Mastomys* species. This is even more important when the species are implicated in applied research, such as in epidemiology or durable interactions.

References

Auffray, J.C., Alibert, P., Latieule, C. and Dod, B. 1996. Relative warp analysis of skull shape across the hybrid zone of the house mouse (*Mus musculus*) in Denmark. Journal of Zoology London, 240, 441–455.

Britton-Davidian, J., Catalan, J., Granjon, L. and Duplantier, J.-M. 1995. Chromosomal phylogeny and evolution in the genus *Mastomys* (Mammalia, Rodentia). Journal of Mammalogy, 76, 248–262.

Chevret, P., Granjon, L., Duplantier, J.-M., Denys, C. and Catzeflis, F.M. 1994. Molecular phylogeny of the *Praomys* complex (Rodentia: Murinae): a study based on DNA/DNA hybridization experiments. Zoological Journal of the Linnean Society, 112, 425–442.

Denys, C. 2002. The problem of species identification in palaeontology and biology: the case of *Mastomys* (Mammalia: Rodentia) and its dental variability. In: Baylac, M., Klingenberg, C.P., Fermon, Y. and Bailly, N., ed., Morphométrie multivariable, systématique et evolution: concepts, méthodes et applications. Paris, Muséum National d'Histoire Naturelle–Institut de Recherche pour le Développement (MNHN–IRD) Editions (in press).

Denys, C. and Jaeger, J.J. 1986. A biostratigraphic problem: the case of the East African Plio-Pleistocene rodent faunas. Modern Geology, 10, 215–233.

Diop, G., Thiongane, Y., Thonnon, J., Fontenille, D., Diallo, M., Sall, A., Ruel, T.D. and Gonzalez, J.-P. 2000. The potential role of rodents in the enzootic cycle of Rift Valley fever virus in Senegal. Microbes and Infection, 2, 343–346.

Dippenaar, N.J., Swanepoel, P. and Gordon, D.H. 1993. Diagnostic morphometrics of two medically important southern African rodents, *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae). South African Journal of Science, 89, 300–303.

Dobigny, G., Baylac, M. and Denys, C. 2002. Geometric morphometrics and diagnosis of sibling species: the complex of West African *Taterillus* (Rodentia, Gerbillinae). Biological Journal of the Linnean Society (in press).

Duplantier, J.-M. 1988. Biologie evolutive de populations du genre *Mastomys* (Rongeur, Muridae) au Sénégal. PhD thesis. Université de Montpellier.

Duplantier, J.M. and Granjon, L. 1988. Occupation et utilisation de l'espace par des populations du genre *Mastomys* au Sénégal: étude à trois niveaux de perception. Sciences et Techniques d'Animalerie et de Laboratoire, 13, 129–133.

Duplantier, J.M. and Sène, M. 2000. Rodents as reservoir hosts in the transmission of *Schistosoma mansoni* in Richard-Toll, Senegal, West Africa. Journal of Helminthology, 74, 129–135.

Granjon, L., Duplantier, J.-M., Catalan, J. and Britton-Davidian J. 1997. Systematics of the genus *Mastomys* (Thomas, 1915) (Rodentia: Muridae). A review. Belgian Journal of Zoology, 127 (suppl. 1), 7–18.

Green, C.A., Gordon, D.H. and Lyons, N.F. 1978. Biological species in *Praomys* (*Mastomys*) *natalensis* (Smith): a rodent carrier of Lassa virus and bubonic plague in Africa. American Journal of Tropical Medicine and Hygiene, 27, 627–629.

Imbert-Establet, D., Moné, H., Tchuem Tchuenté, L.A. and Jourdane, J. 1997. Permissiveness of two African wild rodents, *Mastomys huberti* and *Arvicanthis niloticus*, to *Schistosoma intercalatum*: epidemiological consequences. Parasitology Research, 83, 569-573.

Lecompte, E., Granjon, L., Kerbis-Peterhans, J. and Denys C. 2002. Cytochrome-b based phylogeny of the *Praomys* group (Rodentia, Murinae): a new African radiation? Comptes Rendus de l' Académie des Sciences, Série III (in press).

Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. and Mbise, T. 1996. Forecasting rodent outbreaks in Africa: an ecologi-

cal basis for *Mastomys* control in Tanzania. Journal of Applied Ecology, 33, 937–943.

McCormick, J.B., Webb, P.A., Krebs, J.W., Johnson, K.M. and Smith E.S. 1987. A prospective study of the epidemiology and ecology of Lassa fever. Journal of Infectious Diseases, 155, 437–444.

Mwanjabe, P.S., Sirima, F.B. and Lusingu J. 2002. Crop losses due to outbreaks of *Mastomys natalensis* (Smith, 1834) Muridae, Rodentia, in the Lindi Region of Tanzania. International Biodeterioration and Biodegradation, 49, 133–137.

Swofford, D.L. 1998. PAUP: phylogenetic analysis using parsimony. Champaign, Illinois, Natural History Survey, 177 p.

Verheyen, W.N. and Bracke E. 1966. The influence of ageing on the craniometrical characters of *Praomys jacksoni* (de Winton, 1897). Annales du Musée royal d'Afrique centrale de Tervuren, 144, 91–101.

Volobouev, V.T., Aniskin, V.M., Lecompte, E. and Ducroz, J.-F. 2002. Pattern of karyotype evolution in complexes of sibling species within three genera of African murid rodents inferred from the comparison of cytogenetic and molecular data. Cytogenetics and Genome Research (in press).

Winnepenninckx, B., Backeljau, T. and De Wachter, R. 1993. Extraction of high molecular weight DNA from molluscs. Trends in Genetics, 9, 407.

Wulff, H., Fabiyi, A. and Monath, T.P. 1975. Recent isolations of Lassa virus from Nigerian rodents. Bulletin of the World Health Organization, 52, 609–612.

SYMPOSIUM 9. RODENT BIOLOGY—CONTRASTING PERSPECTIVES

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Market study of meat from field rats in the Mekong Delta

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Abstract. Rats are caught in the field and sold as dressed meat or as live rats for human consumption in the Mekong River Delta region of Vietnam. This study describes six different components of the rat market and the results of surveys of people involved in different parts of the distribution chain. These surveys were focused in six provinces where the rat market is concentrated: Ca Mau, Bac Lieu, Soc Trang, Can Tho, An Giang and Dong Thap. The annual production of rat meat for human consumption was 3300–3600 t of live rats, with a market value of about Vietnamese dong (VND) 25–30 billion (US$2 million). This market provides an important avenue of income for many poor farmers, who are the primary rat catchers. Supply of rats is highest during February to April and lowest in September. Movements in the price of rats showed a pattern similar to the quantity of rats available.

The survey also considered health risks. No person—from rat catcher to processor—was aware of health risks related to the handling of live rats. Analysis for presence of three types of zoonotic bacteria in water samples collected at processing points and in nearby waterways indicated the presence of *Clostridium perfringens* and *Enterococcus faecalis*. Of concern is that the highest concentrations of *C. perfringens* were found in the waterways. More research is required on the health risks to people involved in this trade and to others living near processing plants.

Introduction

Rodents are one of the most important pests of rice and many other crops in the Mekong River Delta. They feed not only on standing crops but also on grain in storage. In rice cropping systems, rats are most prevalent where cropping is more intensive, particularly where two or three crops are grown a year (Sang 1998). Where two rice crops are grown, rats have a greater impact on summer crops. Farmers attempt to control field rats by several means, including use of chemicals, trapping, digging of burrows, electrocution, or a combination of these methods (Singleton et al. 1999).

A peculiar aspect of field rat control in the Mekong Delta is the existence of markets for rat meat for human consumption. In the province of Bac Lieu alone, there are estimated to be as many as 2000 full-time rat catchers, and in all the provinces in the Mekong River Delta there are about 50 specialist rat distributors. Rat meat is popular in this region, not only because farmers have few sources of protein, but also because it is regarded as 'good meat'. In addition, catching rats is an important source of income for some poor farmers. Notwithstanding profit motives or health benefits of consuming rat meat, there are health risks associated with the handling and processing of rats (see Gratz 1994). There have been no studies on the marketing of rat meat in the Mekong Delta or on the health problems related to the handling of live rats. This paper reports on a survey aimed at gathering information on the operation and scale of rat catching and processing as meat for human consumption in the region. The specific objectives of this survey were to:

1. describe the marketing channels of rats caught and marketed as meat from catchers to assemblers or traders to consumers;
2. estimate the volume of rats caught and consumed as meat or as feed; and
3. describe the agents involved in the marketing of rat meat, their operations, their income from rat trading, and their awareness of health risks related to rat processing.

Materials and methods

Rats are caught, assembled and processed at several locations in the provinces of the Mekong River Delta. These assembling places are located near town centres and along the sides of roads or along canals that are used for the transport of goods. An initial survey was conducted to gather general information on the distribution of rat processing and collection. The information was gathered

through interviews with personnel from provincial and district plant protection services, with people they identified as key informants on the rat meat market, and with participants in rat catching and processing in the provinces of Ca Mau, Bac Lieu, Soc Trang, Can Tho, An Giang and Dong Thap. We then surveyed rat dealers and processors to gain detailed descriptions and estimations of marketing channels for rats. From the assemblers and catchers, we traced backwards for information on smaller rat assemblers and rat catchers, and traced forward along the marketing routes for information on rat-meat dealers and end users.

