SYMPOSIUM 3: BEHAVIOUR

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How does rodent behaviour impact on population dynamics?

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

Introduction

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

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

Mechanisms of social limitation

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

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

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

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

Surplus individuals

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

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

Territoriality

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

territory size → population density
population density → territory size

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

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

Recruitment

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

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

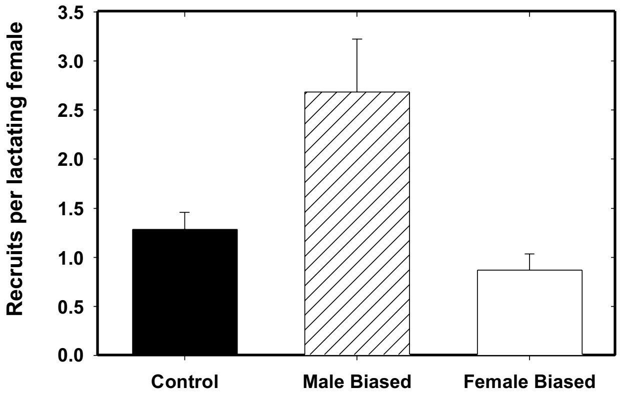

Figure 1. The average recruitment of juvenile *Microtus townsendii* for the summer breeding seasons of 1972 and 1973 on control (unmanipulated), male-biased (80% adult females removed) and female-biased (80% adult males removed) areas. Recruitment was measured as the number of juveniles live-trapped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

Kinship effects

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

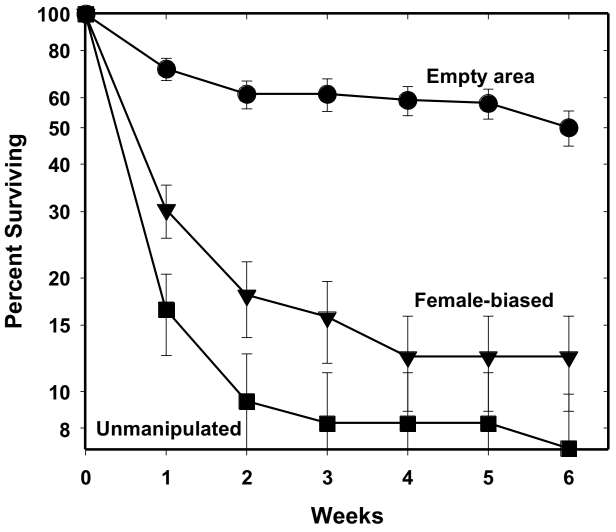

Figure 2. Kaplan-Meier survivorship curves (± 1 se) of juvenile voles (*Microtus townsendii*) introduced in midsummer into three types of areas: an empty grassland from which all adult and sub-adult voles had been removed; an unmanipulated area from which no voles had been removed; and a female-biased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

Infanticide

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

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

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

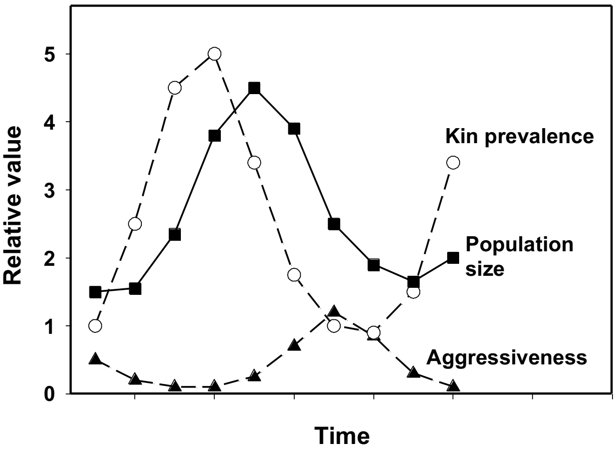

Figure 3. Hypothetical model of the kinship hypothesis of Lambin and Krebs (1991). As the prevalence of kin clusters increases, population density increases with a time lag, with the result of destabilising the dynamics of the population and producing a delayed change in the overall amount of aggression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

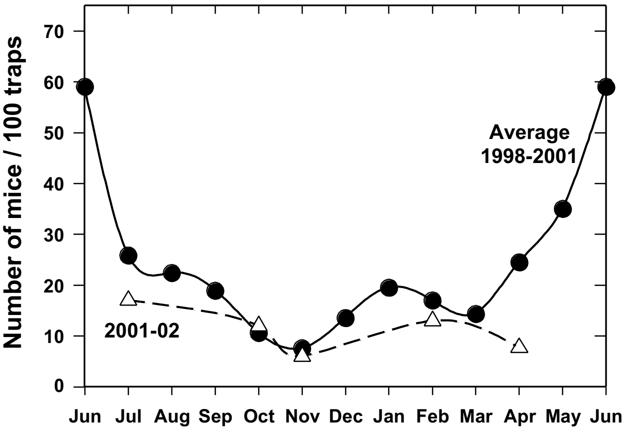

Figure 4. Changes in the abundance of house mice (*Mus domesticus*) in the Murrumbidgee Irrigation Area of New South Wales, Australia, during a series of average years of relatively low abundance. Mice typically decline during the mid- to late-winter months and increase during the summer to reach a peak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

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

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

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

Dispersal

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

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

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

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

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

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

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

Conclusion

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

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Density-dependence and the socioecology of space use in rodents

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

Introduction

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

Female territoriality

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

Mating strategies

Males

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

Females

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

Dispersal and philopatry

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

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

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

Social behaviour and population regulation

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

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

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

Territoriality

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

Dispersal and philopatry

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

Daughters, sexual maturation and reproductive suppression

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

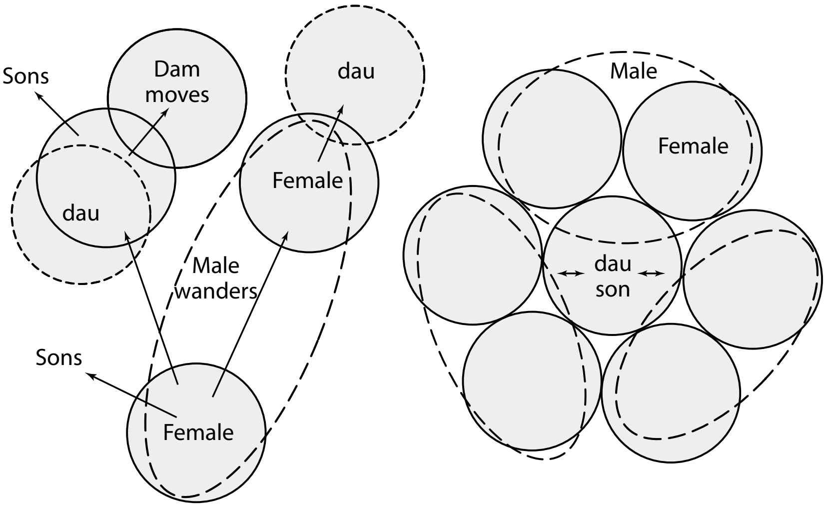

Figure 1. Illustration of spacing and social system of a model rodent, such as many *Peromyscus* and *Microtus* spp. At low density, females (solid circles) are widely spaced and males have large home ranges (dashed ellipses) or wander over large areas to mate with females. Sons disperse relatively far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

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

Reproductive suppression

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

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

The Bruce effect

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

Inbreeding avoidance

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

Infanticide

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

Conclusions

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

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Predator odours as reproductive inhibitors for Norway rats

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

Introduction

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

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

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

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

Materials and methods

Test subjects

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

Reproductive output

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

Determination of implantation sites in utero and post-implantation loss

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

Collection of urine

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

‘Open field’ test with added stress

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

Assay for progesterone and corticosterone

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

Experimental design and protocol

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

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

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

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

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

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

The data were statistically analysed as for the previous experiments.

Results and discussion

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

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

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

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

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

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

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

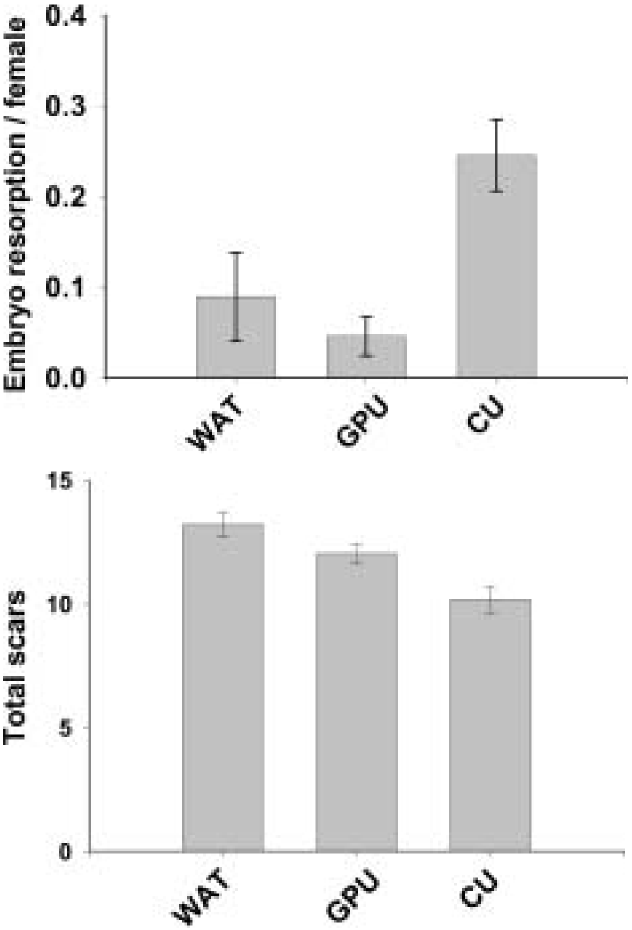

Figure 1. The influence of exposure to urine odours from cats (CU), guinea pigs (GPU) and tap water control (WAT) on (upper) embryo resorption and (lower) implantation in Norway rats. There were no significant differences between the water and guinea pig urine groups.

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

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

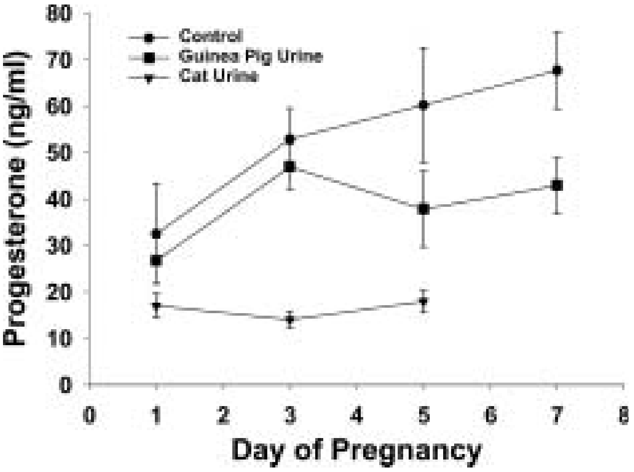

Figure 2. Plasma progesterone levels (mean ± sem) in Norway rats exposed to different urine odours (tap water control, guinea pig urine or cat urine) every other day during gestation.

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

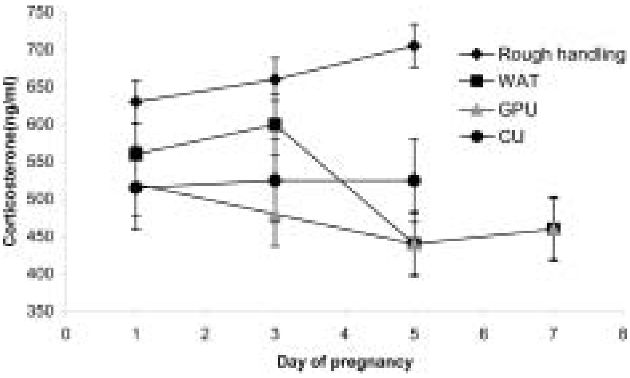

Figure 3. Plasma corticosterone levels (mean ± sem) in Norway rats exposed to urine odours (cat urine, CU; guinea pig urine, GPU; or control tap water, WAT) every other day during gestation or to rough handling in an 'open field' test with added stress.

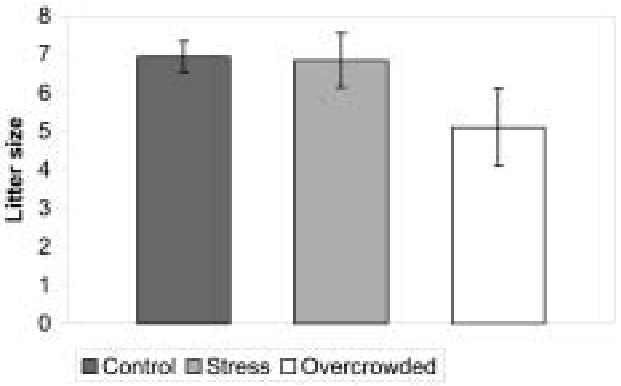

Figure 4. The influence of stress or exposure to urine derived from overcrowded conspecifics on litter size in Norway rats where: control = exposure to tap water every other day during gestation; stress = 'open field' test with added stress; overcrowded = exposure to urine from overcrowded conspecifics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

Conclusion

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

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

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

Acknowledgments

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Boreal vole cycles and vole life histories

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

Introduction

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

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

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

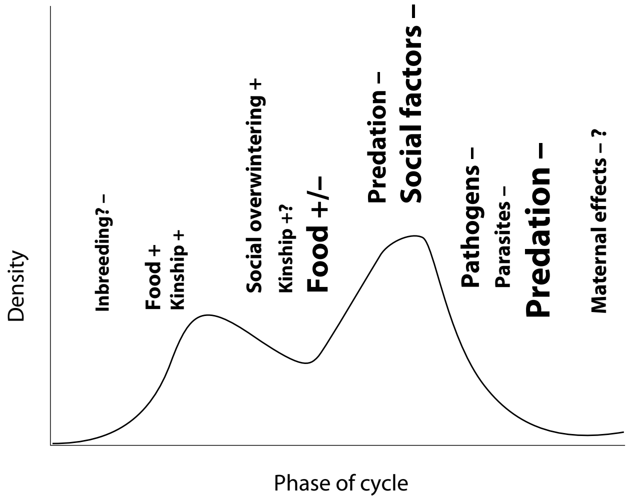

Figure 1. Schematic picture of possible factors having positive effects (+) on population growth rate during different phases of a multi-annual density cycle of voles, or having negative effects (–) on either individual performance or population growth rate during the cycle (after Ylönen 1999). The size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

Fascinating multi-annual cycles

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

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

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

After the decline: the landscape is empty of voles

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

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

Harsh and long winter, but the snow protects

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

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

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

Complicated density-dependent processes during population peaks

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

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

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

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

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

The beast during the decline: the least weasel

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

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

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

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

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

Conclusions

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

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

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

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

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

Introduction

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

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

Reproductive competition

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

Among males

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

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

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

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

Among females

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

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

Mate attraction

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

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

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

Overmarking

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

Conclusions and future directions

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

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

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

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Predator presence affects the reproductive success of prey in outdoor conditions

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

Introduction

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

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

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

Materials and methods

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

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

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

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

Results and discussion

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

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

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

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

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

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

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

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

Conclusion

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

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

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

Introduction

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

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

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

Materials and methods

Experimental animals

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

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

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

Design of experiments

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

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

Urine collection

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

Statistics

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

Results and discussion

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

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

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

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

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

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

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

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

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

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

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

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

Conclusions

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

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

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

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

Introduction

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

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

Materials and methods

Conditions on farms where rats were removed

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

Experiment 1: testing for neophobic behaviour in groups of rats

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

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

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

Experiment 2: testing for neophobic behaviour in individual rats

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

Data analysis

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

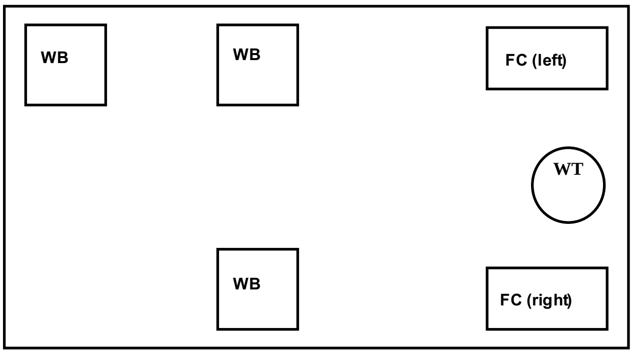

Figure 1. Layout of the experimental room (WB = wooden box, FC = box with feed container inside, WT = water container).

Results

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

Conclusions

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

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

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

Introduction

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

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

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

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

Materials and methods

System description

The automated event-recording system (Francis Scientific Instruments, Cambridge, United Kingdom) was a stand-alone system, capable of functioning in remote locations and after modification was capable of withstanding extremes of weather. It consisted of five main components: a PIT tag, a sensor or antenna unit, a decoding unit, a multi-channel data-logger unit and a power source (Figure 1). The system was designed for Identichip brand PIT tags by 4D Technologies (0.07 g, 11.4 mm long by 2.1 mm diameter, supplied by Veterinary Marketing Network, Wahroonga, New South Wales, Australia). Identichips use Zoodiac H4005 microchips by Sokymat that are energised at the standard International Standards Organisation (ISO) frequency of 134.2 kHz.

For ease of insertion into burrows, rod-shaped antennae measuring 50 mm long and 11 mm diameter were designed and constructed for this study. Each rod-antenna coupled to a decoding electronics box that served as a reader. Antennae and electronics boxes were constructed incorporating weatherproof casings. Four readers were connected to a four-channel data logger via 25 m long cables (cables may be up to 100 m in length without loss of signal). The data-logger and four readers were powered by one 75 Ah 12 V deep-cycle battery that lasted up to 8 days of continual use between recharges. Both battery and data-logger were housed in a ventilated shelter that could be moved between sites. Records stored on each data-logger were downloaded onto a portable IBM compatible computer and records could then be interrogated using commonly available spreadsheet or database software. Four such units were used, bringing the total number of readers to sixteen.

For the system to record the activity of a mouse, the PIT tag must be within the generated electromagnetic field (approximately 50 mm from the antenna) for at least 25 ms (Prentice et al. 1990). If two or more tags are within the field, only the strongest reply signal will be detected with RF-ID technology. The interval between records of detected PIT tags with this system is less than 2 s and records are timed in increments of 1/16th second (62.5 ms). One ‘event’ was considered to encompass the period from when a mouse entered the detected range of the antenna to when it left. In other words, records with the same PIT tag code were considered part of the same ‘event’ if an interval between any two successive records was no greater than 2 s. The duration of each event was determined as the interval from the beginning of the first record to the end of the last record.

Field study

The monitoring study was conducted in the agricultural landscape surrounding the Mallee Research Station, Walpeup, in north-western Victoria, Australia (35°07.5'S, 142°00.5'E). This region has a Mediterranean-type climate with typically cold, wet winters and hot, dry summers. Mice were live-trapped using Longworth traps at the interface between a wheat crop, its boundary stock fence, and an adjacent pasture field. This was conducted at 6 sites, each 100 m long, for 4 consecutive nights on 12 occasions from October 2000, early in the breeding season, to peak population abundance in June 2001. PIT tags were injected subcutaneously by lifting a scruff of skin between the shoulder blades, inserting the 12-gauge needle (3 mm diameter) behind the ears pointed slightly downwards and towards the posterior of the animal. The trigger of the inserter tool was then squeezed, forcing the PIT tag into the space between the skin and the body wall. PIT tags and needles were sterilised in 70% ethanol and dried before use. No anaesthetic or suture was required and animals regained normal activity immediately. A hand-held reader was used to verify that PIT tags functioned after implantation and to record the PIT tag number

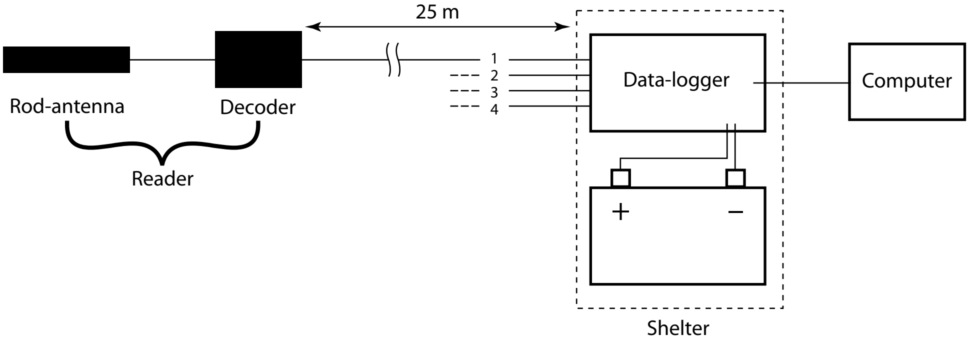

Figure 1. Schematic layout of the automated event-recording system.

of newly captured and recaptured animals. Early in the study, animals with new PIT tags were held for several minutes to ensure the tags were not lost. However, because tags were always retained within this time period, animals were subsequently released at the point of capture without being detained. Tagged animals ranged in body mass from 4.4 g to 35.0 g.

Burrows were monitored with the event-recording system for four consecutive nights immediately after each trapping period at each site. Trapping was never conducted while burrows were monitored. Open burrows with signs of activity were selected for monitoring. The entire antenna was positioned inside each burrow entrance (entrance diameters were approximately 50 mm) then pressed into the base and covered with soil. Therefore, only mice passing into, out of, or deeply investigating a burrow would be recorded. If there were more active burrows than readers at a site, readers were relocated so that as many burrow entrances were monitored within a 4-day period as possible. Each burrow entrance was monitored for at least 24 consecutive hours.

The effectiveness of the system for detecting tags that passed within range of the antennae was assessed by video observations between January and April 2001. A Sony TRV99E video camera with inbuilt infrared light source and time stamp was set on a tripod with a view of the burrow entrance and antenna approximately 30 mins before official sunset. The camera was left to continuously record for 3 hours when mice became active. Events viewed on video were compared to events recorded by the system at the same time and location.

Statistical methods

A two-tailed Kolmogorov–Smirnov goodness-of-fit test was used to determine if distributions of times of activity for each sex belonged to populations with the same distribution.

Results and discussion

PIT tags proved to be an effective marking and identifying technique for mice and are seen to be especially beneficial for long-term studies. Of 1452 PIT tags implanted into mice, 740 were recovered by trapping marked mice. Of the mice recaptured, 13 were missing their PIT tag (1.8%) and 1 animal had a replacement PIT tag missing. There were no observed tag failures. This loss rate is lower than that reported for laboratory mice (5%, Rao and Edmondson 1990), free-ranging *Spermophilus townsendii* (5%, Schooley et al. 1993) or free-ranging voles, *Microtus ochrogaster* and *M. pennsylvanicus* (5%, Harper and Batzli 1996). In the current study, a higher proportion of PIT tags were retained as the handler gained experience in the implanting technique. Of the 14 tags found missing, 8 were inserted by a handler who had inserted less than 200 PIT tags.

The temporal and spatial activity of mice was successfully recorded at multiple burrows. The automated event-recording system detected the activities of 1123 mice on a total of 37,199 occasions ($\bar{X}$ = 33.1 events per animal) over 8 months. Mice were predominantly nocturnal, exhibiting activity throughout the night with the greatest proportion of their activity in the first 2 h after sunset (Figure 2). Event times have been presented relative to sunset because the length of each night varies across the year. Males and females were active in a significantly different distribution of times (D_{max} = 0.069, D_{crit} = 0.014, $p < 0.05$). 26% of male activity versus 20% of female activity was concentrated in the first 2 h after sunset.

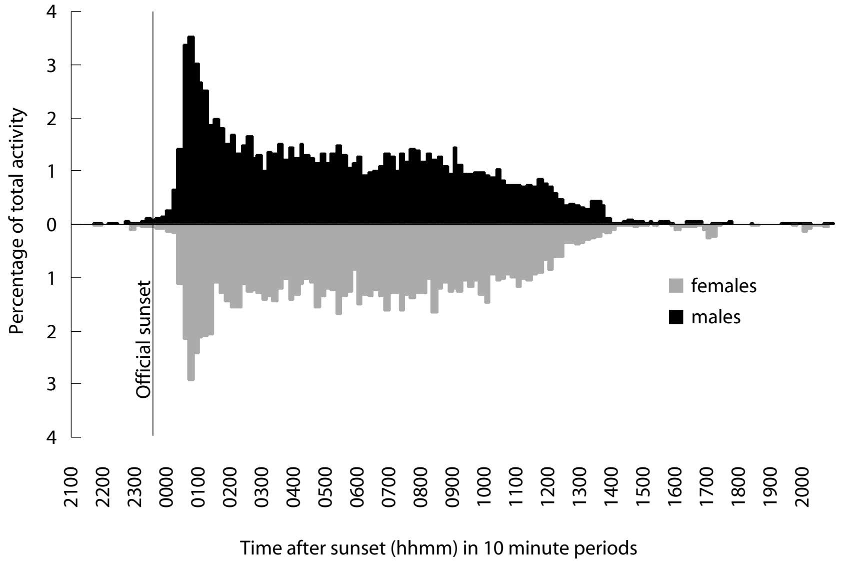

Figure 2. Percentage of the total activity across 24 h that occurred in each 10 minute interval after official sunset for male (black bars) and female (grey bars) mice (*Mus domesticus)* between October 2000 and June 2001. The total number of events recorded was 19,257 for males and 17,942 for females.

Potential interactions between mice may also be observed with this system. Burrow activity was monitored for 1148 reader-nights and activity was recorded at 295 burrows. These data will be analysed in a companion paper in relation to temporal changes in the demography of the population. We found that the number of different individual mice that entered, exited or investigated the same burrow within 24 h ranged from 1 to 44 (median = 3.5, $\overline{X}$ = 4.8; Figure 3). Furthermore, individual mice were detected visiting between 1 and 19 different burrows within a distance of 100 m over a 96 h period (median = 3, $\overline{X}$ = 3.8; Figure 4). We detected a large number of social interactions using this system. This daily activity profile reflects those of previous studies of confined mice. In captivity, many nest boxes are visited by several individual mice per night, either as a territorial patrol or for seeking potential mates (Crowcroft and Rowe 1963). This may have a profound influence on gene flow through the population (Singleton and Hay 1983).

Automated event-recording systems based on PIT technology provide detailed information on the temporal and spatial activity patterns of marked individuals. Such information may be obtained by radio-tracking, however at a far coarser level and not to the same degree of accuracy as PIT technology (activity at one particular burrow entrance to the nearest $1/16^{th}$ second) nor for the same study duration (PIT tags are not limited by battery life). Importantly, studies using automated PIT technology can monitor the activity of a much larger proportion of the population than radio tracking due to the lighter weight of PIT tags, the lower cost of each tag and the relatively less amount of effort required to collect data. Moreover, any animal greater than 4.4 g can be monitored with these systems, whereas there is a weight limitation of 13 g for

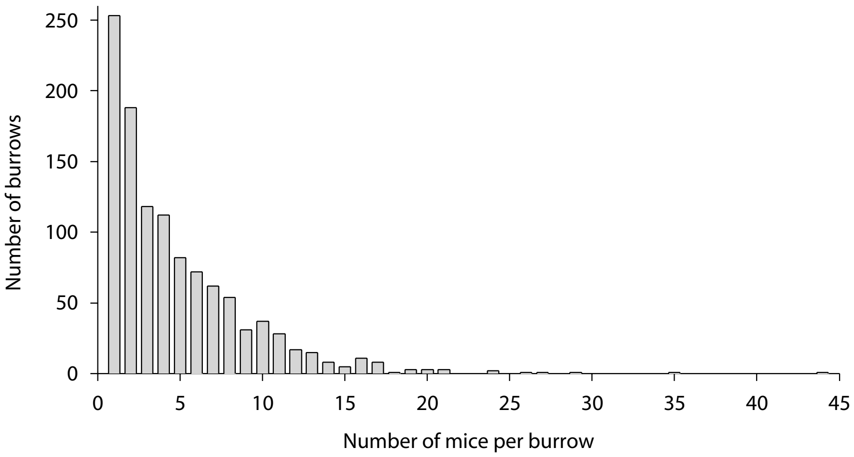

Figure 3. Number of different mice (*Mus domesticus)* tagged with a passive integrated transponder (PIT) tag that visited the same burrow entrance during a 24 h period. The total number of 24 h periods was 1114. Only visits by individuals tagged with a PIT tag were monitored. Mouse density was approximately 100 to 500 mice per hectare during the study

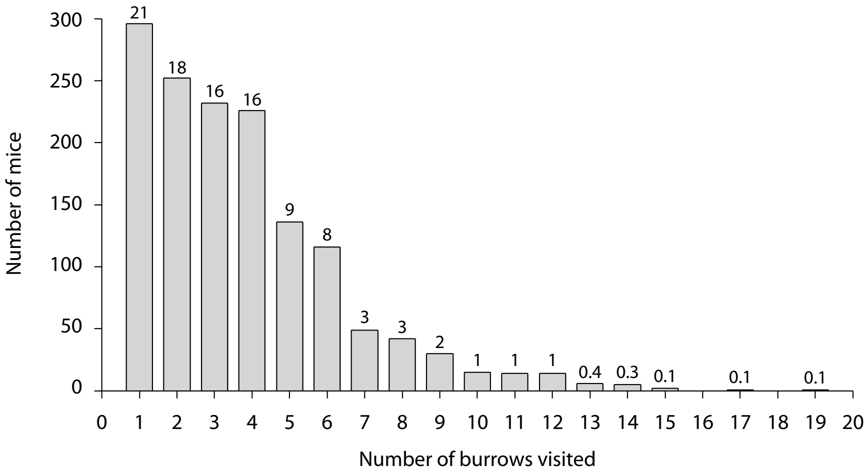

Figure 4. Number of burrows visited by one individual over a 96 h period. The percentage of total monitored mice visiting multiple burrows is indicated above each column. The total number of 96 h periods was 66; the total number of mice monitored was 1437.

mice with current radio-tracking technology (Chambers et al. 2000). Consequently, PIT technology presents the opportunity to monitor important population events such as juvenile dispersal in mice. PIT technology may also enhance a trapping study because it is not necessary to recapture animals to monitor their activity. Individuals within a population that have a low probability of recapture may continue to be monitored for their presence and movements within the study area. In this case study, we were able to monitor the activity of an additional 396 mice that were never recaptured but were detected with the event-recording system. We were also able to repeatedly detect the same individual mice on up to 22 different nights over a period, in one case, of almost seven months. Hence, PIT technology will enable further assessment of mouse activity and of any differences in the trappability of mice both between seasons and between habitats.

In addition, an alternative arrangement of this system can permit the direction of movement to be determined by placing two antennae in series along the path of movement (for examples, see Brannas et al. 1994; Burns et al. 1997). Assuming an animal does not return by some other route, the sequence of successive events will reveal the direction of an animal’s movement. The system was sensitive enough to detect an interval between events of 62.5 ms or greater, however to prevent the two antennae from interfering with the electromagnetic field generated by each, they must be placed at least 200 mm apart. We did not use two antennae in series to determine the direction of movement in this study for two reasons. Firstly, antennae could not be forced 200 mm into mouse burrows due to frequent bends in the tunnels, and secondly, two antennae in series effectively halved the number of burrows that could be monitored at one time. Hence, PIT technology is capable of monitoring similar, yet at the same time quite distinct, information when compared to radio-tracking. When choosing between these technologies, though, it is worth considering that although PIT tags are far less expensive than radio transmitters, the high initial cost of the PIT reader system makes this system comparatively inexpensive only when large numbers of animals will be monitored.

The most significant drawback of the event-recording system is that animals not marked or that have lost their PIT tags are not recorded. The extent of this error will be a function of the trappability, and/or the intensity of trapping effort, of the study population because the rate of tag loss was relatively low. This error was estimated for the period between January and April 2001 by observing activity at 15 monitored burrows for 43 h with a video recorder. The assumption was made that the animals visiting burrows represent a random sample of the population. Video observations revealed that the system was reliably detecting individuals marked with PIT tags, including those moving at great speed and when multiple individuals passed in rapid succession. The activities of mice were recorded 398 times on video within range of the antenna, however only 31% of those events were of mice marked with a PIT tag. It appears that although the system was accurately recording the activities of marked individuals, during the video observation periods a significant proportion of the population was being missed.

Some technical problems were experienced with this automated event-recording system. Firstly, some reader errors were detected, though most were easily accounted for. Most were events containing identification codes with non-numeric characters or zero values. Occasionally, legitimate codes were recorded that did not correspond to PIT tags used to mark mice in the study. The causes of these errors were unknown. Secondly, metal objects interfered with the electromagnetic field generated by the antennae reducing the range of detection. This problem was isolated to large metal objects like fence posts that were within approximately 50 mm of an antenna. Lastly, the data-loggers provided with this system were not waterproof and were sensitive to extremes in temperature and humidity. Therefore, ventilated shelters were necessary to keep the data-loggers and batteries dry and cool. With these modifications, the system continued to function well in ambient temperatures ranging from –1.2 to 43.7°C as well as a maximum 24 h precipitation of 18.4 mm.

Conclusion

The event-recording system with PIT technology as described can monitor the identity, timing and location of activity for a large proportion of a population at fine temporal and spatial scales. Automated systems allow researchers to collect data over extended periods with relatively little effort. Although this system was designed to monitor activity patterns and potential interactions between individuals at burrow entrances, many additional applications exist for this technology. For example, marked individuals can be detected at various focal points of activity such as nests, resting locations, regular paths for movement, latrines, food sources or perhaps bait locations. Any location of interest to the researcher may be used. The direction of movement to or from these points of interest can also be determined, allowing the researcher to determine the location of the individual relative to the antennae. Interactions at these points may be detected both within and between target species. Furthermore, PIT technology is still developing. The reader range is increasing with either larger tags or battery-assisted tags (for examples, see Hutching and Harris 1996; Boarman et al. 1998). The technology may also be integrated with other technologies such as automatic scales (Boisvert and Sherry 2000), temperature probes or infrared motion detectors. The applications found for this technology and the insights gained with its use will only increase.

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Predation risk and behaviour during dispersal: implications for population dynamics of rodents

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Abstract. Models of predation risk assume that animals that are more exposed to predators are at a higher risk of mortality. Young animals may behave in a more 'risky' way than older animals, thereby exposing themselves to a greater degree of risk. But do such behaviours have implications for the population dynamics of a prey species? I explored this idea for juvenile arctic ground squirrels in the boreal forest at Kluane, north-western Canada, from 1992 to 1995. First, I tested whether radio-collared juvenile squirrels that moved further, on average, between regular radio-telemetry fixes during dispersal had higher mortality from predation than those with shorter inter-fix distances. Results supported this hypothesis: (1) movement rates of squirrels that survived to hibernation were significantly lower than movement rates of squirrels that died from predation and (2) juvenile males, which had faster movement rates, were more likely to die from predation than juvenile females. Second, I did a sensitivity analysis using a stage-based simulation model of the population dynamics of ground squirrels to determine which of eight demographic parameters had the strongest effect on the instantaneous rate of population increase (r). Survival of adult and juvenile females had the strongest influence on r in the model, which concurred with a strong relationship between observed survival of juvenile female squirrels and rates of population increase at Kluane from 1992 to 1995. Individuals with behaviours that expose them to predators (such as greater movement rates) increase their chances of mortality. Furthermore, such behaviours can have a strong effect on a prey species' population dynamics, a result that explains the observed multi-annual fluctuation in arctic ground squirrel populations at Kluane, synchronous with the 10-year snowshoe hare cycle.

Introduction

Models of predation risk assume that animals that spend more time exposed to encounters with predators have a higher risk of mortality (Sinclair and Arcese 1995). Animals are assumed to be able to assess the potential risk of being killed by a predator, and alter their behaviour to reduce this risk (Hik 1995). However, behavioural responses to predation risk may change with sex, age, and reproductive condition. For example, young animals may be especially vulnerable to predation because they may not have learned appropriate strategies to avoid predators. Can these observed differences in behaviour be linked to mortality from predation, and subsequently to population dynamics?

Arctic ground squirrels (*Spermophilus parryii plesius*) are a burrowing, ground-dwelling, polygynous sciurid rodent inhabiting much of northern Canada, Alaska, and Siberia. They are found primarily in open meadows and tundra, but part of their range includes boreal forest at Kluane in the south-western Yukon Territory (61°N, 138°W), where the population dynamics of this species are closely linked to the 10-year snowshoe hare (*Lepus americanus*) cycle (Krebs et al. 2001). In terms of biomass, arctic ground squirrels are the second most common herbivore at Kluane, providing an extremely important food source for predators during the summer months (May through to August or September). The main predators of squirrels are lynx (*Lynx canadensis*), coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), and great horned owls (*Bubo virginianus*). Squirrels hibernate for about 7 or 8 months during winter (October through April), so during the short active season, squirrels are primarily concerned with reproduction and fat storage for the coming winter. Juvenile squirrels born in the active season remain in a natal burrow for about 28 days before emerging, and have only a few months to disperse from their natal area, establish a new territory, and gain enough weight to survive to spring.

I measured movement rates and behaviour of dispersing juvenile squirrels in order to quantify the level of risk (exposure to predators) for each individual squirrel during dispersal. Exploratory movements made during dispersal differed between male and female squirrels (Byrom and Krebs 1999). Juvenile males moved in longer increments, whereas females made shorter movements. Here I examine the consequences of these two general types of dispersal behaviour by relating them to a known risk of predation. I also examine the consequences for the population dynamics of the species as a whole, and link this to observed changes in squirrel numbers at Kluane during a snowshoe hare cycle.

Methods

Study sites and field methods

Dispersal movements of 172 juvenile arctic ground squirrels were studied on three 9 ha sites (see Byrom and Krebs 1999 for a description of study sites at Kluane) from 1993 to 1995, and one site from 1992 to 1995. Squirrels were radio-collared on experimental and control sites, but there were no differences in movement rates between treatments or years (A. Byrom, unpublished data) so data were pooled for this paper. Expandable radio-collars were fitted to juvenile squirrels after emergence from the natal burrow at 35–40 days of age and squirrels were radio-tracked through to hibernation (from mid-June to mid-August each year). Each squirrel was radio-tracked by an observer on foot with a hand-held yagi antenna every 2 days. Predation was deemed a relevant cause of death because 97% of radio-collared squirrels died from predation (Byrom and Krebs 1999).