A further survey was conducted from a random sample of rat processors and rat catchers on the rat business system, including methods of capture, price of rats at different stages in the supply chain, labour linked to their part of the rat trade, awareness of health risks, and history of illness that respondents thought might be associated with handling rats.

Estimation of the quantity of rats traded on the market was obtained based on the amount of rats sold as dressed meat or as live rats by the processors and retailers at principal markets.

Disease assessment

The Pasteur Institute in Ho Chi Minh City tested 1 L samples of water collected from either within the area where rats were processed or near the terminal drainage points of canals and streams where the effluent was discharged from processing households. The samples of water (three from households and six from waterways) were collected in Soc Trang and Can Tho. The water samples were cultured to screen for *Clostridium perfringens*, *Yersinia cheopis* and *Enterococcus faecalis*.

Results and discussion

Market agents and their operations

The markets for dressed meat and live rats in the provinces of the Mekong River Delta have well-established routes, with up to five levels of handling before the meat is sold at market (Figure 1).

Rat catchers and trappers

Most rat catchers are poor and landless farmers. Farmers use several methods to catch rats. The most popular are digging them from burrows, driving them into nets, and trapping using wire cages. The methods used vary with season, condition of terrain and vegetation of the area. Only live rats are sold to agents. A premium is paid for rats that look healthy if they are to be kept alive and transported long distances to processors or retailers.

All the rat catchers interviewed use steel traps. These are cheap devices costing less than VND2000 (US$0.15) apiece. Many rat dealers and processors invest in steel traps then lend them to rat catchers or advance them to rat catchers as credit. In return, these people catch rats exclusively for the dealer or processor, ensuring a stable supply of rats.

A professional rat catcher usually owns a boat and operates with about 100 traps. When rat numbers are high, a catcher harvests an average of 15 kg of live rats per day, valued at US$7.

Small-scale rat assemblers

These rat dealers usually operate within a local area, 8–10 km from their home. They buy rats from other farmers and re-sell to dealers. They own a small boat or bicycle, collecting live rats from other catchers, then selling them either to rat dealers in a local area (depot) or to mobile rat collectors.

Rat assemblers

Rat assemblers own a motorcycle or boat and operate within 30 km of their home, collecting rats from small assemblers. Many of these rat assemblers are friends or relatives of rat dealers in the province. They usually receive a cash advance from dealers to buy rats from other assemblers or catchers. The amount of live rats collected per trip is 80–100 kg if using a motorcycle or 200–240 kg if using a boat.

Dealers

There are usually one to three dealers per province buying rats from catchers or other assemblers. These dealers have fixed business premises. They also buy and

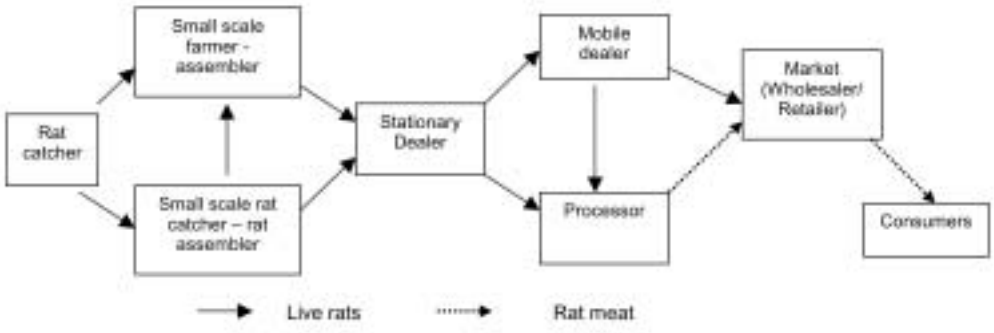

Figure 1. Main collection and distribution channels of live rats and rat meat for human consumption.

sell other animals caught in the field, such as snakes, birds and tortoises.

Long-distance rat assembler-dealers

These operators buy rats from catchers, other local assemblers or from dealers, and sell to rat processors. They operate a motor tricycle with an average of 700–800 kg of rats per trip. Rats are kept in cages 1.2 × 0.8 × 0.2 m that weigh about 50 kg.

Rat processors

Rat processors tend to concentrate in specific places with several households within one hamlet involved in the business. The highest concentrations are 18 households in Xeo Don hamlet of Phung Hiep district, Can Tho, and 36 households in Binh Chien hamlet in Binh Long village of Chau Phu district, An Giang. These two hamlets process about 70% of rats traded daily in the Mekong Delta with highest production occurring from January to May (Table 1). Several households in these hamlets have been involved in rat processing for more than 10 years. In other provinces, such as Bac Lieu, the rat trade is increasing, with many businesses only 2 years old (Table 2).

A large processor can process up to two tonnes of live rat per day or approximately 25,000 rats. The average amount of rats processed daily per household was highest in February (480 kg) and lowest in September (77 kg) (Table 1). Depending on the quantity of rats needed to be processed, one processor will hire 10 to 20 workers—many of them are young children. Processing usually begins at 1700 h and lasts until late in the evening, because live rats are delivered to the processing place late in the afternoon and the meat needs to be brought to market very early the next morning. Workers usually specialise only in one stage of the process and are paid according to the weight of rats processed.

Rat market channels

Principal rat market channels are described in Figure 1. The following routes are the most important channels of live rat transport:

1. Rats collected in Ca Mau are sold in Bac Lieu and Soc Trang.
2. Rats bought in Bac Lieu and Soc Trang are re-sold in O Mon and Can Tho.
3. Rats bought from rat catchers or collectors along the border with Cambodia are re-sold to depots in An Phu district of An Giang province.

About 60–70% of the total traded volume of rats pass through these three channels. From December to April, most of the rat supply comes from the first two routes. From May to July most rats come from grass fields along the Cambodian border.

Rat assemblers in Ca Mau province specialise in buying live rats from farmers or from small rat collectors in the districts. They operate depots in Ca Mau town then

Table 1. Mean quantity of rats processed daily per processor (kg of live rats/day) and mean monthly price (Vietnamese dong (VND) per kg; VND13,000 ≈ US$1).

Factor	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Quantity (kg/day)	367	480	421	336	342	302	191	144	77	101	145	223
Price (VND/kg)	8361	8414	8548	8671	8397	8355	8319	8000	7178	7344	7626	7790

Table 2. Number of living rats (kg) bought monthly at 11 rat businesses (from December 2001 to June 2002) in three provinces (Can Tho, Soc Trang and Bac Lieu) of the Mekong Delta, southern Vietnam.

Province	Shop no.	Years in business	Dec 2001 (kg)	Jan 2002 (kg)	Feb 2002 (kg)	Mar 2002 (kg)	Apr 2002 (kg)	May 2002 (kg)	Jun 2002 (kg)
Bac Lieu	1	4	170,514	170,500	154,120	77,542	56,557	5787	no data
	2	2	8618	12,152	42,165	90,621	48,832	5309	1140
Soc Trang	3	10	3317	2400	29,800	30,000	25,100	23,900	1840
	4	6	7750	8370	6215	16,417	21,655	10,780	2740
	5	8	no data	10,983	21,391	30,452	19,440	9880	570
	6	8	7756	8685	8400	7750	7180	7862	1820
Can Tho	7	12	25,171	24,617	23,400	18,000	21,000	11,500	4500
	8	10	no data	4154	8680	12,400	12,301	10,151	2831
	9	12	4650	4650	11,205	21,724	32,296	22,601	4175
	10	14	9325	15,500	22,436	6226	11,180	19,400	645
	11	3	10,540	13,330	17,645	9345	9178	2851	no data
Total			247,641	275,341	345,457	320,477	264,719	130,021	20,261

sell to traders from Bac Lieu, Soc Trang, Dong Thap, An Giang and Can Tho. In general, rat traders in Ca Mau and Bac Lieu are not involved in rat-meat processing, but sell live rats to traders. These are then processed in Soc Trang, Can Tho (Phung Hiep district) and An Giang (Chau Phu district). Traders in Soc Trang and Bac Lieu buy live rats from assemblers in Ca Mau, Bac Lieu and Soc Trang, and transport them to depots in O Mon, selling them to traders from Cai Dau (An Giang) for processing. Processors in Phung Hiep (Can Tho) buy live rats from assemblers in Bac Lieu and Ca Mau, and then sell meat to dealers in Can Tho.

Rat meat is used for direct human consumption. The survey did not find any other uses of rat meat as in processed food. By-products from processing—heads, skin, tail—are used as feed for fish.

Protection measures and health problems

No labourers who worked at the 69 processing and rat trading units wore protective clothing. Only five processors provided labourers with hand cream to protect skin from long working hours in water, and disinfectant to be applied to rat bites. Workers who participated in rat processing were not aware of health problems related to rat handling. Only 11 of 69 surveyed processors reported that their hired workers had acquired infections from rat bites.