Statistical analyses

For each squirrel, the distance between each radio-telemetry fix and the subsequent fix was recorded using a Trimble Basic global positioning system (GPS) (fix locations were differentially corrected using a base station at Kluane Lake Research Station). Movement rates were estimated by calculating the average distance between fixes for each squirrel. Movement rate data were examined for normality and homoscedasticity and transformed where appropriate. Data that satisfied these assumptions were analysed using conventional parametric tests. Data that violated assumptions of normality even after transformation were analysed using nonparametric tests (Sokal and Rohlf 1995). Movement rates of squirrels that were lost (presumably because they moved far off the study area and the transmitter signal could not be heard) were treated separately.

Simulation model: sensitivity of *r* to demographic parameters

A stage-based simulation model of arctic ground squirrel populations at Kluane (created in Microsoft Excel 5.0) was used to determine the sensitivity of the instantaneous rate of population change (r) to eight demographic parameters (litter size, survival of juveniles below ground, survival of juveniles and adults during hibernation [over winter], survival of adult males and females during the active season [summer], and survival of juvenile males and females during the active season). The annual cycle of activity and hibernation was compartmentalised into 12 one-month periods, with the population densities of adults and juveniles calculated monthly and multiplied by a survival parameter. Juveniles that survived over winter were recruited into the adult population at the beginning of the active season each year. Squirrel population density was calculated in spring each year by adding the separate population densities of adult males and females. The instantaneous rate of population change was calculated as $r = \ln[N(t+1)/N(t)]$. To measure sensitivity of r, each parameter was varied individually while all others were held constant. Parameter values were increased or decreased, for example by ±10%, ±20%, and ±30%. In some cases, it was necessary to change parameter values by 1% increments. Each simulation was run for 20 years or until r reached an asymptote.

Results and discussion

Movement rates of juvenile arctic ground squirrels

All movement rates presented refer to the distance moved by squirrels every 2 days. Juvenile arctic ground squirrels that survived to hibernation moved shorter distances between fixes than squirrels that were killed by predators or were lost during dispersal (Figure 1). The average distance between fixes for surviving juveniles was 51.8 ± 4.6 m (n = 97) (mean ± se) whereas for juveniles that died the average distance between fixes was nearly twice as great, 86.2 ± 11.4m (n = 43). This difference was significant ($t = -3.36$, df = 138, $p < 0.0001$).

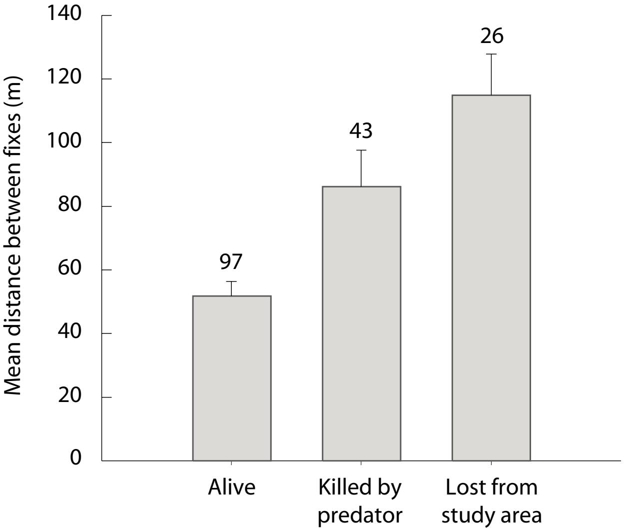

Figure 1. Movement rates (measured as the mean distance between radio-telemetry fixes taken every 2 days, ± se) of juvenile arctic ground squirrels that survived to hibernation in their first active season, squirrels that were killed by predators, and squirrels that were lost (radio-transmitter could no longer be heard and presumably squirrels moved far off the study area). Numbers show sample sizes in each category.

Juvenile males (whether they survived or were killed by predators) had faster movement rates than juvenile females (males: 100.7 ± 9.0 m [n = 69]; females: 47.5 ± 3.9 m [n = 96]). This difference was significant (t = 1.97, df = 162, p = 0.000). Overall, juvenile males that survived moved an average of 93.9 ± 15.5 m (n = 22) between fixes, while juvenile females that survived moved an average of 39.4 ± 2.5 m (n = 75). Juvenile males that were killed by predators moved an average of 105.8 ± 10.9 m (n = 47), while juvenile females that were killed by predators moved an average of 76.5 ± 13.8 m (n = 21). Differences between males and females were significant (surviving squirrels: Welch's t = 3.75, df = 24, p = 0.001; squirrels killed by predators: t = 2.35, df = 66, p = 0.022). Movement rates of juvenile males that survived did not differ significantly from those of males that died (Welch's t = –1.14, df = 32, p = 0.26), but movement rates of juvenile females that survived were significantly lower than those of females that died (Welch's t = –3.22, df = 29, p = 0.003).

The results reported here support the hypothesis that faster movement rates result in increased exposure to predators. Models of predation risk assume that animals that spend a greater proportion of time at risk are more likely to die from predation, but an empirical link between risky behaviour and mortality has rarely been reported. Fitzgibbon (1994) described aspects of Thompson's gazelle (*Gazella thomsoni*) behaviour that increase their susceptibility to predation, such as being more solitary, less vigilant, and more likely to be found at the edge of a group. Sommer (2000) reported lower survival in male rats (*Hypogeomys antimena*) as a result of males moving greater distances and encountering predators more frequently. Holekamp (1984) suggested that frequent exploratory excursions by juvenile Belding's ground squirrels (*Spermophilus beldingi*) might enable individuals to familiarise themselves with an area before settling permanently (although she did not provide an empirical link between survival and movements). Results of this study focus on specific aspects of rodent behaviour during dispersal that predispose individuals to higher rates of predation, and provide a plausible mechanism linking the behaviour of individuals to population-level consequences.

Sensitivity of *r* to demographic parameters: implications for population dynamics

In the model, r was highly sensitive to survival of female squirrels (both adults and juveniles) during summer. For example, a 10% increase in summer survival of juvenile female squirrels resulted in a 13% increase in r. Comparable changes in r with a 10% increase in parameter values were: adult female survival, 37%; survival of adults over winter, 5%; litter size, 4%; survival of juveniles pre emergence in summer, 4%; survival of juveniles over winter, 4%; survival of adult males in summer, 1%; and survival of juvenile males in summer, 0%. This result makes intuitive sense. Female squirrels influence population trends in two ways: directly (higher survival means greater population density) and indirectly (through recruitment). Coupled with the polygynous social structure of arctic ground squirrels, the observed high mortality of female squirrels with the fastest movement rates would create strong selection pressure on females to remain close to their birthplace whenever possible. Conversely, male survival had less overall effect on r. This suggests that the potential fitness benefits for males that successfully establish new territories must be relatively high in order to outweigh the chance of predation as a result of faster movement rates.

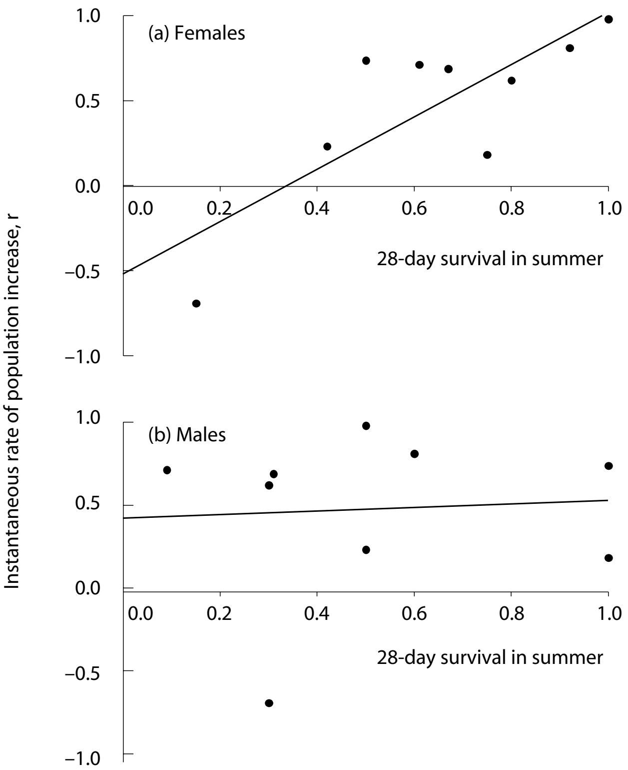

Figure 2. Instantaneous rates of population increase (r; measured annually in spring each year) for (a) juvenile female ground squirrels and (b) juvenile males as a function of survival per 28 days in summer. Rates of increase were measured in each of 3 years at one site (1992/93, 93/94, and 94/95) and in each of 3 years at three sites, giving a total of nine data points.

The findings from the model were verified by plotting observed rates of population increase of arctic ground squirrels from 1992 to 1995 as a function of summer survival of juvenile female and male squirrels (emergence from the natal burrow to hibernation, estimated using Kaplan–Meier survivorship) (Figure 2). There was a strong significant relationship between survival and r for females (r^2 = 0.64, F = 12.29, df = 7, p = 0.01) but not for males (r^2 = 0.004, F = 0.03, df = 7, p = 0.87). This result may explain the observed synchronicity between arctic ground squirrel populations at Kluane and snowshoe hare population cycles. With the decline in snowshoe hare numbers, predation pressure on alternative prey increases dramatically, and arctic ground squirrels provide a substantial biomass of alternative prey during summer (Krebs et al. 2001). Rates of population increase in arctic ground squirrels were lowest when predator numbers were highest (Byrom et al. 2000) and predation during summer was largely responsible for the observed decline in arctic ground squirrel populations (Boonstra et al. 2001).

Conclusion

This study is one of the first to confirm the common assumption of predation risk models that individuals that expose themselves to risk will suffer higher losses from predation. Juvenile arctic ground squirrels with faster exploratory movement rates during dispersal were more likely to die from predation than squirrels with lower rates of movement. The behaviour of individual squirrels and the resultant effect on their survival (through predation) can be linked to observed cyclic fluctuations in squirrel numbers entrained by predators at Kluane during a snowshoe hare cycle. The link between behaviour of individual rodents and their population dynamics has implications for management of rodents both as pests and as threatened species.

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Strategies of aggressive fighting reflect degree of sociality in three species of gerbils

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Abstract. Animals living in communities should develop non-injurious ways of conflict resolution. A comparative study of aggressive fighting strategies in closely related species provides a good approach to investigating this statement. In the present study, we observed intraspecies male–male conflicts in a neutral arena for three species of gerbils, graded on their levels of sociality, from the least social, the pallid gerbil, *Gerbillus perpallidus*, to the much more social Mongol gerbil, *Meriones unguiculatus*, and great gerbil, *Rhombomys opimus*. From videotapes, we estimated winner–loser distances, and the duration of interactions and non-aggressive intervals between them, using 1 s scan sampling method. We found that patterns of aggression showed prominent interspecies differences. Great gerbils used a strategy of conflict delay—using, for the most part, very weak distant threats and standing immobile in static postures for a long time, with rare short blocks of contact threats or overt aggression. Mongol gerbils used a strategy of quick, short interactions, often in tactile contact. Rivals utilised threat postures or moved simultaneously, keeping the inter-individual distance unchanged. Pallid gerbils showed a very hard strategy of fighting, characterised by high levels of overt aggression, with fast changing of both distances between individuals and behavioural actions. We concluded, that male–male fighting strategies are in good agreement with species-specific social organisations in these gerbils.

Introduction

Gerbils (Gerbillinae) are a compact group of rodents, living in desert and semi-desert areas of Asia and Africa. This group has important agricultural and epidemiological significance, because they live on grazing areas, forage on grass and seeds, and are hosts of epidemical diseases that affect both humans and livestock. Gerbils represent a uniform group, possessing similar morpho-physiological adaptations for living in arid environments (Pavlinov et al. 1990). However, different gerbil species show high variability in their use of habitats, construction and use of hides, food, day/night activity and spatial-ethological structure. The discrepancy between similar external appearance and similar physiological adaptations to living in arid conditions, on the one hand, and high variability in social structures, on the other hand, makes this group very promising for comparative behavioural research, such as the evolution of sociality (Goltsman et al. 1994).

Extraction of stereotyped postures from behavioural observations is not the best approach to revealing interspecies differences, because most of important behaviours may be described only by using parameters of the entire behavioural continuum (Golani 1976, 1992; Moran et al. 1981). In our study, gerbils' ethograms are very similar, and behavioural differences are found mostly in kinematic characteristics, such as duration of behavioural actions, speed, and acceleration of speed during movements (Goltsman and Borisova 1993; Volodin and Goltsman 1998). In the present study, we tested aggressive conflicts in three species of gerbils differing in sociality—two social species, the great gerbil, *Rhombomys opimus*, and Mongol gerbil, *Meriones unguiculatus*, and a solitary species, the pallid gerbil, *Gerbillus perpallidus*, in order to compare differences in aggressive behaviour in these species in relation to their sociality.

Materials and methods

We videotaped intraspecies male–male conflicts in a neutral arena. We conducted 21 tests for the great gerbil, 26 tests for the Mongol gerbil, and 20 tests for the pallid gerbil. All of the 15 great, 26 Mongol and 20 pallid male gerbils were adult, captive-born animals, housed with 1–2 females or with females and their offspring (Volodin et al. 1996). Tests were made among unrelated and unfamiliar conspecifics in a plastic enclosure 76.5 cm × 58 cm × 65 cm.

A short time after the beginning of the test, one of the males becomes the winner and the second one becomes the loser, and this asymmetry is retained until the end of the test (Goltsman and Volodin 1997). From videotapes, we measured winner–loser distances, and the duration of aggressive interactions and non-aggressive intervals between them using a 1 s scan sampling method (Altmann 1974). In total, 34,022 s for great gerbils, 29,856 s for Mongol gerbils and 15,308 s for pallid gerbils were sampled. Thus, we analysed 355, 781 and 331 aggressive interactions and 340, 760 and 301 non-aggressive intervals for the great, Mongol and pallid gerbils, respectively.

Results

In all three species, male–male conflicts occurred as aggressive interactions interspersed by non-aggressive intervals (Figure 1). In turn, aggressive interactions could be broken down into distant threats, contact threats, and fighting and chasing.

The percentage of time spent in aggressive interactions decreases progressively in the order great > Mongol > pallid gerbils (Figure 2). However, the severity of the aggressive interactions showed a reversed pattern: fighting and chasing and contact threats took more time in the pallid gerbil in comparison to the Mongol gerbil, and more time in the Mongol gerbil in comparison to the great gerbil, which had the maximum percentage of distant threats. All the differences were significant ($p < 0.001$, White *t*-test).

Aggressive interactions were significantly longer in the great gerbil than both in the Mongol and in the pallid gerbils ($p < 0.001$, Mann–Whitney *U*-test), whose duration of aggressive interactions did not differ (Figure 3). Non-aggressive intervals were the shortest in the Mongol gerbil (Figure 3).

Distant threats were longest in the great gerbil, intermediate in the Mongol gerbil, and shortest in the pallid gerbil and all differences were significant ($p < 0.001$, Mann–Whitney *U*-test; Figure 2). The duration of contact threats and fighting and chasing were more similar between species, but the difference was still significant between the Mongol and pallid gerbils ($p < 0.01$, Mann–Whitney *U*-test) (data not shown).

During aggressive interactions, the great gerbil usually keeps a distance from 0.1 to 0.75 body lengths from his opponent, whereas the Mongol and pallid gerbils maintain a shorter distance of tactile contact. All the differences were significant ($p < 0.001$, White *t*-test) (Figure 4).

Figure 2. Total percentage of time the gerbil species spent displaying different behaviours during aggressive interactions—fighting and chasing, contact threats and distant threats—and non-aggressive intervals between aggressive interactions.

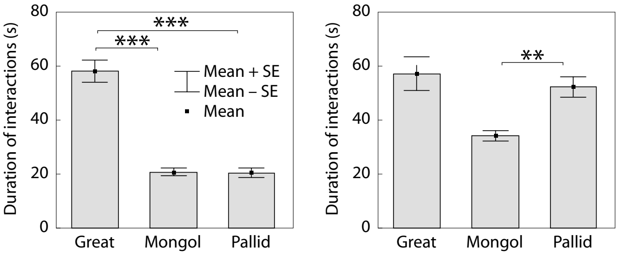

Figure 3. Duration of aggressive interactions and non-aggressive intervals (mean ± se) in the three gerbil species, where *** = $p < 0.001$; ** = $p < 0.01$.

Distance changing rates during non-aggressive intervals were similar in all the three species. In contrast, the distance changing rates during aggressive interactions did differ significantly between the species and graded from the most in the pallid gerbil, through intermediate in the Mongol gerbil, to the least in the great gerbil ($p < 0.001$, Mann–Whitney *U*-test) (Figure 5). It is interesting that in the great gerbil, the distance changing rate was much lower during aggressive interactions than during non-aggressive intervals ($p < 0.001$, Wilcoxon *t*-test); in the

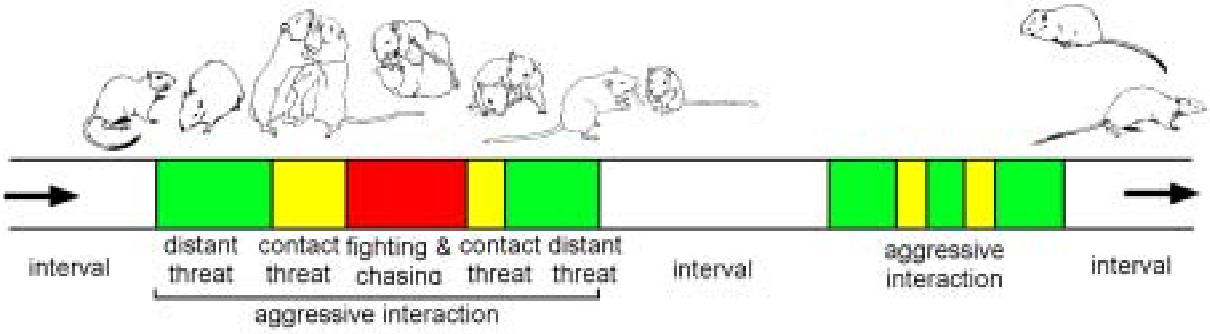

Figure 1. Schematic illustration of a sequence of actions among combatants during male–male conflicts in the three gerbil species observed in the study. Gerbil postures (from left to right): lateral threat posture (distant threat); boxing (contact threat); fighting; displacement (contact threat); frontal threat posture (distant threat); out of aggressive interaction (non-aggressive interval).

pallid gerbil, the relations were reversed ($p < 0.05$, Wilcoxon t-test); and in the Mongol gerbil, the rates were similar in both the cases.

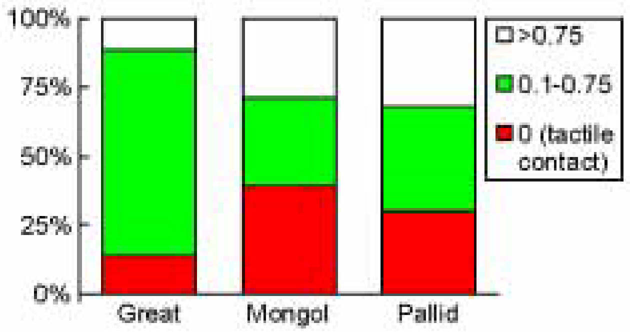

Figure 4. Total percentage of time keeping different winner–loser distances during aggressive interactions in the three gerbil species. Units of body length are the measure of distances.