Wastewater from rat processing was discharged directly into canals (n = 6), rivers (n = 8), enclosed ponds (n = 6), or onto the soil surface (n = 5). Local government did not allow rat processors to discharge wastewater into waterways, except in Binh Long village in An Giang.

Doctors at local hospitals and Red Cross units were sent a questionnaire enquiring about reported human diseases transmitted by rodents. Few questionnaires were completed because the doctors were not familiar with the range of rodent-borne diseases and so had nothing to report. This is surprising given that leptospirosis is relatively common in Thailand and approximately 25% of rodents sampled in a cross-sectional study of rats collected from processors and dealers in Soc Trang were seropositive for leptospirosis (Singleton, Smythe et al., this volume).

The sampling of wastewater from within and outside the processing households returned positive cultures for both *C. perfringens* and *E. faecalis* (Table 3). Both of these bacteria can be transmitted from rats to humans. No samples were positive for *Yersinia cheopis*. The high levels of *C. perfringens* in the waterways are of particular concern. This bacterium is typically associated with decaying animal carcasses. However, this was a pilot study with small sample sizes and with no comparative measures of these bacterial levels in waterways remote from rat processing plants. Further studies are warranted.

Quantity of rats caught and marketed as meat

We covered all the major rat processors and dealers in the selected provinces, with estimates based on the amount of rats sold as meat or as live rats by the processors and retailers at principal markets. This estimation is conservative.

Demand for rat meat appeared to depend on the quality of rat meat and the availability and price of other meat and fish. Rats are more fatty in February to April and very lean in September, coinciding with the highest and lowest quantity of rat processed, respectively. Naturally caught fish are more abundant in September and October. Movement in the price of rats showed a similar pattern as quantity of meat produced (Table 1). These trends for the supply and price of rat meat are unusual since the period of lower supply corresponds with lower prices instead of high prices as in the case of other agricultural commodities. The rats caught and processed annually over the last four years were estimated at around 3300–3600 t (Figure 2).

Conclusion

The rat-meat market in the Mekong Delta of Vietnam provides an important avenue of income for many poor farmers and local businesses. The annual production of rat meat for human consumption (3300–3600 t of live rats) has a market value of VND25–30 billion (US$2 million).

Table 3. Results of analysis of water samples for *Clostridium perfringens* and *Enterococcus faecalis*. Water was sampled from within the households processing rat meat or in the waterways where waste was discharged.

Shop no.	Water sampled at point of rat processing		Water sampled in waterways where waste was discharged	
	C. perfringens (No. bacteria/mL)	*E. faecalis* (No. bacteria/mL)	*C. perfringens* (No. bacteria/mL)	*E. faecalis* (No. bacteria/mL)
1	1	10	1050	10
2	2900	14	2150	10
3	3	10	2250	10
4			2400	10
5			2100	10
6			1800	10

Although there are a number of families that have been involved in the rat trade for up to 20 years, there has been a recent growth in the number of traders, especially in Bac Leiu. It will be interesting to monitor whether this growth of the industry is sustainable.

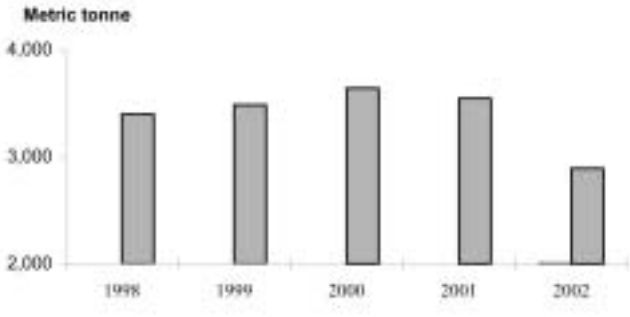

Figure 2. Volume of live rats traded per annum, 1998–2002, in six provinces of the Mekong Delta, Vietnam (data for 2002 only until May).

Despite this level of trade, rats are still the main pre-harvest pest in many provinces in the Mekong Delta. It appears that the rat industry is literally harvesting the rats, with the highest production coinciding with high rat numbers at the end of the main breeding seasons (Brown et al. 1999). Population studies are required to determine the impact of this harvesting operation on rat population dynamics. If a majority of rats are caught at the population peaks, then this may alleviate density-dependent effects on survival, allowing the rat populations to compensate through better survival of remaining rats through to the next breeding season. The impact of the industry on human health also requires urgent attention.

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References

Brown, P.R., Hung, N.Q., Hung, N.M. and van Wensveen, M. 1999. Population ecology and management of rodent pests in the Mekong River Delta, Vietnam. 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, 319–337.

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

Sang, N.D. 1998. Studies of field rat in Ha Tien district, Kien Giang province. MSc Agronomy thesis. Faculty of Agriculture, Can Tho University, Vietnam, 205 p.

Singleton, G.R., Sudarmaji, Tan, T.Q., Jumanta and Hung, N.Q. 1999. 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.

Seasonal variations in metabolism and thermogenic capacity in greater long-tailed hamsters

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Abstract. The aim of this study was to determine the seasonal changes in metabolic properties and thermogenic capacity in the greater long-tailed hamster (*Cricetulus triton*). During seasonal acclimatisation, there were no significant seasonal changes in basal metabolic rate, however non-shivering thermogenesis and maximum metabolic rate increased significantly in winter compared with summer. We also calculated the shivering thermogenesis by subtracting basal non-shivering thermogenesis (NST) from the maximum metabolic rate. Results suggest that shivering thermogenesis plays an important role in total heat production in summer, and NST plays an important role in winter heat production. In the natural environment, greater long-tailed hamsters mainly depend on an increase in NST to adapt to the cold of winter. These physiological adjustments are closely related to this species' biological characteristics, such as being solitary, nocturnal and non-hibernating, and having a seed-dominant, omnivorous food habit.

Introduction

The greater long-tailed hamster (*Cricetulus triton)* is a very common pest rodent in the farmlands of northern China. It is a predominantly seed-eating, omnivorous species, and nocturnal, burrowing, non-hibernating and of solitary habits. In the natural environment, it faces a large seasonal fluctuation in environmental temperatures and unstable food resources because of agricultural activities. However, this species can use stored food during winter and early spring. Although many aspects, such as population dynamics, chemical communication, and other ecological aspects (Zhang and Wang 1998), have been studied, there is no information available on seasonal patterns of energetics and thermogenesis for this species (Wang and Wang 2002). The primary aim of this research was to determine the seasonal changes in metabolism and thermogenesis of *C. triton* in order to understand its physiological survival strategies.

Methods and materials

Animals

Adult greater long-tailed hamsters (males and non-pregnant, non-lactating females) were live-trapped in the farmlands of Hebei province in spring, summer, autumn, and winter. Animals were kept individually in cages under natural photoperiod and temperature conditions, and fed commercial laboratory rat chow pellets plus cabbages. Food and water were supplied *ad libitum*. All determinations were made within 10 days of capture.

Measurement procedure

Rates of oxygen consumption were measured using a closed-circuit respirometer. Temperatures inside the animal chambers (size = 3.6 litres) were measured and maintained with a water bath (±1°C). The body mass and body temperature of animals were recorded before and after each experiment. Body temperature was measured by insertion of a digital thermometer (Beijing Normal University Instruments Co.) into the rectum to a depth of 3 cm.

Measurements of metabolic rates were made at temperatures ranging from 5–36°C. Before each experiment, animals were weighed to the nearest 0.1 g and fasted for 3 h to minimise the specific dynamic action of food. Each measurement lasted for 60 min and oxygen consumption was recorded at 5 min intervals. Animals were allowed to adapt to the metabolic chamber for about 1 h before measurements started. Two consecutive minimum readings were taken for metabolic rate calculations. All measurements were made daily between 0830–1900 h. Metabolic rates were expressed as mL O_2/g.h, corrected to standard temperature and pressure (STP).

After resting metabolic rate measurements had been completed, non-shivering thermogenesis (NST) was stimulated by a subcutaneous injection of a mass-dependent

dosage of noradrenaline. The maximum response to noradrenaline was regarded as the maximum NST.

Maximum metabolic rate was induced using a He:O_2 (80%:20%) mixture and was measured at 0°C and 5°C. When the experiments finished, most of the animals had reduced body temperatures.

Statistics

Data were analysed using the SPSS software package. Differences between temperatures in each season were determined by repeated measure analysis of variance (ANOVA) and seasonal differences were determined by ANOVA, with a statistical significance level of $P < 0.05$.

Results and discussion

Basal metabolic rate (BMR), nonshivering thermogenesis (NST), and maximum metabolic rate (MMR) in greater long-tailed hamsters are shown in Figure 1. The thermal neutral zones for spring, summer, autumn, and winter were 26–32°C, 29–34°C, 26–34°C and 24–34°C, respectively; BMRs (mL O_2/g.h) were 1.68 ± 0.33 (sd), 1.23 ± 0.02, 1.54 ± 0.22 and 1.59 ± 0.22, respectively; NST rates (mL O_2/g.h) were 3.22 ± 0.56, 2.63 ± 0.63, 4.19 ± 0.43 and 4.54 ± 0.31, respectively; and MMRs were 5.02 ± 0.56 mL O_2/g.h in summer and 7.49 ± 0.79 mL O_2/g.h in winter (Figure 1).