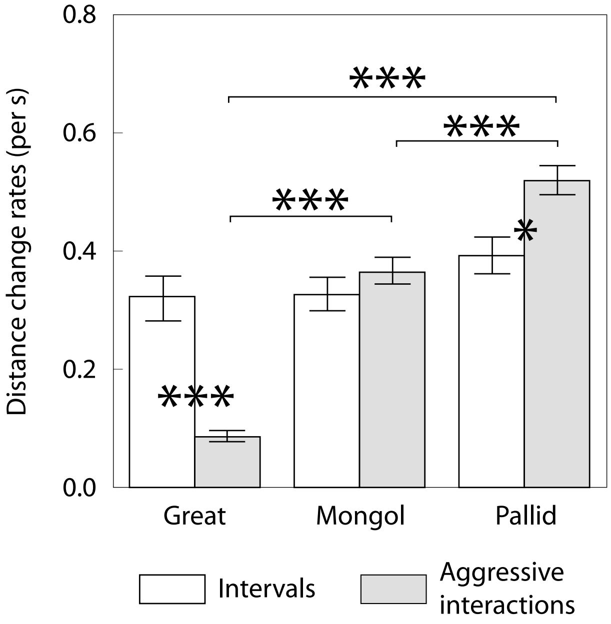

Figure 5. Rate of distance change during non-aggressive intervals and aggressive interactions (mean ± se) in the three gerbil species, where *** = $p < 0.001$; * = $p < 0.05$.

For the great gerbil, aggressive interactions were characterised by long immobility of both combatants, keeping a constant distance apart without body movement (static keeping of a constant distance apart) (Figure 6). In total, the great gerbils remained immobile more than 80% of the time during interactions. The aggressive strategy of Mongol gerbils was intermediate between the great and pallid gerbils: 39% of the time they were immobile, 22% keeping a constant distance by using synchronised movements (mobile but keeping a constant distance apart), and 39% of the time in changing the distance apart. In contrast, pallid gerbils mainly 'danced' around each other, changing the distance apart every 2 s of an interaction. Even when the distance apart was constant, pallid gerbils were immobile only 26% of the time, and spent nearly equal time in synchronised movements that maintained a constant distance apart. All the differences were significant ($p < 0.001$, White t-test, excluding mobile keeping of distances in the Mongol and pallid gerbils).

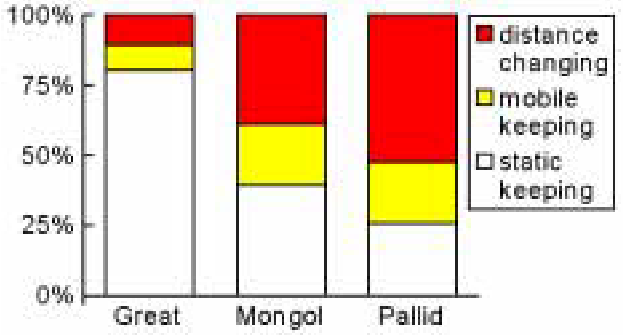

Figure 6. Total percentage of time gerbils spent with the winner–loser distance changing, mobile but keeping a constant distance apart, and static keeping of a constant distance apart during aggressive interactions in the three gerbil species.

Discussion

The differences we found in observing male–male conflicts represent distinctive species-specific strategies of aggressive fighting, graded in severity in accordance with degree of sociality in the species studied. The most social species, the great gerbil, used a strategy of a conflict delay, utilising for the most part prolonged distant threats, with rare, short periods of contact threats or fighting and chasing. Mongol gerbils used a strategy of quick and short aggressive interactions. Rivals showed threat postures or moved simultaneously, keeping a constant distance apart. The solitary pallid gerbils showed a severe strategy of aggressive fighting, with much fighting and chasing, and rapid changing of both distances and orientation.

Psychological intimidation is a very important aspect of aggressive fighting, and these interspecies differences may be discussed from the viewpoint of resistance to social suppression from a conspecific male (Goltsman et al. 1994; Goltsman and Volodin 1997). We hypothesised that more prolonged aggressive interactions demand more resistance from the participants. The time spent in aggressive interactions was the most in the great gerbil, intermediate in Mongol gerbil, and least in the pallid gerbil. Therefore, accordingly to our hypothesis, species-specific strategies of aggressive fighting show that the great gerbil possesses the highest resistance to social suppression, Mongol gerbil an intermediate resistance, and pallid gerbil the lowest one.

The enhancing of resistance may be among the mechanisms that promote the adaptation of animals to exist in social environments of high density. The differences we discovered in resistance to social suppression are in good agreement with the species-specific degree of social density in natural populations (Pavlinov et al. 1990; Goltsman et al. 1994). The observed data on differences in strategies of aggressive fighting in these three species suggest the existence of behavioural mechanisms correlated with social organisation in gerbils. In an ecological framework, these mechanisms may be among the factors that determine population density in gerbils in nature.

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The influence of predator odours and overcrowded mouse odours on regulation of oestrous cycles in house mice (*Mus musculus*)

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Abstract. We investigated the influence of chemical signals derived from different sources—urine of feral cats (*Felis catus*) and urine from overcrowded mice (*Mus musculus*) on regulation of oestrous cycles in *Mus musculus musculus* under laboratory conditions.

Cat urine and urine from mice housed in overcrowded conditions caused very similar effects. Application of urine from feral cats and from overcrowded conspecifics to the bedding of experimental animals for a period of 21 days caused a significant increase in numbers of animals with extended oestrous cycles. Application of cat urine or overcrowded mouse urine to the bedding of female mice caused an extension of oestrous cycles in 56.0% and 62.5% of tested animals, respectively.

The results of the present study and other experimental data from our laboratory may indicate that predator urine and urine from overcrowded conspecifics share the same chemical information.

Introduction

Mammals are known to avoid predator odours (Muller-Schwarze 1983; Weldon 1990; Ylonen et al. 1992; Eppli et al. 1993; Jedrzejwski et al. 1993). More than 10 years ago, the presence of predator urine was shown to decrease activity patterns in rodents (Sullivan et al. 1988). The mechanism of repellency is putatively a fear-induced avoidance response by rodents (potential prey) to the urine characteristics of predators on meat diets, i.e. the double-bonded sulfur and amino by-products of protein digestion (Nolte et al. 1994). In our investigations of the effects of predator urine on rodent behaviour, we found that exposure of rats (*Rattus norvegicus*), mice (*Mus musculus*), and voles (*Clethrionomys rutilus*) to predator urine significantly reduced the reproductive output of these rodents. Previously, we demonstrated that oestrous cycles were extended in Norway rats exposed to mink (*Mustela vison*) anal sac secretions (Voznessenskaya et al. 1992) and urine of feral cats (Feoktistova et al. 2001). Similarly, Kostela et al. (1996) found there was an extension of the duration of oestrous cycles in bank voles (*Cletrionomys glareolus*) exposed to weasel (*Mustela nivalis*) odours.

If food becomes limiting, rodents will begin catabolising their muscle protein and so their urine would contain larger amounts of protein digestion products (Swick and Benevenga 1977; Baracos et al. 1983). These signals could serve to trigger mechanisms that would curtail reproduction.

In the present work, we compare the effects of feral cat urine and urine from mice housed in overcrowded conditions on the regulation of oestrous cycles in house mice under laboratory conditions.

Materials and methods

Test subjects were 36 mice of 4–6 months of age from an outbred laboratory population. Before the experiments, females were housed singly in standard plastic cages. Each cage was placed in individual box (size 70 × 20 × 35 cm) with a separate ventilation system for every animal. Air-flow from different cages did not mix at any stage of the experiment.

Experimental rooms were illuminated on 12:12 hours light:dark schedule, and maintained at 20–22°C. Food and tap water were provided *ad libitum*.

Oestrous cycles were quantified by taking vaginal smears for 21 days before treatments (3–4 complete cycles). After the different types of treatments, oestrous cycles were monitored for a further 21 days. We used two basic treatments: (1) urine from feral cats (*Felis catus*) and (2) urine from overcrowded mice (*Mus musculus*). For the control group of animals (water treatment), we monitored oestrous cycles for the duration of the experiment (42 days).

Urine from feral cats (*F. catus*) was used as a source of predator chemical cues. The cats used in the experiment normally hunt for mice and have mice in their diet. If needed, additional meat was added to their diet. Freshly voided urine was frozen (22°C). Once defrosted, urine was used only 1–2 days. Non-predator urine was obtained from house mice (*M. musculus*). Individuals (*n* = 12) of both sexes were placed in a standard cage for 14 days before urine collection. Food and water were available *ad libitum*. Mice were placed into metabolic stainless steel cages, overnight, and urine was collected and stored using the method described above.

Urine (0.5 mL) (corresponding to specific treatment) or water was put directly onto the bedding of female mice every day for the duration of the treatment. For the first group (*n* = 12) water only was used. For the second group (*n* = 12) water was applied for the first 21 days, then cat urine was applied for the next 21 days. For the third group (*n* = 12) water was applied for the first 21 days, then urine from overcrowded conspecifics was applied for the remaining 21 days. The number of females with extended oestrous cycles relative to both of the controls was recorded. Also we recorded the number of times animals were in oestrus for each group for the period of manipulation (21 days).

Differences among treatment groups were determined using the *t*-test (Student criterion) and Fisher test (STATISTICA, StatSoft Inc., Tulsa, Oklahoma, 1999).

Results and discussion

Cat urine applied every day to the bedding of female mice for a period of 21 days caused a significant ($p < 0.001$) increase in the numbers of animals with extended oestrous cycles relative to control animals (Table 1). Urine from overcrowded conspecifics applied to the bedding of female mice on a daily basis had even greater effect. In this case, 62.5% of female mice had extended cycles relative to the control animals. For both treatments, the duration of the delay to the next oestrus ranged from 2 to 14 days. The average number of oestruses is shown in Table 1. We observed regular cycles for all animals in control group. The number of oestruses was significantly reduced ($p < 0.001$) in animals exposed to the cat urine and in the group treated with urine from overcrowded conspecifics ($p < 0.001$).

Conclusions

The results of the present study suggest that predator (feral cat) urine and urine from overcrowded mice may share similar information about unfavourable conditions for reproduction. The responses are similar to those reported in previous studies on rats, mice and voles (Feoktistova et al. 2001; Voznessenskaya 2002; Voznessenskaya et al., this volume). Mice respond to chemical cues of different origin in the similar manner: reducing numbers of cycling animals and lowering the probability of pregnancy.

The chemical cues of cat urine and urine from mice housed in overcrowded conditions may be due to each containing some similar chemical components as a result of protein digestion in carnivores and muscle catabolism in overcrowded rodents (e.g. sulfur-containing compounds, amino acids, and peptides) (Nolte et al. 1994).

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Table 1. The influence of cat urine and urine derived from overcrowded conspecifics on the number of periods of oestrus during the treatment period in *Mus musculus*.

Treatment	Number of periods of oestrus pre-treatment (21 days)	Number of periods of oestrus during treatment (21 days)	Percentage of animals with extended oestrous cycles
Control (water only)	4.2 ± 0.1	4.3 ± 0.2	0
Cat urine	4.3 ± 0.2	3.0 ± 0.2	56.0
Overcrowded mouse urine	4.8 ± 0.3	3.0 ± 0.3	62.5

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Effectiveness of controlling fecundity and survival on rodents with different life history traits

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Abstract. The finite rate of increase of rodents is sensitive to changes in the key life history traits of fecundity and survival. We used matrix population models to manipulate fecundity (fecundity control) and survival (mortality control) and measured the effectiveness of these two alternative control approaches. Our results indicate that increased mortality through the use of rodenticides is more effective for rodents sensitive to survival, whereas fecundity control is more effective for rodents of high fecundity (frequent recruitment and long breeding seasons). Therefore, different life histories of rodents could influence the effectiveness of fecundity control and mortality control (e.g. use of rodenticides). Knowledge of life history characteristics of species should be considered in estimating population dynamics for management and conservation of different species of rodents.

Introduction

Life history traits of rodents vary considerably and are adapted to environmental influences. Vital rates such as fecundity and survival contribute differently to the population dynamics of rodents. For instance, the finite rate of increase can be more sensitive to changes in fecundity than survival in some rodents, whereas population growth rates are more sensitive to changes in survival in other species. Hereafter, we use the term ‘fecundity-sensitive’ to refer to the former, and the term ‘survival-sensitive’ to refer to the latter. The management or control of pest rodents is aimed to either reduce fecundity with contraception or increase mortality by applying rodenticides (Chambers et al. 1997; Sinclair 1997). However, differences in the sensitivity to changes in fecundity and survival to population growth rate may cause differences in the effectiveness of fecundity control (decreasing reproduction) and mortality control (decreasing survival) among rodent species. It seems reasonable to hypothesise that the fecundity-sensitive rodents would suffer greater reduction in population growth rate from fecundity control than from mortality control, but the survival-sensitive rodents would undergo a larger reduction in population growth rate from mortality control. This hypothesis has not been tested. Our objective was to test the above hypothesis using matrix population models. Mathematical models have been shown to be useful in formulating pest control strategies (Stenseth 1981).

Methods

Study species

We chose three rodent species, *Microtus californicus, Clethrionomys rufocanus* and *Mastomys natalensis,* for this study. *M. californicus* is a fecundity-sensitive species, whereas *C. rufocanus* and *M. natalensis* are survival-sensitive species (see the Results section). In addition, we created a hypothetical ‘super’ fecundity-sensitive species (SFS) using the 6-month wet season matrix of *M. californicus* for the monthly transition matrix of SFS. Thus, SFS is not only fecundity-sensitive, but also breeding-intensive (12 months a year). We also recreated a hypothetical species (HS) using the wet season matrix of *M. natalensis* as monthly matrix (A_m) for the entire year. As a counterpart of SFS, HS is survival-sensitive and has a long breeding season (12 months a year).

Model development and simulations

We used the stage-structured matrix model to project annual finite rate of increase (λ) for the three rodent species, HS, and SFS. Transition matrices (A) of the three species were obtained from Harding (2002), Yoccoz et al. (1998), and Stenseth et al. (2001), respectively (Figure 1). In a transition matrix,

$$A = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & a_{22} & a_{23} & a_{24} \\ a_{31} & s_2 & a_{33} & a_{34} \\ a_{41} & a_{42} & s_3 & s_4 \end{bmatrix},$$

f_1, f_2, f_3, and f_4 are the fecundity rates of females (number of female offspring per reproducing female) at each stage (e.g. juvenile, sub-adult, adult etc.), s_1, s_2, s_3, and s_4 are the survival rates of animals to next stage, and subscripts 1, 2, 3, and 4 represent stages. a_{ij} is the transition rate of animals from j stage to i stage. For instance, a_{22} is the rate, at which animals remain at stage 2, and a_{23} is the rate at which an animal changes from stage 3 to stage 2. In vertebrates, a_{31}, a_{41}, a_{32}, a_{42}, and a_{34} are zeros. The projection of population size in matrix models is the result of survival of animals and juvenile recruitment to the next time step.

We derived an average monthly transition matrix (A_{wm} and A_{dm}) for *M. natalensis*. Annual finite rates of increase of *M. californicus* (λ_{MC}), *C. rufocanus* (λ_{CR}), and *M. natalensis* (λ_{MN}), HS (λ_{HS}), and SFS (λ_{SFS}) were determined as follows. First, we derived annual transition matrices for the three species, HS, and SFS using equations:

$$A_{MC} = A_w * A_d$$

$$A_{CR} = A_f^{\,2} * A_s^{\,4} * A_w^{\,6}$$

$$A_{MN} = A_{dm}^{\,6} * A_{wm}^{\,6}$$

$$A_{HS} = A_m^{\,12}$$

$$A_{SFS} = A_m^{\,12}$$

And then, λ_{MC}, λ_{CR}, λ_{MN}, λ_{HS} and λ_{SFS} were computed as the dominant eigenvalues of annual transition matrices, respectively (Caswell 2001).

Sensitivity to vital rates were determined by elasticity analysis (Caswell 2001) using transition matrices of breeding seasons and the formula,

$$\text{Elasticity } (e_s) = \frac{s}{\lambda}\frac{\partial\lambda}{\partial s}$$

where s is a vital rate and $\partial\lambda/\partial s$ is a partial derivative of λ with respect to s. If the sum of elasticity of all stage-specific survival is greater than that of all stage-specific fecundity rates, we classified the species as survival-sensitive; otherwise, as fecundity-sensitive.

We simulated mortality control (applications of rodenticides) and fecundity control by reducing either survival or fecundity, respectively, to 80%, 70%, 60%, 50%, 40%, and 25% of the average values for entire effective periods. We assumed that lethal effects of rodenticides would last for one month (January) and assumed no multiple applications. The effects of contraception would last for the entire breeding season or year. Rodenticides and contraceptives had the same effects (or percentage reduction) on survival and fecundity to all age stages, respectively. We did not simulate fecundity suppression and application of rodenticides simultaneously. The effectiveness of fecundity control and mortality control was measured with the proportion of post-control finite rates of increase compared with the finite rates of increase of control populations that were not exposed to any chemicals and contraception agents. To demonstrate the influence of the length of breeding season to the effectiveness of fecundity control, we determined the proportional drop in the rate of population increase of *M. natalensis* with 20% reduction in fecundity rate for the breeding seasons of 4, 6, 8, 10, and 12 months, respectively.

Results and discussion

The sum of elasticity of all survival entries was greater than that of all fecundity entries in *M. natalensis* and *C. rufocanus*. On the other hand, the sum of elasticity of all fecundity entries was greater than that of all survival entries in *M. californicus* (Figure 2). In some rodent species, the elasticity might have seasonal changes (Haydon et al. 1999). In addition, biases in the estimation of survival and fecundity rates might undermine the effectiveness of elasticity analyses (Haydon et al. 1999).

Under mortality controls, fecundity-sensitive *M. californicus* and SFS underwent less reduction in population growth rate; however, survival-sensitive *M. natalensis*, HS, and *C. rufocanus* exhibited greater reductions in population growth rate (Figure 3a). Moreover, mortality control had similar effectiveness on *M. natalensis* and *C. rufocanus* (Figure 3a).

Fecundity control had similar effectiveness on *M. natalensis* and *C. rufocanus*, which have similar life histories (Figure 1), but fecundity control had a greater effect on HS compared with *M. natalensis* and *C. rufocanus* (Figure 3b). Although *M. natalensis*, *C. rufocanus*, and HS were all survival-sensitive (Figure 2), HS was more breeding intensive and had recruits 12 months a year. By contrast, *M. natalensis* and *C. rufocanus* had recruits only 6 months a year in our models. In fact, *M. natalensis* can have a greater fecundity than one in our model (Figure 1). *M. natalensis* can breed as early as in January and has an average litter size of 6.67. In our model, *M. natalensis* begins to breed in April and has an average litter size of 4.01. Stenseth et al. (2001) also found that fecundity control could effectively prevent the outbreak of *M. natalensis*. In our simulations, with a 20% reduction in fecundity, the population growth rate of *M. natalensis* was reduced to 0.769, 0.715, 0.661, 0.618, 0.602 of that of non-control populations for 4-, 6-, 8-, 10-, and12-month breeding seasons, respectively. The longer the breeding seasons, the greater reduction in population growth rate under the fecundity control. *M. californicus* had the least reduction in population growth rate under fecundity control (Figure 3b). This is probably because *M. californicus* had only one-time recruitment over 6 months in the matrix model. SFS, a hypothetical, fecundity-sensitive, and breeding-intensive species suffered the greatest reduction in the population growth rate (Figure 3b). SFS had recruits 12 months a year in our matrix population model. Therefore, fecundity control is more effective in rodents of high fecundity (long breeding season and frequent recruitment).