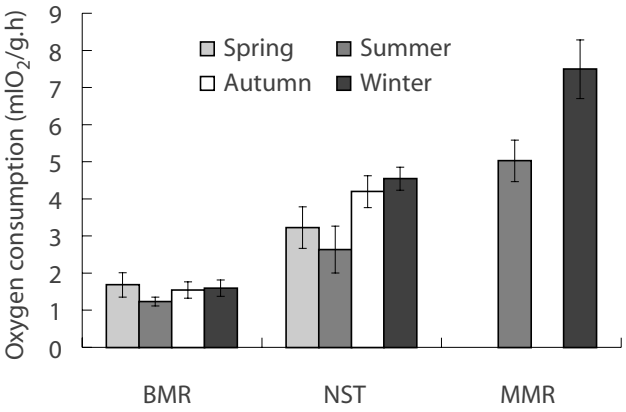

Figure 1. Seasonal variations in basal metabolic rate (BMR), non-shivering thermogenesis (NST) and maximum metabolic rate (MMR) in greater long-tailed hamsters (mean ± standard deviation).

BMR increased by 29% in winter compared with summer, maximum NST increased by 73%, MMR increased by 49%, regulatory NST (maximum NST–BMR) increased by 111%, and shivering thermogenesis (MMR–maximum NST) increased by 23%. In summer, hamsters' BMR contributed 25% of MMR, regulatory NST contributed 28%, shivering thermogenesis contributed 48%, and maximum NST contributed 52%. In winter, hamsters' BMR, regulatory NST, shivering thermogenesis, and maximum NST contributed to MMR by 21%, 39%, 39%, and 61%, respectively. During seasonal acclimatisation, there were no significant seasonal changes in BMR (although it tended to increase in winter), however NST and MMR increased significantly in winter compared with summer.

Many small mammals inhabiting fluctuating and cold environments display enhanced capacity for seasonal changes in NST and MMR, such as the Djungarian hamster (*Phodopus sungorus*) (Heldmaier et al. 1989), short-tailed shrew (*Blarina brevicauda*) (Merritt 1986), red-backed vole (*Clethrionomys rutilus*) (Feist and Rosenmann 1976), plateau pika (*Ochotona curzoniae*) and root vole (*Microtus oeconomus*) (Wang and Wang 1996). However, a fossorial rodent (*Spalacopus cyanus*), which is not faced with cold stress, has a relatively low physiological plasticity which is in accordance with a fossorial mode of life—it has a remarkably high NST, low MMR and, surprisingly, nearly no shivering thermogenic capacity compared to other rodents (Nespolo et al. 2001). Feist and Rosenmann (1976) showed that the arctic–subarctic red-backed vole has a greater capacity for NST than rodents from temperate latitudes, probably because this species is acclimatised to colder seasonal conditions. Holloway and Geiser (2001) showed that BMR and thermal conductance were lower in winter in the sugar glider (*Petaurus breviceps*), a marsupial, but maximum heat production was raised significantly in winter, suggesting that, despite the apparent lack of functional brown adipose tissue, sugar gliders are able to significantly increase heat production in winter.

In conclusion, our present study suggests that shivering thermogenesis plays an important role in total heat production in summer and NST plays an important role in winter heat production for greater long-tailed hamsters. In its natural environment, this species mainly depends on the increase in NST to adapt to the cold winter. These physiological adjustments are closely related to the living habits of this species, such as living singly, being nocturnal and non-hibernating, and having seed-dominant, omnivorous food habits.

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References

Feist D.D. and Rosenmann, M. 1976. Norepinephrine thermogenesis in seasonally acclimatized and cold acclimated red-backed voles in Alaska. Canadian Journal of Physiology and Pharmacology, 54, 146–153.

Heldmaier, G., Steinlechner, S., Ruf, T., Wiesinger, H. and Klingenspor, M. 1989. Photoperiod and thermoregulation in vertebrates: body temperature rhythms and thermogenic acclimation. Journal of Biological Rhythms, 4, 251–265.

Holloway J.C. and Geiser, F. 2001. Seasonal changes in the thermoenergetics of the marsupial sugar glider, *Petaurus breviceps*. Journal of Comparative Physiology, B, 171, 643–650.

Merritt, J.F. 1986. Winter survival adaptations of the short-tailed shrew (*Blarina brevicauda*) in an Appalachian mountain forest. Journal of Mammalogy, 67, 450–464.

Nespolo, R.F., Bacigalupe, L.D., Rezende, E.L. and Bozinovic, F. 2001. When nonshivering thermogenesis equals maximum metabolic rate: thermal acclimation and phenotypic plasticity of fossorial *Spalacopus cyanus* (Rodentia). Physiological and Biochemical Zoology, 74, 325–332.

Wang D.-H. and Wang Z.-W. 1996. Seasonal variations in thermogenesis and energy requirements of plateau pikas (*Ochotona curzoniae*) and root vole (*Microtus oeconomus*). Acta Theriologica, 41, 225–236.

Wang D.-H. and Wang and Z.-W. 2002. Metabolic rate, thermoregulation and distribution of greater long-tailed hamster (*Cricetulus triton*) in China. Folia Zoologica (Sppl.) (in press).

Zhang, Z.-B. and Wang, Z.-W. (ed.) 1998. Ecology and management of rodent pests in agriculture. Beijing, Ocean Publishing House, 286 p.

Rodent physiological ecology in China

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Abstract. In China, studies of the physiological ecology of rodents began in the 1950s and developed rapidly from the 1980s. Some areas have been well covered for some, but not all, species. Most of the work has focused on thermogenesis, temperature regulation and digestive physiology. Almost 20 small mammal species have been studied and these species are mainly distributed in northern China. Because the majority of these species are rodents, much basic research work must be done before we can test hypotheses and/or make predictions or generalisations. It is essential to continue to develop excellent hypotheses and then undertake experimental manipulations to obtain robust, repeatable and precise results. This paper reviews the status and development of rodent physiological ecology in China, including the history of studies, current trends in research on physiological ecology, and areas for development in the near future.

Introduction

Physiological ecology combines the disciplines of physiology and ecology, and focuses on studies of individuals. Physiological data are used to answer ecological questions, which are related to the animal's survival and reproduction, and to explain their distribution, abundance and richness in the natural environment. Since the 1940s, physiological ecology has become a mature discipline. In this paper, we briefly review the developments in studies of physiological ecology of rodents in China.

History of studies in China

The first systematic studies on the physiological ecology of small mammals appear to be those of Professor Zhao Yibing of Peking University in the 1950s on thermoregulation in hedgehogs. In the late 1950s and early 1960s, Professor Sun Ru-Yong, Beijing Normal University, studied geographical variations in the physiological properties of *Clethrionomys rufocanus* and *Microtus agrestis* at Moscow University in the former Soviet Union (his work was published in the Bulletin of Beijing Normal University). In the 1970s, Sun Ru-Yong measured the metabolism of Chinese white-bellied rats (*Rattus niviventer confucianus*) and Norway rats *(Rattus norvegicus*), two farmland rodent species. He introduced analysis of covariance (ANCOVA) to account for the effect of body mass in studies of metabolism. In the late 1970s, Professor Wang Zu-Wang, Northwest Plateau Institute of Biology (now Institute of Zoology), Chinese Academy of Sciences, and his colleagues measured seasonal changes in metabolic rates and digestibility for two field small mammals (plateau pika, *Ochotona curzoniae*, and plateau zokor, *Myospalax bailyei*) in the Qinghai–Tibet Plateau. This was the first work on seasonal acclimatisation in metabolic rates in China.

Since the 1980s, studies in physiological ecology in China have progressed rapidly. Some new areas and more rodent species have been reported and studied, including: a comparative study on the metabolic rates of three rodent species of the southern Yangtze River; the effects of huddling on the metabolic rates in the lesser rice-field rat (*Rattus losea*); the development of homeothermy in Mongolian gerbils (*Meriones unguiculatus*) and root voles (*Microtus oeconomus*); the relationship between average daily metabolic rates and resting metabolic rates; the metabolic properties and the average daily metabolic rate for root voles in the Qinghai Plateau; the seasonal changes in mass, structure and composition of brown adipose tissue and capacity for non-shivering thermogenesis in plateau pikas and root voles; the metabolism and thermoregulation during hibernation and the non-hibernation period in Daurian ground squirrels (*Spermophilus daurica*) and hedgehogs; and seasonal variations in digestibility in root voles in the Qinghai Plateau.

In the 1990s, Li Qing-Fen, Beijing Normal University, and her group studied the molecular thermogenic mechanisms for Brandt's voles (*Microtus brandti*) and Mongolian gerbils in the laboratory (Liu et al. 1998; Li et al. 2001). Wang De-Hua (1993) examined the effects of photoperiod and temperature on thermogenesis in plateau pikas and root voles after acclimation in the laboratory. Wang Zheng-Kun (1996) studied the thermogenic capacities of tropical and subtropical small mammal species. Wang Yu-Shan (1997) determined energetic constraints on survival, reproduction and growth and development for alpine small mammals. Liu Xiao-Tuan (1998) first studied the molecular adaptive thermogenic mechanisms in Mongolian gerbils and Daurian ground squirrels. Bao (1999) compared the characteristics of ecophysiology and water metabolism in four rodent species from the Ordos Plateau of Inner Mongolia. Wang De-Hua and his colleagues determined the seasonal changes in thermogenesis and thermoregulation in Brandt's voles, Mongolian gerbils, and greater long-tailed hamsters (e.g. Wang De-Hua et al., this volume). Pei (2000) measured the effects of food quality on digestibility and retention time of digesta in Brandt's voles and Mongolian gerbils. Liu He (2002) was the first to systematically determine the reproductive energetics of Brandt's voles and Mongolian gerbils. Nearly 20 rodent species have been studied for their ecophysiology. These species are distributed in the alpine meadows of the Qinghai–Tibet Plateau; across regions of farmland and grassland, the Ordos Plateau of Inner Mongolia; the farmlands of the Northern China Plain; the tropical and subtropical area in Yunnan province of southern China; and some agricultural areas of the southern Yangtze River.

Current trends in research in China on physiological ecology

Today, there are some important trends in our studies of physiological ecology. With the globalisation of research, we are able to test theories in energetics, especially in comparative physiology. We are also able to contribute our ideas on the effects of evolution in the area of evolutionary physiology. Functional ecology and functional morphology and the search for mechanisms that regulate physiological processes using modern molecular biology techniques and instruments are considered very important. It is essential to continue to develop excellent hypotheses and then undertake experimental manipulations to obtain robust, repeatable and precise results. Multi-disciplinary research combines many approaches and techniques (e.g. telemetry to measure the body temperature, metabolic rates and food intake and/or activity of the individual). Individual differences and the relationship between different physiological parameters, structure and function are also important, as is the evolutionary significance of geographical differences in physiological parameters.

Areas for development in the near future in China

The following topics of rodent physiological ecology should be developed strongly in China for the majority of our native rodents. For the testing of hypotheses and/or making predictions or generalisations, much more work must be done in the areas of (1) water balance, especially for desert rodent species; (2) hibernation (torpor) and ecophysiology; (3) individual differences and genetic differences in physiological parameters; (4) relationships between characteristics of physiological ecology and population biology; (5) digestive tract morphology and digestive strategies; (6) reproductive energetics; (7) physiological limitation and its evolutionary significance; and (8) body weight maintenance, regulation and energy balance (leptin and its role in body weight regulation). More rodent species need to be studied for their ecophysiology. We should also expand our knowledge on those species for which we have some information, such as small mammals in the alpine meadows and Inner Mongolian grasslands.

Acknowledgments

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References

Bao, W.D. 1998. Comparative studies on metabolism and water balance for four rodent species from Ordos Plateau. PhD thesis. Institute of Zoology, Chinese Academy of Sciences.

Li, Q., Sun, R., Huang, C., Wang, Z., Liu, X., Hou, J., Liu, J., Cai, L., Li, N., Zhang, S. and Wang, Y. 2001. Cold adaptive thermogenesis in small mammals from different geographical zones of China. Comparative Biochemistry and Physiology A, 129, 949–961.

Liu He 2002. Reproductive energetics for two rodent species of Inner Mongolian grassland. PhD thesis. Institute of Zoology, Chinese Academy of Sciences.

Liu, X.T. 1998. Adaptive thermogenic mechanism of ground squirrels and Mongolian gerbils. PhD thesis. Beijing Normal University.

Liu, X.T., Lin, Q.S., Li, Q.F., Huang, C.X. and Sun, R.Y. 1998. Uncoupling protein mRNA, mitochondrial GTP-binding, and T4 5'-deiodinase activity of brown adipose tissue in Daurian ground squirrel during hibernation and arousal. Comparative Biochemistry and Physiology A, 120, 745–752.

Pei, Y.X. 2000. Effects of food quality on digestibility and digesta retention time for two rodent species of Inner Mongolia. Master Degree thesis. Institute of Zoology, Chinese Academy of Sciences.

Wang, D.H. 1988. Seasonal changes in the mass and structure of brown adipose tissue and nonshivering thermogenesis for two small mammals on the Qinghai–Tibet Plateau. Master Degree thesis. Northwest Plateau Institute of Biology, the Chinese Academy of Sciences.

Wang, D.H. 1993. Physiological adaptations to alpine environments of small mammals. PhD thesis. Beijing Normal University.

Wang, Y.S. 1997. Constraints of energetics on survival, reproduction, growth and development for alpine small mammals. PhD thesis. Institute of Zoology, Chinese Academy of Science.

Wang, Z.K. 1996. Comparative studies on physiological ecology and thermogenesis for tropic and subtropic small mammals. PhD thesis, Beijing Normal University.

Wang, Z.-W. and Wang, D.-H. 1996. Rodent energetics. In: Wang, Z.W. and Zhang, Z.B., ed., Theory and practice of rodent management. Beijing, Science Press.

Myth, dogma and rodent management: good stories ruined by data?

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Abstract. Many beliefs exist on what influences the population dynamics of rodent pests. In some instances, these beliefs get mentioned so often that they become dogma and in too many instances national policies on rodent management are based on dogma. We review five dogmas that have varying degrees of influence on policies for rodent management in Australia and Southeast Asia. Three are associated with regional or local movement patterns of rodents, one with the efficacy of predators as biological control agents, and one with the influence of farming systems on rodent dynamics. We provide results of experimental studies conducted to test the three dogmas associated with movement patterns. Two of these dogmas were rejected and one accepted. We conclude that rodent management requires a scientific approach, and the science of rodent management requires managers to conduct experiments.

Introduction

In a cogent review of the science and practice of wildlife management, Sinclair (1991) succinctly stated: "A scientific statement is one which can be tested and disproved. If it cannot potentially be disproved than (sic) that statement falls into the realm of religious belief. Such beliefs have no place in a scientific decision-making process for management, because they involve value judgements, subjectivity, bias and dogma." In rodent management, both in developed and developing countries, there are many beliefs surrounding what leads to outbreaks of rodent populations or to their chronic nature. Mention that you work on rodent pests when visiting a local bar or coffee shop, chatting with farmers or attending a scientific workshop, and you will be soon inundated with unsolicited (but well meaning) advice on why these rodents are pests and on how to control them (see Singleton et al. 1999 for discussion of the range of techniques used in Southeast Asia). In some regions, these beliefs have been around so long or been repeated so often that they become dogma. Yet when one examines the rationale for these dogmas, the scientific data cupboard is usually bare.

The paradigms for scientific studies for wildlife management may be based on the density-dependent school of thought focusing on regulation (see Sinclair 1989) or a more empirical approach focusing on limitation (see Krebs 1995). Regardless of which paradigm one adopts, the proponents of the differing paradigms agree that the way ahead is to adopt an experimental approach with clear alternative hypotheses (McNab 1983; Sinclair 1991; Krebs 2002). In the case of rodent management, we are not arguing that this experimental approach be adopted simply to provide scientific rigour to our art. In too many instances, national policies on rodent management or the beliefs of farmers are based on these dogmas, and therefore it is important that these beliefs are addressed scientifically to assess their worth. If this is not done, then governments and farmers will not be receptive to other, possibly more effective, management regimes.

We review five dogmas of rodent pest management prevalent in Australia and Southeast Asia. We have applied the experimental approach to three of these dogmas and report on our findings. We also briefly review the scientific basis for the other two.

Materials and methods

We describe experimental field studies we conducted to test alternative hypotheses for the first three dogmas. The last two dogmas will be described and reviewed in the Results and Discussion section.

Dogma 1

In Australia, mouse populations undergo aperiodic outbreaks resulting in densities of >1000 mice per ha (Singleton and Redhead 1989). Many farmers attest that mouse populations build up in the south-west (South Australian wheatfields or in areas of natural woodland) and move *en masse* to the north-east to invade the grain

fields in Victoria and New South Wales (NSW), devouring crops in their path. Stories of fish (Murray cod) caught in the Murray River, which defines the southern boundary of NSW, with mice in their stomach supposedly provides positive evidence that mice swim across the Murray River to invade NSW.

A 6-year replicated study was designed to distinguish between the following hypotheses:

- Hypothesis A: Mouse populations build up in areas of natural woodland (*Eucalypt* or *Callitris* dominated woodland) and then invade the adjoining cereal-cropping regions. (Accept dogma 1.)
- Hypothesis B: Mouse populations build up in both natural woodlands and cereal-cropping habitats. (Neither accept nor reject dogma 1.)
- Hypothesis C: Mouse populations build up in cereal-cropping regions and then invade the natural woodlands (Reject dogma 1.)

The study site was the central mallee region of Victoria centred around Walpeup (35°08'S, 142°02'E), which is characterised by an extensive strip of cereal-cropping land with woodland to the north and the south (Figure 1). From March 1983 to March 1988, a grid of 7 × 5 Longworth live-capture traps was set on average every 7 weeks in eucalypt woodland (three replicates), *Callitris* woodland (three replicates) and in crops (six replicates) (Figure 1). A line of 35 traps was set also along the margin of the crop (three replicates). This was a capture–mark–release study with trapping conducted for three consecutive nights, or for two consecutive nights per trapping session when greater than 75% of traps were occupied. Each mouse was sexed, breeding condition noted (see Singleton 1983), marked with a uniquely numbered ear-tag, weighed, head–body length measured, and then released at the site of capture.