(a) Average monthly matrix of *M. natalensis*

Wet season

$$A_{wm} = \begin{bmatrix} 0 & 0 & 2.01 \\ 0.5 & 0.37 & 0 \\ 0 & 0.25 & 0.62 \end{bmatrix}$$

Dry season

$$A_{dm} = \begin{bmatrix} 0 & 0 & 0 \\ 0.5 & 0.37 & 0 \\ 0 & 0.25 & 0.62 \end{bmatrix}$$

(b) Seasonal matrices of *M. californicus*

Wet season

$$A_w = \begin{bmatrix} 1.33 & 1.33 \\ 0.58 & 0.58 \end{bmatrix}$$

Dry season

$$A_d = \begin{bmatrix} 0.49 & 0.49 \\ 0.2 & 0.2 \end{bmatrix}$$

(c) Seasonal matrices of *M. rufocanus*

Summer

$$A_s = \begin{bmatrix} 0 & 0.93 & 1.86 & 1.86 \\ 0.75 & 0 & 0 & 0 \\ 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0.75 & 0.75 \end{bmatrix}$$

Fall

$$A_f = \begin{bmatrix} 0 & 0 & 0.93 & 0.93 \\ 0.75 & 0 & 0 & 0 \\ 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0.75 & 0.75 \end{bmatrix}$$

Winter

$$A_w = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0.80 & 0 & 0 & 0 \\ 0 & 0.80 & 0 & 0 \\ 0 & 0 & 0.80 & 0.80 \end{bmatrix}$$

Figure 1. Projection matrices of stage-structured population models for *Mastomys natalensis* (a), *Microtus californicus* (b) and *Clethrionomys rufocanus* (c).

(a) Elasticity matrix of *M. natalensis*

$$\begin{bmatrix} 0 & 0 & 0.19 \\ 0.19 & 0.11 & 0 \\ 0 & 0.19 & 0.32 \end{bmatrix}$$

(b) Elasticity matrices of *M. californicus*

Wet

$$\begin{bmatrix} 0.81 & 0.09 \\ 0.09 & 0.01 \end{bmatrix}$$

Dry

$$\begin{bmatrix} 0.50 & 0.21 \\ 0.21 & 0.08 \end{bmatrix}$$

(c) Elasticity matrices of *M. rufocanuss*

Summer

$$\begin{bmatrix} 0 & 0.1 & 0.1 & 0.1 \\ 0.29 & 0 & 0 & 0 \\ 0 & 0.2 & 0 & 0 \\ 0 & 0 & 0.1 & 0.11 \end{bmatrix}$$

Fall

$$\begin{bmatrix} 0 & 0 & 0.07 & 0.13 \\ 0.21 & 0 & 0 & 0 \\ 0 & 0.21 & 0 & 0 \\ 0 & 0 & 0.13 & 0.25 \end{bmatrix}$$

Figure 2. Elasticity matrices of stage-structured population models for *Mastomys natalensis* (a), *Microtus californicus* (b) and *Clethrionomys rufocanus* (c).

We are aware that rodent populations are affected by density-dependent feedback and climate (Stenseth et al. 2001) as well as environmental and population stochasticity (Wang et al. 2001). One limitation of our study was that our model did not incorporate the effects of these factors. Also, lower fecundity could result in higher survival of those young that are recruited into the population (Sinclair 1997). Twigg and Williams (1999) found that the productivity of European rabbits (*Oryctolagus cuniculus*) decreased with increasing sterility levels, but the recruitment of offspring was enhanced with high levels of sterility. Thus, additional factors can be incorporated into the model that would affect population growth rates. This modelling exercise emphasises different responses of rodents with different life history traits to fecundity control and mortality control. However, in practice, the two alternatives are not always possible in some rodent species. In many cases, an integration of all available control techniques as a part of pest control strategy is needed (Twigg and Williams 1999).

Conclusions

Survival-sensitive and fecundity-sensitive rodents responded differently to manipulations of these two life history traits. Rodenticides are more effective in reducing population growth rate in survival-sensitive species, whereas reduced fecundity has a greater impact on reducing population growth rate in fecundity-sensitive species. Rodents that have large litter sizes and long breeding seasons should be effectively controlled by contraception. Additional factors, such as those subject to density-dependence, can be incorporated into the model to obtain a better predictor of population consequences of manipulating life history traits.

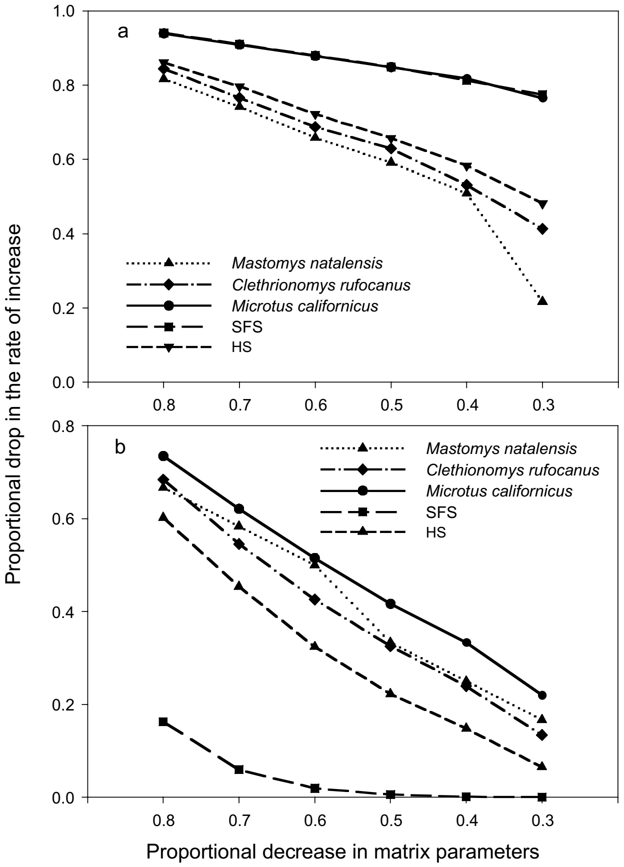

Figure 3. Effectiveness of rodenticides (mortality control) (a) and fecundity control (b) on *Mastomys natalensis*, *Microtus californicus*, *Clethrionomys rufocanus*, a hypothetical species using the parameters of the wet season matrix of *M. natalensis* (HS), and a hypothetical super-fecund species (SFS). The Y-axis represents the proportion of post-control finite rate of increase for experimental populations compared to that of control or pretreatment populations.

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SYMPOSIUM 4: MANAGEMENT—FIELD

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Management of rodents in crops: the Pied Piper and his orchestra

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Abstract. Few rodent species do very well in agricultural fields, but with nevertheless dismaying consequences. The amounts of food that are lost due to damage by rodents in crops are large and there is a pressing need for effective in-field rodent management. A number of reasons make this a very difficult task. Some of these are related to the nature of the fields, which provide optimal habitats for the pest species. The ecology of those rodents, often with a very high fecundity that contributes to high population numbers, forms another but closely connected side of the problem.

The analysis of the ecology of rodent species that are a problem in crops in different parts of the world shows a considerable diversity of ecological traits. Ecologically based rodent management, aiming to reduce damage below an acceptable level, thus must be tailored to each individual species. This may mean that fundamentally different approaches, such as a focus on fecundity or mortality control, the attraction of predators, the reduction of dispersal, combined or alone, may be relevant for one species but not for another. Economic circumstances may render one strategy beneficial in some crops or regions, but not in another. Ecologically based management is a generic approach but its application is site- and species-specific. Management of rodents in crops cannot rely on a single Pied Piper's technique, but requires a directed and concerted strategy.

> "Please your honours," said he, "I'm able,
> "By means of a secret charm, to draw
> "All creatures living beneath the sun,
> "That creep or swim or fly or run,
> "After me so as you never saw!
> "And I chiefly use my charm
> "On creatures that do people harm,
> "The mole and toad and newt and viper;
> "And people call me the Pied Piper."
>
> R. Browning 1888,
> *The Pied Piper of Hamelin*

Introduction

The Pied Piper had a wonderful tool: a single flute to lure all vermin away. Alas, he was no more than the product of wishful thinking, but the tale remains a good illustration of the awe that rats have inspired for thousands of years. As long as history goes back, rodents have had a bad reputation as agricultural pests, on the field and in the store. Old Indian scriptures, dating back 5 millennia, testify to this (Prakash 1988) and myths and stories are found in all cultures.

Also in our day, rodents cause major losses to agricultural production, despite the availability of very effective rodenticides and other techniques to kill rodents. Estimates of damage vary widely: for a country like Tanzania, the average annual yield loss of maize is 5–15%. This corresponds to more than 400,000 tonnes of maize, equivalent to an amount that could feed 2.3 million people for a whole year, representing a financial loss of around US$40 million (Food and Agriculture Organization of the United Nations (FAO) 1998 data). In Indonesia, rodents cause annual losses in rice production between 10–20%, in Malaysia 2–5% (Singleton and Petch 1994), in Vietnam >10% (Singleton et al. 1999b), in Thailand 6–7% (Boonsong et al. 1999) and in India and Bangladesh 5–10% (Islam et al. 1993; Parshad 1999). Even when using a conservative estimate of 5% for the whole of South and Southeast Asia, the losses in that region amount to 16 million tonnes of rice, enough to feed almost 50 million people (Riceweb 2002).

Predictions about human population growth indicate that the world will have about one billion more mouths to feed by 2025. Regional food shortages will cost the lives of many people through starvation and cause social and political instability, with global consequences. Increasing world food production is a complex task, but it is obvious that rodent pests in agriculture will be a serious hurdle on the way. There is a pressing need for effective in-field rodent management.

After the first International Conference on Rodent Biology and Management in Beijing, China, in 1998, Singleton et al. (1999a) edited a book on ecologically based rodent management. This concept of using ecological knowledge to design management techniques, rather than just focusing on techniques for killing rats, has been picked up by a number of projects and researchers. One of the consequences has been the enthusiastic adoption of a number of ecologically based rodent management strategies that seem sustainable and environmentally friendly and are therefore attractive to the authorities. The question that I want to discuss in the present paper is whether it is such a good idea to use the same methods everywhere.

Agricultural fields as a rodent habitat

Rodents form a very diverse group of mammals, ranging from tiny pigmy mice to big capybaras, from arboreal flying squirrels to subterranean mole rats, from opportunistic omnivores (e.g. Norway rats) to specialist feeders (e.g. the North African fat sand rats that feed on a single family of plants only). It is therefore no surprise that some species thrive well under the conditions that are found in agricultural fields.

Generally, agricultural fields are fairly homogeneous patches in the landscape, with a plant community highly dominated by one or two crop species. The crop species that are grown have been selected for high productivity, and farmers attempt to increase soil fertility and water availability. As a result, plentiful amounts of energy-rich food become available in the fields. On the other hand, most crops are harvested every year, meaning that the availability of food and cover in the fields change drastically over the seasons. At the same time, these changes are closely linked to seasonal changes in light, temperature and precipitation, and thus are fairly predictable. Similar effects also occur in natural conditions, and many species have developed methods to use environmental clues for predicting seasonal changes (Boyce 1979). Rodent species that can take advantage of the temporarily abundant food, and at the same time somehow overcome periods when conditions are poor, make good candidates for agricultural pests.

The above general description holds best for fields with cereal crops, which take up the largest part of the total area used for agriculture in the world (FAO 2002). For some other crops, especially perennial crops like many root and tuber crops and tree crops, the temporal variability may be less strong. However, also here, the point remains that agricultural fields are very productive habitats. Rodent pest management in fields is limited by the fact that the same conditions that favour the presence of pest rodents are to a large extent also the conditions that farmers desire for their fields.

A rat is a rat is a rat?

There are almost 2000 species of rodents, but only a limited number of them cause problems in agriculture. In Africa, for example, with 406 species belonging to 11 families (Wilson and Reeder 1993), there are 77 species that have been reported to cause damage to agriculture, most of them in the Family Muridae (Fiedler 1988). But even in this group, most species only occasionally damage crops and just a handful (<20) cause serious damage over most of their distributional range. In Australia, only 4 out 67 species are clearly pest species, in India 12 out 128 species, and in Western Europe 5 out of 61. Still, being a pest species is not an inherent characteristic of these animals. Hamsters (*Cricetus cricetus*) are intensively controlled as pests in grain fields in eastern Europe, but in western Europe the species is endangered, and legally protected (Nechay et al. 1977). Understanding the diversity of the species that are involved in rodent damage, and those that are not involved, is crucial. There is no point in controlling an irrelevant species, and control strategies must target the right species.

A rodent species' status as a pest is a combination of its own biology and the nature of the agro-ecosystem in which it occurs. Although pest species are often thought to have a number of common features, such as a high fecundity and a fast rate of increase, there are some differences that are worth considering.

Rodent biology

The population dynamics of agricultural pest rodents can show at least three different basic patterns (Figure 1). Populations may be relatively stable or irregularly fluctuating, as in *Rattus tiomanicus* in oil palms; they may show strong seasonal fluctuations combined with interannual differences, as in the African multimammate mouse, *Mastomys natalensis*, in maize fields; or they may be eruptive with irregular peak years alternated with periods when there are hardly any mice (e.g. house mice, *Mus domesticus*, in Australia; see Singleton 1989; Singleton and Brown 1999; Davis et al., this volume). Regular cyclic populations seem to be rare in agricultural crops. I suggest that this could be due to the fact that feedback mechanisms in trophic interactions, a common explanation for cyclic population dynamics (Stenseth 1999), rarely occur in agricultural fields. Plant–herbivore interactions, where plant quantity and quality vary between years as a result of herbivory, can of course not be very important in annually planted crops. Predator–prey interactions are rare because predators are rare or even actively hunted in many agro-ecosystems (because they are considered pests themselves). Social regulation, an alternative explanation for cyclic population dynamics (Krebs 1996), is unlikely in agricultural fields because the instability of the environment, caused by frequent disturbances such as ploughing, weeding or harvesting, does not allow stable social structures to develop.

Different patterns of population dynamics are the result of differences in life history and interactions with the environment. The African multimammate mouse shows a strict breeding seasonality, closely linked to rainfall periods, probably through the stimulating effect of germinating grasses (Leirs et al. 1994). This induces maturation of sub-adult females, which then can produce a large number of young in a short period due to the high litter size (up to 24 young, with an average around 11). The young, however, do not start reproducing until the next wet season and in the meantime there is no reproduction while survival is low (Leirs et al. 1993, 1997). The usual demography of the Australian house mice is not well documented due to the very low densities that occur in most years, but particularly favourable conditions of food and cover lead to high population numbers that escape the normal density-dependent regulation and lead to an eruption (Pech et al. 1999).

Rodent management strategies are clearly dependent on the population dynamics of the targeted species.

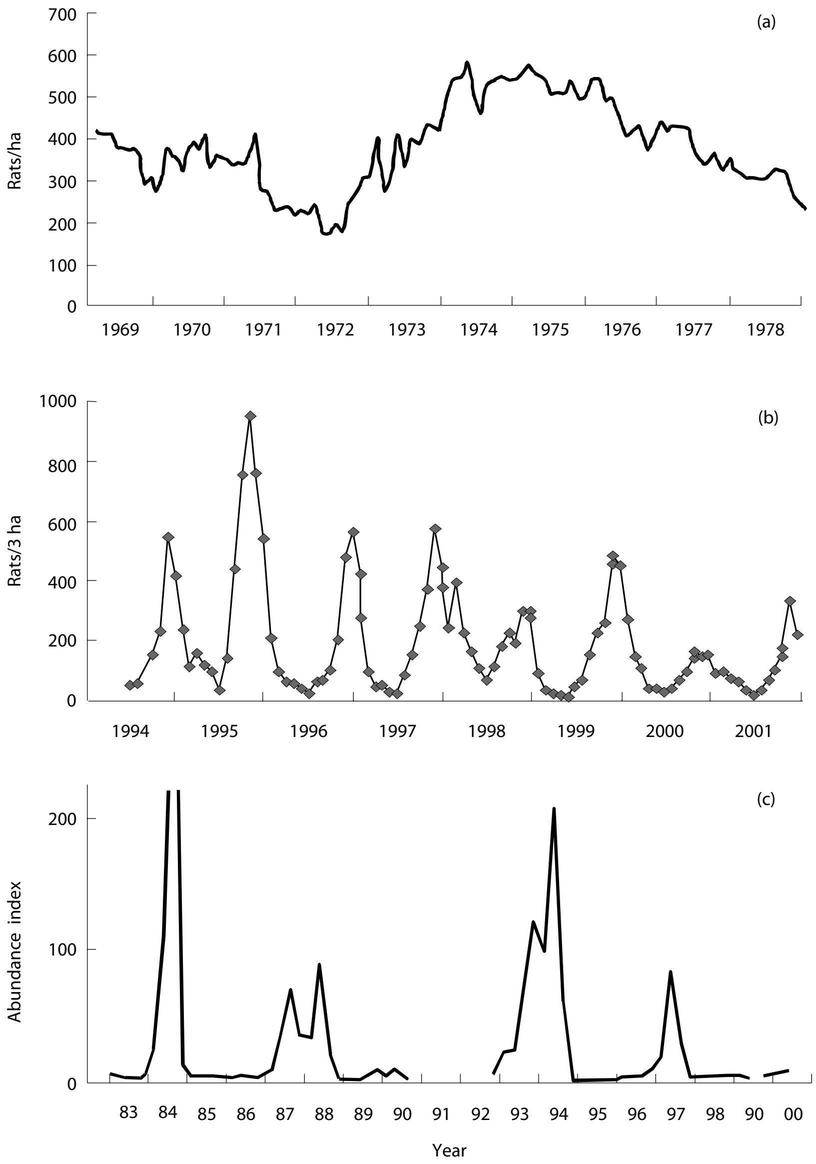

Figure 1. Multi-year population dynamics patterns in three different agricultural rodent pests: (a) wood rats, *Rattus tiomanicus*, in oil palm plantations in Malaysia, population size estimates (redrawn from Wood 1984); (b) multimammate mice, *Mastomys natalensis*, in a maize fields–fallow land mosaic in Tanzania, population size estimates based on robust design capture–mark–recapture (CMR) analysis (own data); (c) house mice, *Mus domesticus*, in cereal fields in Australia, abundance index based on adjusted trapping success (redrawn from Singleton et al. 2001).

Rodents with a stable pattern are kept within restricted limits by density-dependent mechanisms. In species with a clear seasonal pattern, density-independent environmental mechanisms cause the observed regular patterns, and the objective of rodent management will normally be to lower the long-term equilibrium around which population size fluctuates. Such a strategy seems irrelevant in eruptive species where population sizes are usually low anyway. In these species, rodent management will focus on avoiding the build-up of eruptions, or at least the initiation of control early in the build-up phase. It is worth noting that some species may have relatively high average population sizes and consequently cause considerable damage every year, but also in addition show irregular outbreaks (Leirs et al. 1996).