Abundance indices for mice were calculated using trap success per 100 trap nights, adjusted for frequency using the method of Caughley (1977, p. 20).

Dogma 2

On the Southeast Asian ‘mainland’, rats invade from neighbouring countries, so farmers feel powerless to manage the problem and are only interested in developing palliative (crisis) management rather than tactical management. Since our research on rodent pests began in Southeast Asia in 1995, we have had numerous reports of rats moving across borders from Cambodia to Vietnam, Cambodia to Thailand, Laos to Thailand, Burma to Thailand, and Thailand to Laos.

A 2-year study was designed to distinguish between the following hypotheses:

- Hypothesis A: Rats invade Vietnam from Cambodia. (Accept dogma 2.)
- Hypothesis B: Rats invade Cambodia from Vietnam. (Accept dogma 2.)
- Hypothesis C: Rats show seasonal movements that track the different crop stages with no consideration of national borders. (Reject dogma 2.)

The study was conducted in the Ha Tien district, Kien Giang province (10°23'N, 106°23'E), Vietnam, from 29 September 1996 to 22 March 1997, and from 26 December 1997 to 3 March 1998. These periods were chosen because Vietnamese farmers report migration from Cambodia of rats around the lunar New Year. This is a politically sensitive region and politics influenced the length of the study periods. The region has dry (December to March) and wet (April to November) seasons; 97% of the rainfall occurs during the wet season. The average annual rainfall is 1500 mm.

In Ha Tien (Vietnam), there are two rice crops grown per year, each with a short growing season (90–105 days). In both years, the dry season crop was planted in December and harvested in mid to late March, and the wet season crop was planted in April and harvested in August. In Cambodia, there is one rice crop per year with a 6-month growing season: transplanted in August and harvested in January and February.

Drift fence plus traps

A 1.5 km plastic fence (0.70 m high) was established within 50 m of the Vietnam–Cambodia border. The bottom 50–100 mm of the fence was buried. A live-multiple-capture cage trap made of wire (600 × 300 × 300 mm) was placed every 30 m flush with, and opening to, a hole in the fence. The rats enter a wire cone, squeeze through and are unable to return (see Singleton et al. 1998 for details). Alternate live-capture traps faced either Vietnam or Cambodia. Rats caught only in the central 1 km of the fence (n = 35 traps) were included in the analyses. Rats were necropsied upon capture, identified to species, sexed and females examined for breeding condition (number of embryos, presence of uterine scars).

Dogma 3

Rats invade from neighbouring villages and devour crops. Farmers feel that the rodent problem is beyond their control because it originates from elsewhere. This is in essence the same as dogma 2, except at a more local scale.

A 4-year study was conducted to distinguish between the following hypotheses:

- Hypothesis A: Rats show seasonal movements that track the different crop stages with no consideration for village borders. (Accept dogma 3.)
- Hypothesis B: Rat populations build up only within a village and stay within these bounds. (Reject dogma 3).

The study was conducted in West Java, Indonesia (6°20'S, 107°39'E) from 1995 to 1998. The movements of rats were monitored between two large holdings, a research farm of 400 ha and seed farm of 1400 ha. Share farmers grow the rice on the seed farm and on two-thirds of the research farm with most farmers responsible for 1–5 ha of crop (mean of 2 ha). The two holdings share a common boundary of 3 km that is separated by the national highway. There are two rice crops grown per year, a wet season and a dry season crop The research farm has a short fallow of approximately 1 month between the wet

season and dry season crops and a 3-month fallow after the dry season crop. The fallow seasons were more evenly spaced on the seed farm, which led to the crops being planted asynchronously (Figure 2). The main rat access between the two farms was large stormwater drains that ran under the highway. A high flow of traffic on the highway 24 h a day limited the movements of rats across the surface of the road. High rat damage was reported in 1995–97 to the dry season rice crop in May and June. To monitor the level of rat movement to the research farm from late May to mid-June, rat access via the drain was channelled into wire multiple-capture cage traps. These traps were cleared each day and the number of rats recorded.

Results and discussion

Dogma 1: Australia and mouse plagues

The rate and timing of the population increase of mice across the four habitat types shows that populations in woodlands are 2–4 months behind the on-farm habitats

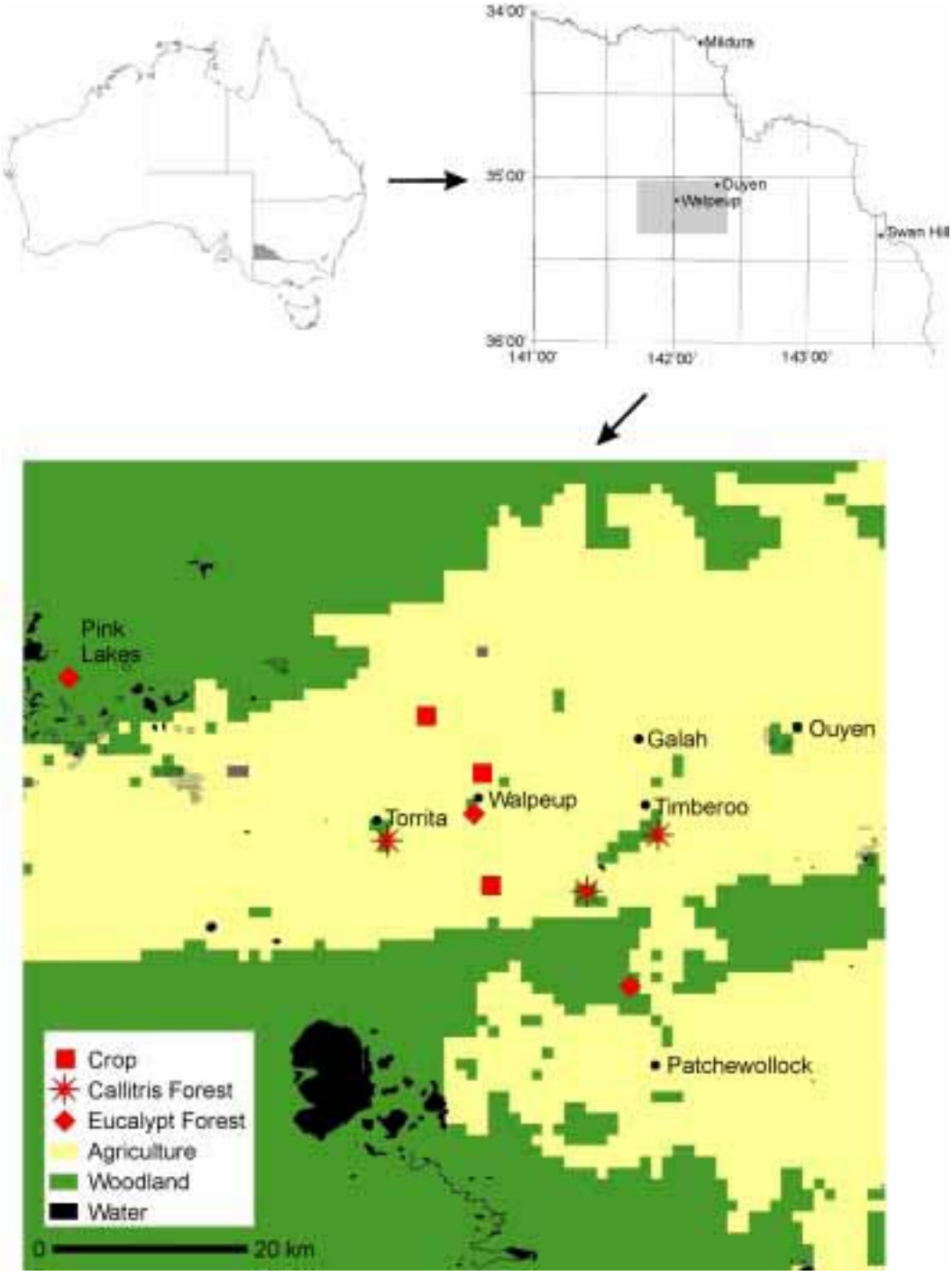

Figure 1. Location of nine study plots in woodland and crop habitats in the central mallee region of Victoria, Australia.

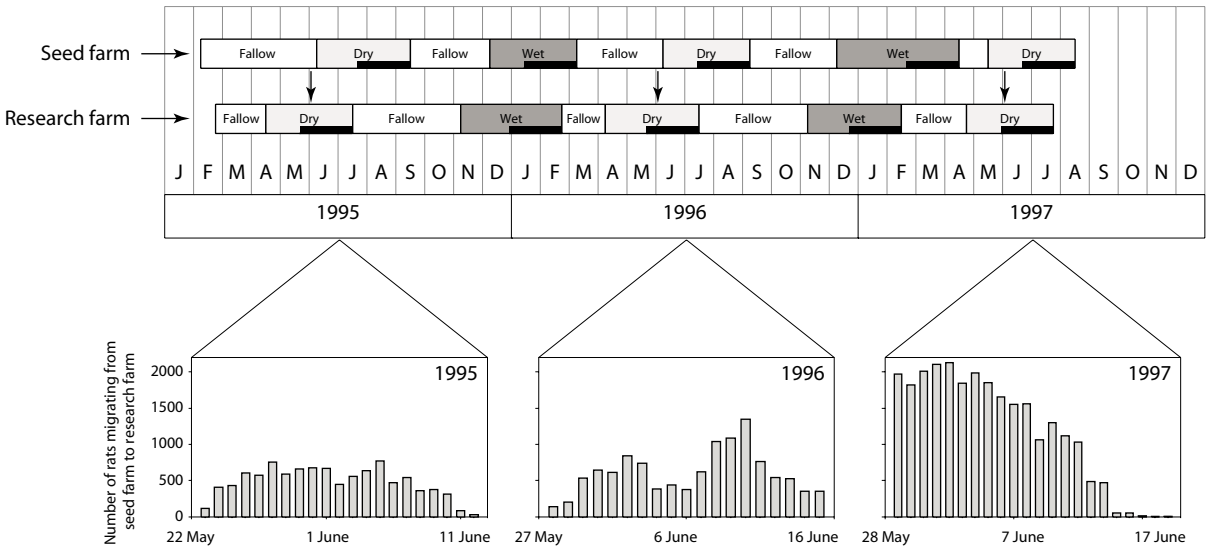

Figure 2. A schematic illustration of the timing of crops on the seed farm and the research farm at West Java, Indonesia, for 1995–97. The histograms show how many rice-field rats moved from the seed farm to the research farm during late May and June of each year. Movement between the farms was highest in 1997 when the time lag was short between harvest of the seed farm wet season crop and planting of the research farm dry season crop. The black bars indicate the period of crop development that is most attractive to rats (Dry = dry season rice crop; Wet = wet season rice crop).

(Figure 3a). Also, the populations in the woodlands increase with few, if any, females in breeding condition (pregnant and/or lactating) in the sample before the increase (Figure 3b). Together these results suggest that crop habitats are source habitats for mice, whereas woodlands are sink habitats.

There have been five detailed studies of changes in the demographic machinery of mice during the formation of a mouse plague in Australia. Three studies were conducted in irrigated crops in NSW (Redhead 1982; Boonstra and Redhead 1994; Twigg and Kay 1994), and two on rain-fed cereal farms: one in South Australia (Newsome 1969) and one in Victoria (Singleton 1989). A further study in South Australia reported changes in mouse abundance, breeding performance and habitat use of mice over a 10-year period (Mutze 1991). The live-trapping components of all of these studies were conducted either in one or two paddocks of a single farm or in a number of habitats but still within the borders of a single farm. Mutze (1991) conducted snap-trapping over large geographic areas, but these studies were restricted to monitoring changes in abundance and breeding of mice for three habitat types: cropped areas, roadsides and grassland/pasture. All of these studies highlighted the importance of seasonal use by mice of different habitats within a cropping landscape. However, the current study is the first to address the issue of whether native woodland is a source or sink habitat for mice. It is clear that mouse populations build up in cereal-cropping regions and then invade the natural woodlands. This leads us to reject dogma 1.

Dogma 2: border region of Vietnam and Cambodia

In 1996/97, rats began moving primarily from Vietnam into Cambodia after the harvest of the wet season crop in Vietnam and at the onset of annual flooding of the Mekong delta (October/November). These movements appeared to be associated with the stage of the crop on either side of the border. Before flooding, 2544 rats were caught migrating from Vietnam and only 49 from Cambodia. After flooding, the trend reversed: 279 rats were caught migrating from Vietnam and 3718 were caught migrating from Cambodia. The movements from Vietnam corresponded to completion of harvest of the rice crop in Vietnam and the flowering/booting stage of Cambodia's rice crop. After waters had subsided in Vietnam (January/February), rats began moving from Cambodia. This coincided with the harvest of Cambodian rice and burning of rice straw. At the same time, the Vietnamese dry season crop was approaching the tillering/booting stage (Table 1).

In the 1997/98 wet season, the fence was erected only in late December so we could monitor the movement patterns of rats only after the floods had receded. As in 1996/97, most rats (2021 of 2367 rats caught in the 6 weeks after 19 January) migrated from Cambodia to Vietnam. However, in 1998, the migration began in mid-January and peaked at the end of January, one month earlier than in 1997. The earlier timing of movements was most likely related to the rainy season ending in late December 1997 with the floods subsiding a month earlier than in 1996/97 and harvesting beginning earlier in Cambodia.

In summary, these seasonal rat migrations appear to track the availability of high-quality food on a local geographical scale (Table 1). National borders did not define a high net flow of rats in one direction, indicating that dogma 2 could be rejected.

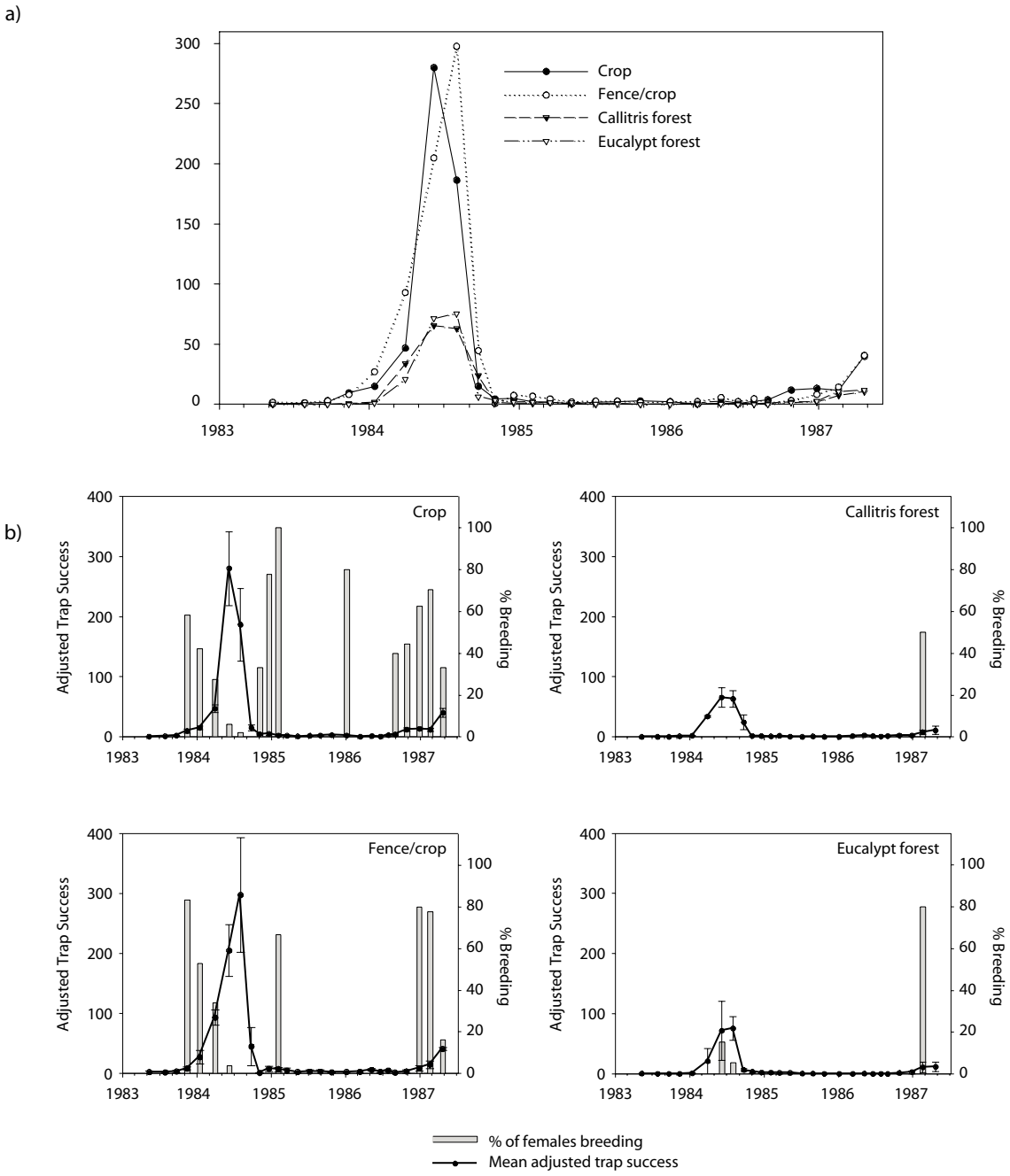

Figure 3. (a) Trap success of house mice in four habitat types in the Walpeup region shown in Figure 1. Population changes in the forest habitats lag behind the agricultural habitats by several months. (b) Percentage of female mice breeding and trap success in each habitat type. Breeding mice were captured in the forest habitats only after the population had increased; indicating the forest habitats are sinks rather than sources.