Diet is another aspect in which rodent species show considerable diversity. Many rodent pests are opportunistic omnivores. They can live on a variety of foodstuffs (green plant materials, seeds, fruits, or insects) and thus survive in many different types of crops, but they can also take advantage of a single food item, e.g grain seed, that becomes available in large amounts (e.g. multimammate mice in Africa (Leirs et al. 1994) or house mice in Australia (Bomford 1987)). However, this is not a general feature: other species, like the rice-field rat, *Rattus argentiventer*, have more specialised dietary requirements and thrive only in grasslands such as rice fields (Singleton and Petch 1994). Mole rats are specialised on roots and tubers and cause major problems in cassava fields (Sidorowicz 1974). Such variation means that some rodent species will be very sensitive to changes in crop choices, land use and field management, while others will be affected only marginally.

Crop ecology

Rodent damage is rarely uniform in time, but follows crop phenology. Rice-field rats cause more damage to some stages in the growth of rice than to others (Tristiani and Murakami 1998, 2000), multimammate mice dig up planted maize seeds but are no problem during the growth of maize plants until cobs start ripening (Makundi et al. 1999), and wood mice, *Apodemus sylvaticus*, are a threat to sugar beet fields only in the two weeks after they have been sown (Pelz 1989). In perennial crops, such as coconut or cocoa, rodent damage is more continuous but can vary, e.g. to coincide with fruiting (Williams 1985).

Changes to the phenology of the crop may exacerbate rodent damage. Damage by rodents in rice agro-ecosystems increased from 18,640 ha of total damaged area in 1992 to over 500,000 ha in 1999 (Brown et al. 1999; Singleton 2001). A major factor involved in this increase was the introduction of fast-growing rice varieties which allowed two or even three crops per year, rather than the traditional single crop. While rice-field rats earlier had to survive a long fallow period from mid-January to mid-August, that fallow period is now considerably shorter (from August to December, but during more than 3 months of this period the fields are flooded anyhow). Moreover, the rats now experience twice per year the good conditions provided by specific crop stages that are needed for reproduction (Brown et al. 1999). When irrigation is not synchronised over a large area, adjacent fields will have crops of different ages and rats may move between fields to benefit from the optimal crop stages during a prolonged period (Brown et al. 2001).

The way in which fields are managed will strongly affect the rodents living there, and the damage they cause. Integrated pest management schemes for rodent control rarely fail to mention how important it is to keep fields and field edges clear of weeds, and active weeding strategies have been promoted as rodent control measures (Green and Taylor 1975; Drost and Moody 1982). Maize fields in Tanzania that have been disc ploughed before planting show less damage by rodents than fields that are prepared with a slash-and-burn technique (Massawe et al., this volume). Moreover, fields are not isolated entities from which rodents can be excluded. The fields may be interspersed with different vegetation types and, even when they are large, they are associated with structural variation around hedges, fence lines, roads, irrigation canals, and wind shelters. Such elements increase the attractiveness but also the accessibility of the fields for rodents, since they may serve as refugia or dispersal corridors (Fenn et al. 1987; Brown et al. 2001). Large monocultures in Tanzania experience less rodent damage than smallholder fields that are interspersed with fallow land (Myllymäki 1987).

Rodent management strategies

Given the diversity among rodent pests and the agro-ecosystems where they occur, a number of management strategies have been designed in the past. Most of them have been very successful under specific conditions and this has encouraged people to also try to apply them elsewhere in very different ecosystems. However, none of them is a panacea, and while the people who designed those methods mostly are very well aware of that, policymakers do not always appreciate the subtleties that make a strategy useful in one area but not necessarily elsewhere. Without presenting the strategies in detail, I want to present some examples and discuss why they seem appropriate for some combinations of pest rodents and agro-ecosystems, while they are less appropriate for other conditions. The list is not exhaustive, and strategies such as field sanitation, hunting in various ways, use of repellents, and control with pathogens are not discussed, although some may be very useful and effective under specific circumstances.

Rodenticides

Rodenticides provide a very effective tool for increasing mortality, one of the key demographic processes in population dynamics. A variety of compounds and ways of delivery exist, with second-generation anticoagulants giving the best results (Buckle 1994). Despite some public concern about the use of chemical compounds, rodenticides certainly will continue to play a role in rodent management in agriculture (Buckle 1999). When using rodenticides against different species, the most appropriate product should be chosen, based on information about toxicology and bait preference for the targeted species. Unfortunately, commercial compounds are largely designed to work optimally for a few commensal species of *Mus* and *Rattus*.

A common misconception with the use of rodenticides (and all other lethal control methods) is that the number of killed rodents is a relevant measure of success. An important reason why this does not hold is that density-dependent effects on recruitment and natural mortality may compensate for the mortality caused by the rodent control so that the population size as such is hardly affected. Another, and less often recognised reason, is that the relationship between rodent numbers and damage is not necessarily linear. In maize fields in Tanzania, it is sigmoidal, indicating that there are density ranges where a reduction in rodent numbers does not reduce significantly the level of damage (Mulungu et al., this volume).

In order to be effective, rodenticides must be applied at the correct point, both in space and in time. Rodenticides should be used at the appropriate places: for example, in macadamia orchards, rodenticides were broadcast on the ground until studies revealed that the rats doing the damage only foraged in the trees, and placing the rodenticides there led to a more effective control (Tobin et al. 1997). Likewise, the timing of rodenticide applications is crucial for their effect on a rodent population as, for example, clear in model simulations with *M. natalensis* (Stenseth et al. 2001).

Biocontrol with predators

Attracting predators is probably one of the oldest ways of controlling pests. Under field conditions, promising results using perches and nesting boxes to attract owls and raptors have been obtained in forestry (Munoz and Murua 1990), cereal fields (Kay et al. 1994) and in oil palm plantations (Smal et al. 1990). However, there are a number of questions to be raised. One misconception is that the trophic interactions between predators and prey are symmetrical; because mice are an important dietary item for a certain owl species, for example, does not mean that this owl is a significant mortality factor for the mouse population. Moreover, density-dependent mechanisms may compensate for the additional mortality that is caused by the attraction of predators. In Tanzania, keeping raptors and owls out of 0.5 ha field plots, or attracting them there, does not make a difference for the population size of rodents that is reached (S. Vibe-Petersen, unpublished data). In Kenya, on the other hand, experiments with nesting boxes in maize fields seem promising (Ojwang this Oguge, this volume). Predators also have problems in surviving periods with low rodent numbers. Studies with nest boxes for barn owls in oil palm plantations in Malaysia showed that, in the experimental phase, owls dispersed to neighbouring areas when densities of rats dropped and then reoccupied the nest boxes when densities of rats increased again. When more plantations took over the nest box idea, the density of owls became very large and when rat densities dropped, owls found no vacant territories, the owl population crashed and could not be re-established quickly when rat densities increased again (Smal et al. 1990; C.M. Smal, pers. comm.). Such mechanisms may actually lead to the introduction of cyclic population dynamics in the rodent pest.

Trap–barrier system

The trap–barrier system plus trap crop (TBS+TC) is an elaborate trapping method for the physical removal of rats from rice fields in Southeast Asia (for an overview, see Singleton et al. 1999b). Basically, a small plot of about 30 × 30 m is planted with a rice crop, a few weeks in advance of the surrounding fields. The plot is surrounded by a plastic fence in which holes with multiple live-capture traps are placed. Rats are attracted by the presence of the early crop and get caught. Large numbers of rats can be trapped and this reduces the damage to crops in the surrounding fields considerably. There is a lot of interest in promoting this method since it seems straightforward, does not require rodenticides, yields visibly high numbers of captured rats, and experiments have shown good results.

There are a few conditions, however, that must be met before this strategy can be used effectively. First of all, the cropping system must allow the planting of an early crop. In irrigated systems this may be feasible, but in rainfed systems, this might be difficult. Secondly, the targeted rodents must be attracted to the trap crop. This requires that they can detect the trap crop and are willing to actively move there over reasonably large distances. If those two conditions are not met, only rats accidentally entering the TBS plot will be trapped and although the plot itself may be protected, damage in the surrounding area will not be reduced and the cost of the fence and traps will not be economically justified. A complex situation may occur if the rodent fauna in the rice fields is diverse and only some of the species are attracted to the TBS+TC. This may result in the capture of many individuals of some species, but it may also reduce the competition for the other species that do not respond. The result could be that damage to rice is only slightly reduced.

Another point is that the TBS+TC plot provides protection to a relatively large area but only is economical if the damage reduction in that area is included. This means that the strategy will be sustainable only if farmers have large enough fields, or if a community-based approach is possible, where all those who benefit from a TBS+TC will contribute to it, even though it is not placed close to their own fields. This is not that easy to implement everywhere.

Diversionary feeding

Rodents cause damage because they select the food sources that at a certain place and time give them the best net benefit when balancing energy intake versus the cost of searching and handling food items (taking into account the risk for predation). This insight is the basis for diversionary feeding tactics, whereby the rodents are offered alternative food sources, which they will prefer over the crops to be protected. This has been tested in orchards and forestry (Sullivan 1979; Sullivan and Sullivan 1988) and is now a common strategy in sugar beet fields (Pelz 1989). In such fields, seeds are drilled in the soil in long rows, and wood mice, *A. sylvaticus*, simply go along these lines and dig up the planted seeds. The management method consists of providing alternative seed on the surface along the edges of the fields. The wood mice prefer to use the seeds on the surface and by the time these seeds are finished, the planted seeds have grown to a stage where they are no longer at risk.

The prime condition for having the diversionary feeding method work is that the economic cost of the alternative food is sufficiently low compared with the reduction of losses that can be realised. That condition is met when the crop has a relatively high value or when it has to be protected during a short time only. Surprisingly few experiments have been carried out with this technique. This may be because most crops need protection for a longer time, but also because the uneasy feeling that people may get because they are feeding rather than killing rodents. However, we must remember that the objective of pest management is reduction of damage, not necessarily reduction of rodent numbers.

Fertility control

Ecological theory predicts that reducing reproduction should be as least as effective as increasing mortality in order to reduce population size in the long term. Model simulations and experimental work confirm this for a variety of species (Chambers et al. 1997; Courchamp and Cornell 2000; Stenseth et al. 2001; Davis and Pech 2002; Shi et al. 2002). Fertility control has a number of advantages over lethal control for species with a high fecundity and a high natural rate of mortality, and at the same time can be considered to be a more humane management strategy than killing rodents. A number of different techniques for reducing fertility has been designed, but only immunocontraception seems to hold promise for real field efficacy (Chambers et al. 1999). Large efforts are under way to develop this strategy for the management of house mice in Australia.

Immunocontraception is based on the induction of an immunological response of animals (mostly females) to proteins of their own reproductive cells. This prevents successful fertilisation. The immune response is triggered by incorporating the protein in a virus which is then delivered to the animal as an infectious and self-disseminating organism, or as a deactivated oral vaccine. Ideally, both the protein and the mode of delivery should affect only the targeted rodent species, and hence the engineered micro-organisms cannot be used to control other species.

A more fundamental issue is that not all populations will be equally sensitive to fertility control. Recent analysis of survival and recruitment in the African multimammate mice, *M. natalensis*, and the South American leaf-eared mouse, *Phyllotis darwini*, shows that the annual population growth rate of these species is more affected by changes in mortality than by changes in fertility (M. Lima et al., unpublished results). This suggests that in order to keep these populations at a lower average density, mortality control may be more effective than fertility control. On the other hand, within-year population growth is dependent on reproduction and therefore fertility control may be an excellent tool to avoid the build-up of outbreaks. Again, how appropriate this strategy is will depend on the rodent species and the objectives that one wants to achieve.

Outbreak forecasting

Irregular eruptions of rodent populations come mostly unexpectedly and farmers are rarely well prepared. This has stimulated a lot of research on the causes of such outbreaks and the development of predictive models (see, for example, Leirs et al. 1996; Pech et al. 1999). Intuitively, it will be beneficial to be able to predict the outbreak and take preventative measures to reduce damage (e.g. order rodenticides in time, organise prophylactic control treatments, or plant a crop that is less prone to rodent damage).

However, the benefit of a predictive model is not necessarily clear cut. Due to stochasticity in the population dynamics of the rodents, any prediction will be probabilistic, meaning that there still will be outbreaks that are not predicted or predicted outbreaks that do not occur. Moreover, how advantageous it is to rely on predictions is not only dependent on the quality of the model, but also on economics. The cost of using the model and applying control measures whenever an outbreak is predicted must be outweighed by the benefit (i.e. reduced losses) that one can expect if action is undertaken and a predicted outbreak actually occurs. Depending on the relationship between costs and expected benefit, predictions should be more, or less, conservative. When control is cheap and the crop very valuable, it is better to apply control often. When control is expensive and the crop less valuable, then it may be better to accept losses caused by some outbreaks that were not predicted. The quality of the model depends on the biology of the rodents (and the skills of the researchers), while the economics depends on the agricultural system and the rodent biology (through the link between rodents and damage). We are currently working on a more formal analysis on the value of outbreak predictions. Preliminary results show, for example, that with house mice in south-eastern Australia, farmers may benefit more when they always apply control rather than never, while with multimammate mice in Tanzania, it would more beneficial never to do control than always (S. Davis et al., unpublished results).

Conclusion

The above examples have illustrated that smart strategies for rodent control do not necessarily work always and everywhere. The biology of rodents is diverse and complex and so is the ecology of the fields in which they live. Ecologically based rodent management is a sound concept, but it does not provide a ready-made solution. Specific approaches must be identified, based on the ecological characteristics of the agro-ecosystem and the pest species involved. Different techniques must be combined and fine-tuned to work optimally in each system. Management of rodents in crops cannot rely on a single Pied Piper's technique, but requires a directed and concerted strategy.

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Ecologically based management of rice-field rats on a village scale in West Java: experimental approach and assessment of habitat use

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Abstract. A major constraint to rice production in Southeast Asia is pest rodents. In a large-scale replicated field study, we are examining the effect of ecologically based rodent pest management on rodent numbers, pre-harvest rodent damage, yield and the use of chemicals. This paper describes the rationale for including community rat campaigns as a management tool in this study. We present data on the spatial and temporal patterns of habitat use by rice-field rats (*Rattus argentiventer*), which are the major mammalian pests in lowland irrigated rice in Indonesia. Rat numbers showed similar fluctuations in rice fields, crop margins and village garden habitats. Most rats were caught during fallow and land preparation, possibly as a result of increased movements post-harvest. At this time, many more rats were captured in crop margins and village garden habitats than in rice fields. Similar numbers of rats were present in all habitats at tillering, ripening and harvesting of rice. We conclude that community rat campaigns targeted at refuge habitats (crop margins, village gardens) shortly before transplanting rice from nurseries into the rice fields should considerably decrease the founding population of rice-field rats for the next cropping season. This refuge campaign, combined with the application of community trap–barrier systems during the standing crop should minimise rat damage to rice crops and increase yield.

Introduction

Habitat use by pest rodents

Mobile animals select habitats actively to achieve maximum fitness (Fretwell 1972). Habitat choice of an individual takes into account intrinsic factors including intraspecific competition (Myllymäki 1977; Hodara et al. 2001), as well as extrinsic factors including interspecific competition (Hodara et al. 2001), predation (Newsome 1969; Lima and Dill 1990) and weather conditions (Vickery and Rivest 1992).

For rodent pests in agricultural systems, habitat use may be linked to patterns of land use (Twigg and Kay 1994; Leirs et al. 1997). Seasonal changes in food supply may cause movements of animals between refuge habitats and impact habitats (crops) (Hansson 1977; Redhead and Singleton 1988). Knowledge of the spatial activity of rodent pests is vital to developing appropriate management strategies because control should be conducted at key times in the source/refuge habitats where high numbers of the pest species are generated (Stenseth 1977; Singleton 1989; Twigg and Kay 1994).

The role of pest rodents in Southeast Asia

Rodent pests are a worldwide problem, and are responsible for considerable damage to crops, food stores and human property. Some rodents are also significant carriers of diseases transmitted to humans (e.g. leptospirosis, tularaemia, rickettsiosis, bubonic plague) (e.g. Gratz 1994), and thus have a further economic impact related to losses in worker productivity and health-care costs.

Rodents are one of the main causes of pre-harvest losses in Southeast Asian rice crops (Singleton and Petch 1994). In Indonesia, rodent pests are the most important pre-harvest pests, causing annual losses of 17% in rice crops (Geddes 1992). Generally, pre-harvest rodent damage is patchy with localised losses of 70% or even 100% occurring in particular fields. In other Southeast Asian countries, similar levels and patterns of rodent damage occur (reviewed in Jacob et al. 2002).

Ecologically based rodent management

Ecologically based rodent management (EBRM) aims to manage the target species based on sound knowledge of farming systems and natural factors, such as the availability of food and shelter, that contribute to the limitation of pest rodent populations. In manipulating these factors, control is spatially and temporally focused on the target species and non-target impacts are reduced. Key refuge habitats (banks of irrigation channels, irrigation levee banks) are modified to minimise the availability of food and shelter for pest rodents by controlling the growth of grasses and height and width of banks as well as by synchronising planting and harvesting (Leung et al. 1999).

Community trap–barrier systems (CTBSs) are simple, affordable structures used by farming communities in some Southeast Asian countries to control rats. A CTBS consists of multiple-capture cage-traps associated with a rectangular plastic fence, typically (25 × 25 m) that encloses a lure crop planted 2–3 weeks earlier than the surrounding crop. It is therefore more nutritious and attracts rats from the surrounding area, which are caught in the traps. In lowland flood-irrigated rice, one TBS protects up to 16 ha (Singleton et al. 1998). The CTBS method has significant advantages: it is environmentally sustainable because non-target species can be released and there are no residues left in the rice field after removal of the structure; and the technique is simple and can be easily transferred from scientists to extension officers and farmers (Singleton et al. 2001). However, the use of the CTBS entails a large maintenance effort (Jacob et al. 2002). Moreover, it is only effective until the surrounding crops reach their generative stage because the efficacy of the CTBS technology relies on the presence of an early-planted crop.

Best results in controlling pest rodents are likely if a combination of several management techniques—including CTBSs, community rat campaigns and habitat manipulations—are applied (Singleton et al. 2001). The choice of methods and timing of activities will depend on the biology and ecology of the target species. In contrast to lowland irrigated rice systems in Vietnam and Laos, where several rodent species occur, rice fields in West Java harbour almost exclusively rice-field rats (Singleton et al. 1998). Management in this ‘one-species system’ is therefore more easily targeted on the culprit and effects at the population level are more easily detected than in ‘multi-species systems’.

Effectiveness of ecologically based rodent management

Ultimately, farmers in Indonesia control pest rodents (and other pests that damage rice) in order to increase their net income. This can be achieved in two ways. First, if the cost of pest rodent management is lower than the monetary benefits from an increased yield, there is a direct increase in income. The cost of rodent management includes the materials and equipment use and the time spent conducting rodent control. Second, if improved management techniques are less time-intensive, then a farmer may spend the time gained in other cash-generating activities.

In addition, there may be an important environmental benefit if the use of EBRM measures results in a decrease in the use of poisons. In West Java and other regions in Southeast Asia, a large proportion of farmers use unregistered poisons (Sudarmaji, Rochman et al., these proceedings). These poisons include potent broad-spectrum chemicals such as endosulfan, aldicarb and dichloromethane.

A study of the effectiveness of EBRM should therefore include measurements of rodent damage to rice crops, crop yields, and the use of chemicals, as well as the time and money spent on rodent control.

Spatial and temporal scale

Pest rodents can be highly mobile (e.g. Krebs et al. 1995; Leirs et al. 1997). Despite relatively small home ranges of c. 1–2 ha during the breeding season (Brown et al. 2001) rice-field rats can travel large distances (>700 m) post-harvest (Jacob, Nolte et al., this volume). Rice-field rats are also thought to travel between refuge/nest habitats (channel banks, road verges) and impact habitats (rice crops). During the breeding season, there may be pronounced activity of pregnant and lactating female rice-field rats in rice fields (J. Jacob et al., unpublished data). These changes in spatial activity need to be considered for the management of populations of rice-field rats, but little is known about their spatial dynamics and habitat use.

A number of studies on large holdings not typical for Java have provided detailed information on the efficacy of certain aspects of EBRM such as the use of CTBSs and fumigation (e.g. Singleton et al. 1999). Studies at a village level are required to examine the effects of EBRM for traditional cropping systems. Implementation of EBRM there may lead to the application of additional techniques and to the temporal and spatial coordination of traditional and additional techniques.

In 2000, we began a replicated, manipulative village-level study of the efficacy of EBRM in lowland irrigated rice fields in Cilamaya, West Java. One management tool we planned to use was community rat campaigns instigated at key times. Therefore, as a prelude to the village-level study, we monitored the numbers of rice-field rats by capture–mark–recapture trapping during the wet season 1998/99 and dry season 1999. The aim of the study was to identify specific habitats and key times for community rat campaigns.

Materials and methods

The study was conducted in lowland irrigated rice crops near the town Cilamaya (06°14'51"S, 107°34'05"E), Subang province, West Java, Indonesia. The climate in the region is tropical. Annual variation of the average temperature (28°C) is low. About 75% of the annual rainfall (1450 mm) occurs during the wet season (November–April) but rain is also frequent during the dry season (May–October).

The West Javanese agro-ecosystem is characterised by smallholder lowland irrigated rice fields (average family holding of 1–1.5 ha). Individual holdings are partitioned by small distribution channels and larger rice-growing areas are separated by dikes and irrigation channels. Villages are located along roads. One rice crop is grown in each of the two seasons. Rice is transplanted from nurseries in the fields after 2–3 weeks. The main crop stages are tillering (55 days after sowing), booting (75 days), ripening (95 days) and harvesting (120 days).

We used a typical rice-growing area of about 750 ha for this study. Rice-field rats were trapped monthly for three consecutive nights from January 1999 until December 1999 in the vicinity of the villages Pasirukem, Sukatani and Tegalurung. We captured rats with multiple-capture wire-cage live-traps (20 × 20 × 50 cm). Six traps were set along a 120 m long drift fence (Leung and Sudarmaji 1999) in each of three habitats: rice fields, crop margins (irrigation channel banks and road verges) and village garden (Figure 1).

In rice fields, the drift fences were located either close to creeks or small irrigation channels that were 50–60 cm wide and 20–30 cm deep or about 50 m into the fields (Figure 1). Volunteer crops, which emerged from the stubbles after harvest, grew along the creek banks for 3–4 weeks after harvest. During the planting season, farmers usually did not manage the vegetation along these watercourses, but controlled weeds regularly in the fields. Drift fences with traps were also set along road verges and irrigation channel banks. In these habitats burrowing activity is usually high. Grassy vegetation 1–2 m wide occurred on either side of the channels and the roads, providing ground cover of 80–90%. Village garden habitats were located between villages and rice fields. In the village gardens, farmers grew bananas, mangoes, coconuts and vegetables.

In January, April, June and from August to November 1999 we set one drift fence in each of four rice fields, four crop margin habitats and in two village garden habitats. In February, March, May, July and October 1999 we set one drift fence in each of eight rice fields, eight crop margin habitats and in four village garden habitats.

The plastic drift fences were 60 cm high, stabilised by bamboo poles and dug into the ground about 20 cm deep. The openings of the traps were flush with holes at the base of the fence. The traps were on either side of the fence facing alternate directions and were held in place with bamboo sticks. The distance between traps was 20 m; the first and last trap along a drift fence were 10 m away from the ends of the fence. The distance between the drift fences was >300 m. Traps were checked every morning at sunrise. Rats were marked with a uniquely-numbered brass ear-tag (Hauptner, Germany) and released at the point of capture.

Rice-field rats are extremely trap-shy after first capture and can usually not be caught more than once, so that estimators of population size that rely on recaptures could not be applied. We therefore compared the minimum number of rats known to be alive (MNA) between seasons (wet and dry season), habitats (rice field, crop margin and village garden) and crop stages (tillering, maximum tillering, ripening, harvest and land preparation) using ln-transformed data in an accumulated analysis of variance (ANOVA) (general linear regression). MNAs at fallow

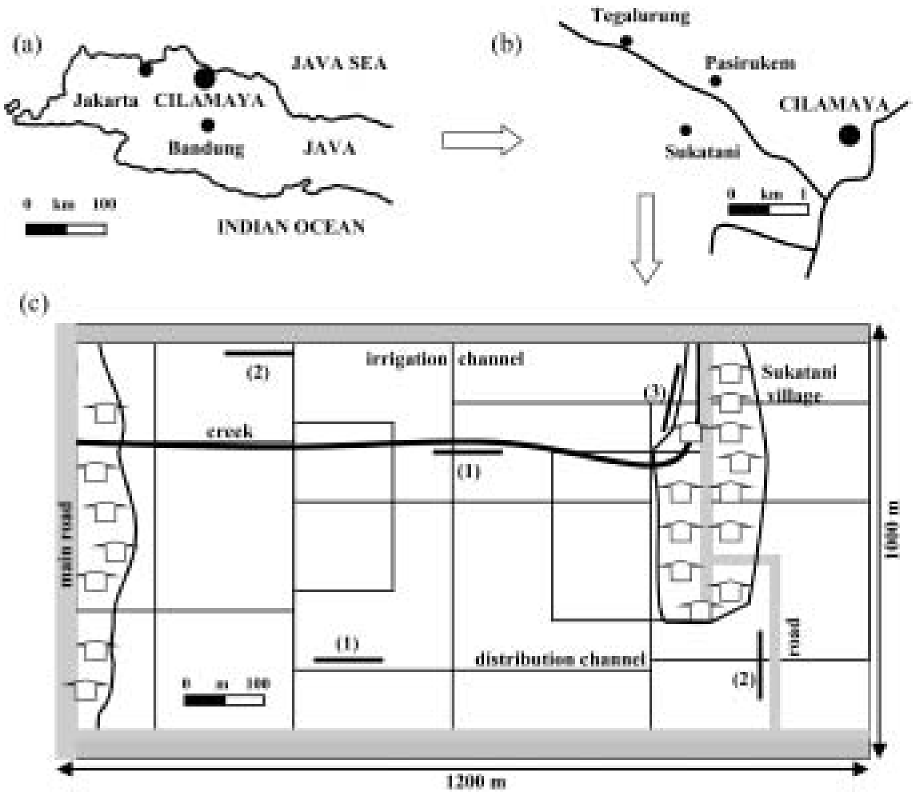

Figure 1. (a, b) Location of the study area in West Java, Indonesia. (c) Examples of the location of drift fences with traps (short black lines) for live-trapping rice-field rats in rice fields (1), crop margins along irrigation channels and roads (2), and in village garden habitats (3) near the village of Sukatani.

and transplanting were not considered in the statistical analysis because sampling at these crop stages was not conducted in both seasons. Variance is stated as standard error throughout the paper.

Results and discussion

We caught 1564 rice-field rats during 3060 trap nights. Captures of non-target mammals were rare (<2%) and included *Bandicota* sp., *Suncus* sp. and *Rattus rattus*.

There was no difference in the MNA between seasons ($F_{1,120}$ = 0.03, p = 0.862) (Figure 2). Across habitats, the average MNA was low (<10) at tillering, maximum tillering, ripening and harvesting, high (>26) at land preparation ($F_{4,120}$ = 37.18, p < 0.001) and highest (>37) at fallow (Figure 2). The breeding activity of rice-field rats commences about two weeks before maximum tillering (Leung et al. 1999) and should have led to recruitment of rats into the trappable population at ripening and harvesting. However, this was not reflected in the MNA. This could have been due to abundant high-quality food provided by the rice crop resulting in small home ranges and low trapping probability. In California voles (*Microtus californicus*), for example, plentiful food leads to small home ranges (Ostfeld 1986). High background food availability may also have reduced trappability because the rats' exploratory behaviour in their search for food may have been low.

The high number of rats caught at fallow and land preparation was probably due to increased movements activity of rats during and after the disturbance by harvest (Jacob, Nolte et al., this volume). Harvesting rice not only removed much of the food, it also removed the rats' shelter from predators. The reduction of shelter exposes small mammals to increased predation risk (Jacob and Brown 2000; Sheffield et al. 2001). Some small mammals such as common voles (*Microtus arvalis*) respond to the removal of shelter with decreased spatial activity (Jacob and Hempel 2002) but rice-field rats relocate quickly after harvest to unharvested rice fields (Jacob, Nolte et al., this volume). During fallow and land preparation, no unharvested patches were available and the rats may have been forced to move more often than in the standing crop in search for shelter and food. These movements and the relatively high number of rats at the end of the breeding season may have been the reason for the high MNAs.

In addition, trappability could have been influenced by the breeding activity because low MNAs coincided with the breeding season (maximum tillering until shortly after harvest) and high MNAs coincided with the non-breeding season (fallow and land preparation). When breeding, female rats may have stayed close to their offspring in the burrows, lowering the probability to encounter and enter a trap. This seems likely as several small mammals have relatively small home ranges in the breeding season compared to the non-breeding season (e.g. Krebs et al. 1995).

The number of rats caught was higher in crop margins and village gardens than in rice fields ($F_{2,120}$ = 6.63, p = 0.002) and the fluctuations in the MNA of rats showed similar trends in all three habitats (Figure 2). However, in contrast to crop stages when few rats were caught

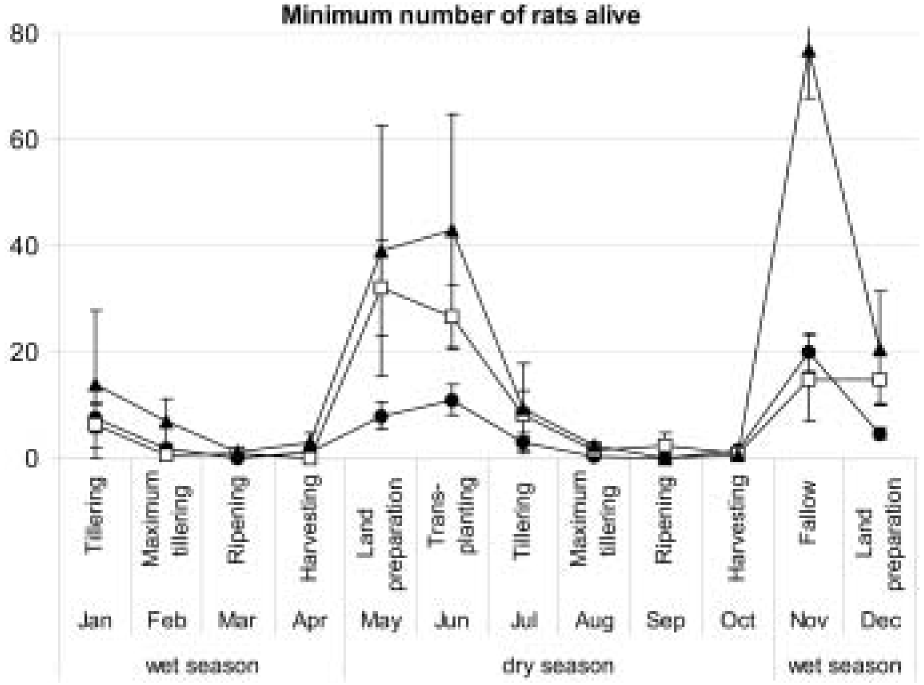

Figure 2. Relative abundance of rice-field rats as minimum numbers alive at monthly capture–mark–recapture trappings in rice fields (black dots), crop margin habitats (open squares) and village garden habitats (black triangles) in Cilamaya, West Java, Indonesia. Error bars are standard errors.

(maximum tillering, ripening and harvesting), there was a difference in MNAs between habitats at fallow, land preparation and transplanting (Figure 2) ($F_{8,120}$ = 2.01, p = 0.05). While few rats were caught at these crop stages in the rice fields, relatively high numbers of rats were usually caught in crop margin and village garden habitats. The latter habitats were relatively undisturbed during harvesting of rice and land preparation. In addition, shelter was not removed there and grass seeds and invertebrates may have been sufficient to sustain the rats until the next rice crop was transplanted.

The reproduction of rice-field rats usually ceases 2–3 weeks after harvesting of rice (Leung et al. 1999) and at that time the population size reaches its maximum. The high number of rats at that time does not pose a threat to the rice crop until transplanting because the only areas with rice plants present at this time—seed nurseries—can be successfully protected with fences (Sudarmaji, Rochman et al., this volume). Therefore, management actions to decrease rat numbers in crop margin and village garden habitats could be delayed until shortly before transplanting the rice from the nurseries into the fields. This timing would allow ‘natural mortality’ to decrease rat numbers for as long as possible before management actions are applied to minimise the founding population for the following planting season. However, management of rats in the crop margin and village garden habitats needs to be conducted before the rats recolonise and damage the freshly transplanted crop.

Rat management during community rat campaigns or bounty systems can remove high numbers of rodents from agricultural land within short periods of time. In these campaigns, rats are removed mainly by fumigation with sulfur gas and physical methods such as flooding burrows, digging, hunting, netting and trapping (Jacob et al. 2002). In Vietnam, a rat bounty scheme applied in 1998 in 47 provinces yielded 179 million rats (source: Plant Protection Division, Ministry of Agriculture and Rural Development, Vietnam). Bounty systems also are used occasionally in Indonesia. In regions where farmers are accustomed to rat campaigns on a community level, it may be relatively easy to conduct rat drives as a component of EBRM. We predict that the combination of traditional control methods applied during 2–3 week rat campaigns and follow-up control using CTBSs will result in lower damage to rice crops, higher yield and higher net income for farmers.

The cost of these management actions will have to be balanced with potential benefits. If rat numbers in refuges are low at early tillering of the rice crop, management actions may not be justified. However, one has to keep in mind that rats concentrate in refuge habitats at early tillering and, as a consequence, management can be targeted in smaller areas and possibly with much lower cost than at other times of the cropping cycle.

Conclusions

Based on our findings, we decided to use community rat campaigns in treatment areas in the village-level study as an additional tool for managing rice-field rats in lowland irrigated rice fields in West Java using EBRM. The campaigns are to be conducted in major refuge habitats (village gardens, channel banks, road verges) shortly before transplanting, when rat numbers are high at the end of the fallow. In conducting these studies, we will assess the effectiveness of using a combination of community rat campaigns and CTBSs for rodent pest management in lowland irrigated rice fields.

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Impact of village-level rodent control practices on rodent populations and rice crops in Vietnam

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Abstract. In Vinh Phuc, Vietnam, data on the species composition, population abundance, breeding, and habitat use of the main rodent pest species were obtained. Four sites were selected for a replicated field experiment to examine the effectiveness of ecologically-based rodent management at a village-level scale. We present 14 months' data from the beginning of the experiment, the first 11 months of which were before any management actions were imposed. Live-trapping was conducted every month within three different habitats of the rice-growing area. The main rodent species present were *Rattus argentiventer* (58%), *R. losea* (22%) and *R. rattus* (12%). There were two main peaks in population abundance, each following harvest of the main rice crops. Captures of rats were very low from March to May, at the end of the winter crop season when vegetable crops were grown. Breeding was evident from maximum tillering to just after harvest for each of the spring rice crops and summer rice crops. The use of habitats was slightly different for *R. argentiventer* and *R. losea*, with more *R. argentiventer* trapped along big channel banks compared with small banks and big banks. When the abundance of *R. argentiventer* was low, more *R. losea* were trapped along big channel banks, and when more *R. argentiventer* were trapped, *R. losea* favoured small banks, which suggested interspecific competition. It will be important, therefore, that any practice imposed to manage *R. argentiventer* also manages *R. losea*. Based on our understanding of the rodent community and population dynamics, we developed a series of rodent management practices to reduce damage to crops. These included targeting rodent management within refuge habitats early in the growth of the rice crop and the application of a community trap–barrier system.

Introduction

Rodents are a significant problem for agriculture in Vietnam. Rats are considered the number one pre-harvest pest of lowland irrigated rice crops, especially in the Mekong and Red River Deltas. Recent changes in the economic structure of agricultural production have led to a doubling of rice production in the Mekong and Red River Deltas. An important factor behind these increases is intensification of cropping from two to three crops per year. Rodents have benefited from this because of the increase in food supply and an extension of the time that high-quality food is available (Singleton and Petch 1994). The latter would extend the period within each year that breeding occurs because the breeding season of the principal pest species of rats is linked with the availability of rice from its maximum tillering stage to ripening (Lam 1980, 1983; Tristiani and Murakami 1998). It is not surprising, therefore, that rat problems have been serious in Vietnam since 1995 (Figure 1).

The rice-field rat, *Rattus argentiventer*, is the single most important pest to rice crops in Vietnam, and it is an important pest of rice crops in other parts of Southeast Asia, including Malaysia and Indonesia. In Indonesia, it causes annual pre-harvest losses of around 17% (Geddes 1992; Leung et al. 1999). Other rodent species inhabiting rice fields in Vietnam include *Rattus losea*, *R. rattus* and *Bandicota indica* (Brown et al. 1999). Little is known about how these pest species interact within the rice-growing areas or how management should be implemented to mitigate damage to rice crops. Currently, most farmers are reactive in their actions, only implementing management once the rat problem is moderate to severe.

Methods for controlling damage caused by rodents in rice agro-ecosystems include the application of rodenticides (Buckle 1999), hunting, fumigation, physical barriers such as the trap–barrier system (TBS, Singleton et al. 1998, 1999), and cultural practices such as synchronised cropping, sanitation of fields and encouraging predators (such as barn owls) (Leung et al. 1999).

Our research is aimed at understanding the ecological factors influencing rodent populations in rice ecosystems in the Red River Delta, Vietnam. This ecological understanding has led to the identification of key management actions and the subsequent decision analysis of their feasibility and timing of application, their likely economic and environmental impact, and the required scale of implementation. The impact of integrating these management actions is currently under assessment at the village level through close cooperation with farmers in a replicated, controlled field experiment. As this study is in progress, the purpose of this paper is to (a) present background data on the species composition of the rodents inhabiting the rice fields of Vinh Phuc Province, (b) examine the population dynamics and breeding seasons of the most common species and relate these to the cropping system, (c) compare capture rates of rats in different habitats, and (d) describe the basic design and implementation of treatments for the village-level study.