Dogma 3: local rodent movements in Java

Large numbers of rats were caught within a 3-week period each year from 1995 to 1997. These pulses of movements from the seed farm to the research farm were associated with the harvest of the rice crops and subsequent land preparation on the seed farm. The rats moved to the research farm where the crop was beginning the generative stage of development. The shorter the fallow following the wet season crop on the seed farm, the higher the number of rats caught moving towards the research farm (Figure 2). In 1998 and 1999, the seed farm and the research farm decided to plant both their wet and dry season rice crops synchronously. There were so few rats moving from the seed farm to the research farm in those years that it was decided by the farm managers (with input from scientists who had valuable research plots to protect) that there was no need to set up a barrier plus rat traps.

We accept dogma 3 that rats show seasonal movements that track the different crop stages with no consideration of village borders. Similar *en masse* movements have been reported by Saucy and Schneiter (1997) in juvenile water voles, *Arvicola terrestris*. In this case, it

was natal dispersal of a species that spends much of its time as an adult in underground burrows. We know of no other well-documented reports of *en masse* dispersal of rodents.

Dogma 4: predators and rats

Predators, particularly barn owls, have been proposed as a biological method for limiting rodent pest populations in rice agro-ecosystems below levels that cause economic hardship to farmers (Lee and Ho 1999). The reason that barn owls are not able to do so is the lack of nest sites. Provision of nest boxes (one per 6–8 ha) will lead to recruitment of barn owls into an area where they will raise young and the resulting increase in barn owl predation will limit rodent populations (Smal et al. 1990). However, many of these studies were done in conjunction with rodenticides, where they were aiming to poison 90% of the rat population. This high knock-down rate is required because models indicate that owls are unlikely to be able to limit rat populations if there are >60–70 rats/ha (Smal et al. 1990). There is evidence that avian predators are a major cause of density-dependent (see Sinclair et al. 1990) or delayed density-dependent (Lima et al. 2001) mortality of rodents, however too few studies have examined the ability of rodent populations to compensate for predator removal (see discussion by Singleton and Petch 1994).

In the Red River delta of North Vietnam, it is claimed that a reduction in cat numbers (allegedly through trade to China for body parts but also from misuse of poisons) has led to substantial increases in rodent populations. Although there is no scientific evidence to support or refute this allegation, the Vietnamese government is encouraging farmers to raise cats and research is in progress on the breeding performance of different breeds of cats. Promoting predators, particularly cats, was part of a Prime Ministerial Decree on 18 January 1998 (number 09/1998/CT) to encourage farmers to manage rodent pests.

There are insufficient replicated studies, with appropriate controls, to assess the impact of predators on rodent populations. This dogma therefore requires more research.

Dogma 5: farming intensification and rats

Changes in farming systems, especially intensification of rice production in Asia and greater heterogeneity of crops and continuous-rotational cropping in Australia, lead to extension of breeding seasons of rodents and better survival, which in turn is responsible for increased rodent problems in agricultural systems (Singleton and Brown 1999). In Southeast Asian countries, increases in areas of irrigation and changes to their market economies have led to two rice crops per year being grown where there was previously one grown, and three crops where there were previously two. Also, many of the crops are now grown asynchronously within a region.

The Mekong delta in Vietnam is a region that would provide a good test of the effect of farming intensification on rodent populations. Before 1990, rodents were not considered a major pre-harvest pest to rice. In the following decade, rats became a serious pest. In two provinces, Bac Lieu and Soc Trang, the rat situation is so severe that enterprising farmers have taken advantage of the situation by 'harvesting' millions of rats each year and processing them for rat meat. In 2001, we visited two rat-processing businesses and knew of one other. In 2002, the number of businesses had grown to at least eight, with production of dressed rat meat in the vicinity of 1 tonne per day per business from February to April.

Table 1. Summary of patterns of cropping systems on either side of the Vietnam and Cambodia border in Kien Giang province, Vietnam, and the migratory responses of rats from 29 September to 20 March in 1996/97 and 26 December to 2 March in 1997/98.

	Vietnam side	Cambodia side	1996/97	1997/98
Terrain	Low terrain (<5 m above sea level)	Higher terrain, small mountains, 4 km from border		
Cropping system	Irrigated; two crop seasons/year	Rainfed; one crop season/year		
Land preparation	April and November	July		
Rice variety	Improved, dwarf variety of rice; 90–115 days growing season; two crops per year	Local, 'traditional' variety of rice; 180–240 days growing season		
Planting time	15 April – early May 20 November – early December	End of July – early August		
Harvesting time	August 15 March–15 April	Mid to late February in 1997 Mid to late January in 1998		
Fallow	September to October	March to July		
Migration periods			*Migration to:*	
October	Fallow before floods	Vegetative rice	Cambodia	No data
January–February	Vegetative rice	Harvesting and straw burning	Vietnam	Vietnam
March–May	Harvesting and then fallow	Fallow	No migration in March	No data

That farming intensification leads to more rodent problems is an emerging dogma that is vitally important to sustainable agriculture and needs to be examined further. The more we know about the effects of changes in farming systems on rodent population dynamics, the better equipped we will be to not only tackle existing problems but also to anticipate the responses of rat populations to new or proposed agricultural production systems.

Conclusion

This review has considered five beliefs associated with rodent pest biology and management. This is but a subset of the beliefs that have become dogma for rodent managers in both developed and developing countries. This brief review is telling because of the three dogmas for which we had reasonable scientific data, two were rejected. No matter how simple or unrealistic beliefs may appear to a wildlife biologist, it is of paramount importance to make a scientific assessment of those that become dogma. Too often in our experiences in Australia and Southeast Asia, dogmas form the foundation of policies for rodent management adopted by government or agricultural industries. These dogmas are of particular concern because governments often adopt the consequent management approaches to the exclusion of emerging practices or do not invest funds to develop and test alternative management practices because they think they already have the solution.

We end by paraphrasing the concluding statement of Sinclair (1991)—rodent management requires a scientific approach, and the science of rodent management requires managers to conduct experiments.

References

Boonstra, R. and Redhead, T.D. 1994. Population dynamics of an outbreak population of house mice (*Mus domesticus*) in the irrigated rice-growing area of Australia. Wildlife Research, 21, 583–598.

Caughley, G. 1977 Analysis of vertebrate populations. London, Wiley, 234 p.

Krebs, C.J. 1995. Two paradigms of population regulation. Wildlife Research, 22, 1–10.

Krebs, C.J. 2002. Beyond population regulation and limitation. Wildlife Research, 29, 1–10.

Lee, C.H. and Ho, D.T. 1999. Barn owls—field biology and rat control. In: Symposium on biological control in the tropics. Selangor, Malaysian Agriculture and Research Development Institute, 77–81.

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 climate. Journal of Animal Ecology, 70, 761–775.

McNab, J. 1983. Wildlife management as scientific experimentation. Wildlife Society Bulletin, 11, 397–401.

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.

Newsome, A.E. 1969. A population study of house-mice temporarily inhabiting a South Australian wheatfield. Journal of Animal Ecology, 38, 341–359.

Redhead, T.D. 1982. Reproduction, growth and population dynamics of house mice in irrigated and non-irrigated cereal farms in New South Wales. Unpublished PhD thesis. Canberra, Department of Zoology, The Australian National University, 304 p.

Saucy, F. and Schneiter, B. 1997. Juvenile dispersal in the vole *Arvicola terrestris* during rainy nights: a preliminary report. Bulletin Société Vaudoise des Sciences Naturelles, 84, 333–345.

Sinclair, A.R.E. 1989. Population regulation in animals. In: Cherrett, J.M., ed., Ecological concepts. Oxford, Blackwell Scientific Publications, 197–241.

Sinclair, A.R.E. 1991. Science and the practice of wildlife management. Journal of Wildlife Management, 55, 767–773.

Sinclair, A.R.E., Olsen, P.D. and Redhead, T.D. 1990. Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. Oikos, 59, 382–392.

Singleton, G.R. 1983. The social and genetic structure of a natural colony of house mice, *Mus musculus*, at Healesville Wildlife Sanctuary. Australian Journal of Zoology, 31, 155–166.

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. and Petch, D.A. 1994. A review of the biology and management of rodent pests in Southeast Asia. Canberra, Australian Centre for International Agricultural Research, 65 p.

Singleton, G.R. and Redhead, T.D. 1989. House mouse plagues. In: Noble, J.C. and Bradstock, R.A., ed., Mediterranean landscapes in Australia: mallee ecosystems and their management. Melbourne, CSIRO Publications, 418–433.

Singleton, G.R., Sudarmaji and Suriapermana, S. 1998. An experimental field study to evaluate a trap–barrier system and fumigation for controlling the rice field rat, *Rattus argentiventer*, in rice crops in West Java. Crop Protection, 17, 55–64.

Singleton, G.R., Sudarmaji, Tan, T.Q., Jumanta and Hung, N.Q. 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.

Smal, C.M., Halim, A.H. and Amiruddin, M.D. 1990. Predictive modeling of rat populations in relation to use of rodenticides or predators for control. Palm Oil Research Institute of Malaysia, Occasional Paper No. 25, 55 p.

Twigg, L.E. and Kay, B.J. 1994. The effects of microhabitat and weather on house mouse (*Mus domesticus*) numbers and the implications for management. Journal of Applied Ecology, 31, 651–663.