Materials and methods

Study site

The study areas were all within Vinh Phuc Province, in northern Vietnam, 40 km north of Hanoi (21°08'N, 105°45'E). Four study sites were selected in March 1999 and comprised part of a main village or sub-villages. Each site was 0.5 to 1 km apart. The sites were set up to monitor the population dynamics of rats before implementation of ecologically-based rodent management. Each site was about 100–150 ha in size. Within each site, families manage small plots of land (called 'sao', which are 360 m^2). Each family generally owns 0.5–0.7 ha of land. The principal crop grown in the area is rice. There are two main rice-growing seasons each year, the spring rice season (transplanted late February and harvested mid-June), and the summer rice season (transplanted mid-July and harvested late September). Other crops grown are vegetables (broccoli, Chinese cabbage, kohlrabi, onion, pumpkin, tomato) and flower crops (chrysanthemum, rose). Summers are hot and wet, and winters are cool and dry. The annual average rainfall is approximately 1600 mm, most falling between May and September. Farmers irrigate their crops using water supplied by channels originating from large storage dams in nearby hills.

Monitoring of rat populations

Live-trapping for rats was implemented every month from April 1999 until May 2000 using single-capture wire traps (100 × 100 × 300 mm) baited with vegetables. Twenty traps were set for four nights across each of three trap-lines with two replicates of each line. The trap-line habitats investigated were: (1) 'big channel banks', large earth banks for transporting water, each bank 2 m high by 3 m wide; (2) 'small banks', 300 mm high by 300 mm wide for retaining water within paddies and for walking between fields; and (3) 'big banks', large earth banks for paths 1–2 m high and 2–5 m wide. There were 480 trap nights per census. Traps were placed at 10 m intervals, and trap lines were placed 50–100 m apart. Each captured rat was marked with an ear punch, identified for species, sexed, breeding condition determined for females (evidence of lactation or pregnancy), and measured (tail length, ear length, hind foot length, body weight). All animals were released at the site of capture.

Breeding samples were collected from 15 adult female *R. argentiventer* and 15 *R. losea* per month (the two main species caught). These animals were euthanased and assessed for uterus size, number of embryos, and size of embryos (trimester of development). These data were used to determine the commencement and cessation of breeding, percentage of adult females in breeding condition, and the average number of embryos per pregnant female.

Results and discussion

Species composition

The most common rat species caught was the rice-field rat (58%), followed by the lesser rice-field rat (22%) (Table 1). In total, seven species of rodent were captured, as well as an insectivorous shrew (*Suncus murinus*).

Population dynamics

There were two peaks in abundance—the first after harvest of the spring rice crop in July and the second after

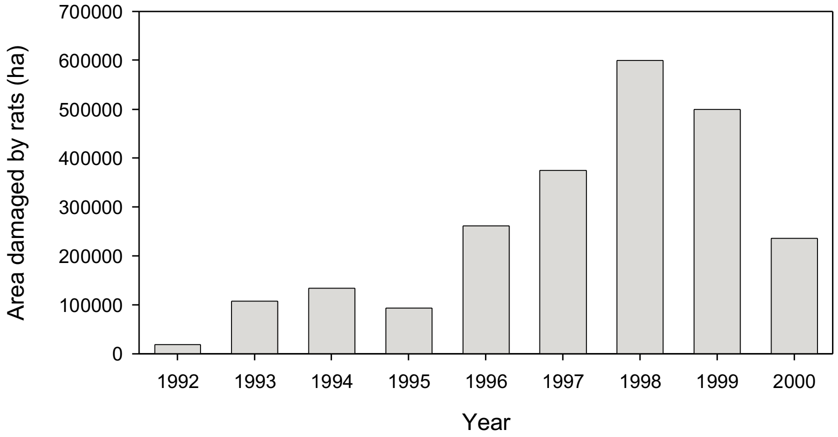

Figure 1. Area of rice crops (ha) damaged by rats in Vietnam since 1992. Data from Brown et al. 1999 and Ministry of Agriculture and Rural Development (2000).

harvest of the summer rice crop in October (Figure 2). *R. argentiventer* was more common than *R. losea* ($F_{1,60}$ = 9.38, $P < 0.01$), and the abundance of the rats was higher in July and October 1999 than other months ($F_{13,60}$ = 3.496, $P < 0.001$). The peak in abundance in October coincided with the damage observed to kohlrabi crops at that time (Tuan et al., this volume). Captures of rats were lowest during March, April and May after harvest of the winter crops and during the early growth phase of the spring rice crop. No marked animals were recaptured. *R. argentiventer* are well-known for their low recapture rate (Brown et al. 1999; Leung et al. 1999).

Breeding was evident from maximum tillering of the rice crop through to a few weeks after harvest during each rice crop. Very few adult female rats were in breeding condition during the winter period (<5% of captures). The average litter size of *R. argentiventer* was 9.0 pups (se = 0.30, *n* = 83), with 7.5 pups for *R. losea* (se = 0.30, *n* = 53).

Habitat use

Consistently more *R. argentiventer* were trapped on the big channel banks compared with the other habitats ($F_{13,90}$ = 3.693, $P < 0.05$) (Figure 3). Likewise, *R. losea* were more commonly trapped on big channel banks than other habitats ($F_{2,90}$ = 5.545, $P < 0.01$). The abundance of both *R. argentiventer* and *R. losea* was higher during June, July, August and October compared to other months ($F_{13,90}$ = 8.834, $P < 0.001$; $F_{13,90}$ = 8.480, $P < 0.001$, respectively), but the interactions were not significant ($F_{26,90}$ = 0.457, P = 0.987; $F_{26,90}$ = 1.403, P = 0.123, respectively). A Pearsons correlation analysis between captures of *R. argentiventer* and *R. losea* in each habitat showed that the highest correlation coefficient was for the relationship between the captures of *R. argentiventer* on big channel banks and captures of *R. losea* on small banks (R^2_{14} = 0.931, $P < 0.001$), and that the lowest correlation was for the relationship between

Table 1. Main small mammal species caught at Vinh Phuc Province, northern Vietnam, from April 1999 to May 2000.

Species	Common name	Vietnamese name	Number	%
Rattus argentiventer	Rice-field rat	Chuot dong lon	541	58.0
Rattus losea	Lesser rice-field rat	Chuot dong nho	204	21.9
Rattus rattus	Black rat	Chuot nha	110	11.8
Bandicota indica	Great bandicoot rat	Chuot lon	42	4.5
Mus sp.	Mouse	Chuot nhat	13	1.4
Rattus norvegicus	Norway rat	Chuot cong	5	0.5
Suncus murinus	Shrew	Chuot chu	2	0.2
Other rodent species not accurately identified		Cac loai chuoj chua xac dinh ten	16	1.7
Total			933	100

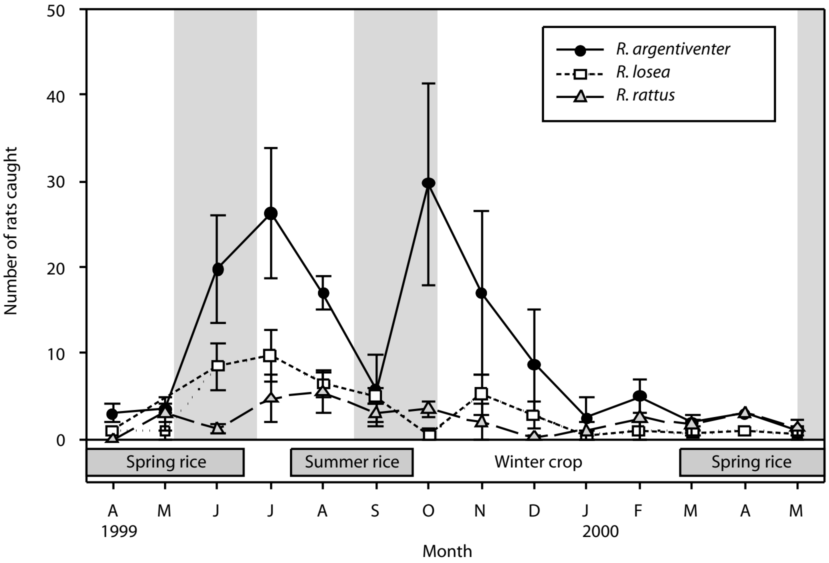

Figure 2. Population dynamics of the three common *Rattus* species at the Vinh Phuc study site from April 1999 to May 2000 in four sites trapped (means ± standard error). The shaded bars represent each breeding season. Crop stages are indicated for spring and summer rice crops and winter crops. The horizontal bars represent the duration of the rice crops.

captures of *R. losea* in small banks and *R. losea* in big channel banks ($R^2_{14} = 0.662$, $P < 0.01$). This suggests that when captures of *R. argentiventer* were low on big channel banks in September, there was a corresponding increase in captures of *R. losea*. *R. losea* favoured big channel banks only when fewer *R. argentiventer* were present. When relatively more *R. argentiventer* were trapped on the big channel banks, *R. losea* was predominantly found on small banks. These results indicate that interspecific competition for resources is occurring, with *R. argentiventer* considered the dominant species. Further research involving diet studies, monitoring habitat use through radio-tracking, and manipulative studies where only *R. argentiventer* are removed could assist our understanding of the interactions between the two species.

Development of village-level rodent control

Based on the results described above on the dynamics, breeding patterns and habitat use of the main rodent species, a series of management practices were developed for farmers to implement. From the four study sites, two treatment sites (farmers are encouraged to conduct the rodent management practices) and two untreated sites (farmers are not influenced in their rodent management practices) were selected. The selections were based on the abundance of rats and damage to rice crops and on discussions with village-heads on the willingness of farmers to conduct and implement the rodent control practices. This work is ongoing.

Before implementation of treatments, a meeting with farmers at the treatment sites was held to discuss the different rodent management practices available. These included routine actions (field sanitation, synchronous land preparation, TBS, reducing refuge around villages, and cleaning up after harvest), and actions if high numbers are forecast (trapping and hunting, using rodenticides, bounty on rats, and digging burrows). A survey of rodent control practices used by farmers at the Vinh Phuc study sites was summarised by Tuan et al. (this volume). Although various control methods are available to reduce the impact of rats on rice crops, the main control techniques traditionally used by farmers are poisoning and trapping (Tuan et al., this volume). The effectiveness of rodenticides is often compromised because the bait is not mixed properly, is placed in inappropriate locations, or is poorly timed to the rodent breeding cycle. Farmers frequently use poison baits after rodent damage has occurred rather than to prevent damage. Furthermore, the cost of chronic poisons is usually prohibitive for farmers, and there are serious risks of non-target poisoning (P.R. Brown and N.P. Tuan, personal observations).

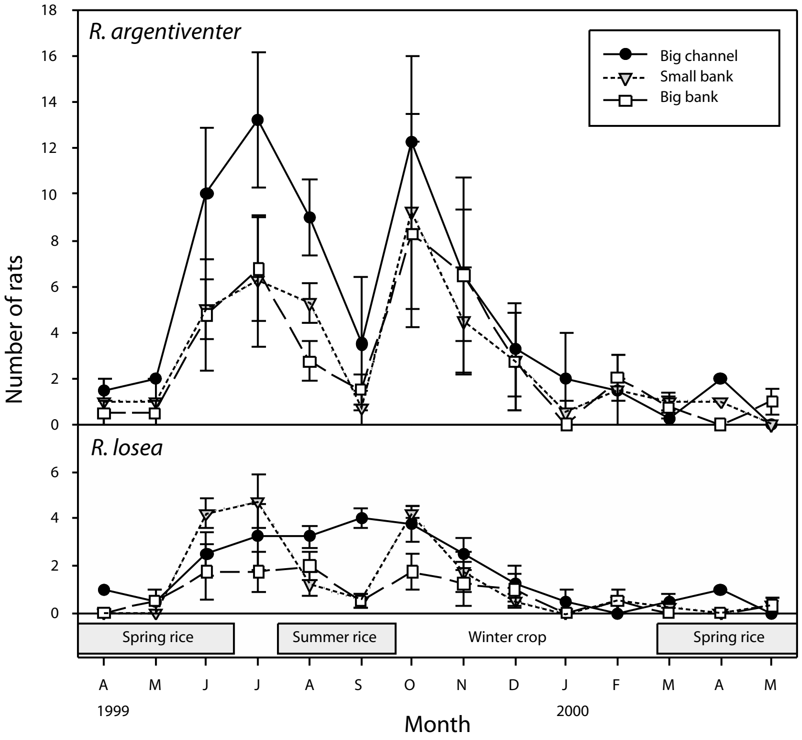

Figure 3. Habitat use of *Rattus argentiventer* and *R. losea* in Vinh Phuc Province from April 1999 to May 2000 as the average number of rats captured in trap lines set along big channel banks, small banks and big banks (means ± standard errors). Crop stages are indicated for spring and summer rice crops and winter crops. The horizontal bars represent the duration of the rice crops.

Table 2. List of farm management practices for managing rodents in the Red River Delta, Vietnam.

Management action	Timing[a]	Feasibility	Scale of adoption	Priority
Routine actions				
Field sanitation	LP	Yes	Farmer	High
Synchronise land preparation, seeding and planting	LP, SB, TP	Availability of labour	Village	Medium
TBS by farmer group[b]	TP	Yes	Village	High
Reduce bund size within rice fields	LP	Yes	Village	High
Encourage natural predators	All	?	District	High
Reduce refuge around villages	All	Yes	Village	High
Clean up after harvest	H, F	Yes	Village	Medium
Actions if high numbers are forecast				
Trap and hunt	All	Yes	Farmer	High
Apply chemical baits in field and houses	TP–MT	Yes	Village	Medium
Bounty system on rat tails/heads	LP–TP	? ($)	Commune	High
Dig burrows	LP–TP	Yes	Commune	Medium
Monitor rat activity in field	All	No	Village	Low

[a] LP = land preparation, SB = seed bed, TP = transplanting, MT = maximum tillering, H = harvesting, F = fallow.
[b] The trap–barrier system (TBS) needs to be planned in advance and set up 3–4 weeks before surrounding rice crops.

Research trials to develop rodent management practices for Indonesia (Leung et al. 1999) and the Mekong Delta region of Vietnam (Brown et al. 1999) indicated that a similar set of management actions for farmers in the Red River Delta would be appropriate (Table 2).

The management actions were assessed for their feasibility of implementation, including whether the action was economical, socially acceptable, environmentally friendly and sustainable, the scale of likely adoption, and its priority for farmers to implement. These management actions were developed by scientists and extension officers, through combining scientific knowledge on the biology and management of the rodent pest species with the concept of ecologically-based management defined by Singleton (1997).

Success of the rodent management practices will be assessed through comparing differences in the abundance of rodents between treated and untreated sites, the level of damage inflicted on crops, and differences in yields obtained by farmers. The use of chemical rodenticides and plastic barrier fences by farmers in the survey areas (without traps or a lure crop) is also under assessment.

Conclusion

The data collected are providing valuable information on the species composition, habitat use and abundance of the main rodent species in Vinh Phuc Province. This knowledge will help refine the rodent management practices that farmers will use, and to target key rodent habitats at key times. The benefits of this project will be demonstrated if there are increases in crop yields and less reliance on chemical rodenticides.

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Rodent problems in India and strategies for their management

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Abstract. Rodents are major vertebrate pests due to their endemicity and propensity to damage major crops at the farm level and in storage in India. Analysis of the reviews on pre-harvest losses indicates a range of 5–15% damage to major cereal crops of rice and wheat. Instances of rodent outbreaks also occur due to bamboo flowering in the north-eastern states, and prolonged dry spells followed by heavy rains and flash floods in other states. Reports also exist on increased incidence of zoonotic diseases such as plague and leptospirosis. The lesser bandicoot rat, *Bandicota bengalensis*, is predominant in irrigated crops throughout the country including arable areas of the Thar Desert. The Indian gerbil, *Tatera indica*, soft-furred field rat, *Millardia meltada*, and field mouse, *Mus booduga*, are widespread in both irrigated dryland and dryland crops in the country, except in the north-eastern states. Due to the research support extended by the Indian Council of Agricultural Research (ICAR) All India Network Research Project on Rodent Control, Jodhpur, adequate technology for effective rodent management is available. The use of rodenticides is the most common approach to the rodent problem, but environmental and cultural techniques, such as clean cultivation, proper soil tillage and crop scheduling, have had long-lasting results. A National Programme on Rodent Pest Management, launched during 1976, with trainers' training, community preparation, technology and actual control operations, produced significant results in preventing rodent damage. With planning on rodent management by the Government of India, the emerging rodent-related problems could be controlled effectively. Currently, problems occur due to increases in intensive cropping in expanding irrigation areas, changing agricultural practices resulting in replacement of desert rodents with lesser bandicoot rats, increased coconut cultivation failing to follow proper spacing, cultivation of oil palm in rodent-endemic areas, and natural calamities like flash floods and drought spells followed by heavy rains.

Introduction

Indian agriculture has progressed a long way from an era of frequent droughts and vulnerability to food shortages to become a significant exporter of different agricultural commodities. This can be attributed to harnessing a larger portion of the land for agricultural purposes and introduction of new technologies. A spectacular rise in food grain production took place from 1949–50 to 1999–2000 (from about 55 to 206 million t). The thrust in intensive cropping, coupled with increased fertiliser use, resulted in an increase in pest problems with a crop loss of 10–20% annually, amounting to rupees (Rs)60,000 million in field and storage situations (Rajak 1993).

Economic importance of rodents

Agriculture

Rodents cause direct damage to various crops/commodities by gnawing and feeding, and indirect damage by spoilage, contamination and hoarding during on-farm and post-harvest stages (Rao and Joshi 1986; Parshad 1999). However, the pattern and level of rodent infestation, and the extent of damage, vary in different crops and geographical regions (Table 1). Most of the estimates of damage relate to isolated studies in smaller plots and extrapolated to larger areas. Hart (2001) reported that overall losses of grain to rodents in India were approximately 25% in pre-harvest and 25–30% in post-harvest situations, bringing the loss to at least US$5 billion annually in stored food and seed grain in India. Often chronic losses go unrecognised and these losses are economically more important.

Rodent outbreaks

Population explosions of rodents sometimes result in rodent outbreaks (Chauhan and Saxena 1985; Rao et al. 1998) (Table 2), on occasion resulting in famines. Reasons attributed to outbreaks are: (i) prolonged drought/dry spell followed by heavy rains increasing the reproductive propensity of the rodent pests, as happened in Saurashtra region of Gujarat state; (ii) failure of the monsoon in the preceding year, resulting in a favourable environment for rodent breeding, as in Cauvery Delta area of Pondicherry (Karaikal region) and Tamil Nadu (Tanjor and Nagapattinam districts) states; (iii) flash floods leading to unusual increases in the subsequent carrying capacity of the environment and to the absence of predators in the delta areas, as happens in Andhra Pradesh (East Godavari and West Godavari districts); and (iv) flowering of species of bamboo (*Melocanna bambusoides* and *Bambusa tulda*), leading to increased carrying capacity in *jhum*[1] cultivated fields in Arunachal Pradesh, Manipur, Mizoram and Nagaland states.

Cereal crops

Analysis of reviews on pre-harvest losses indicate a range of 5–15% damage to cereal crops like rice and wheat (Sridhara 1992; Chopra et al. 1996; Parshad 1999; Singleton 2001). The lesser bandicoot rat, *Bandicota bengalensis*, is the predominant rodent pest in these crops. The vulnerable crop period is the boot leaf stage, due to the availability of sweaty mucilage. Crop compensation does not occur after this stage.

Sugarcane

Gnawing lower internodes of sugarcane causes direct damage at the sugar formation stage of the crop. Even incisor injury to the cane is often associated with secondary losses in yield and quality because of red rot caused by *Physalospora tucamanesis*. Christopher (1987) reported a yield loss of gur (dark, unrefined sugar) at 45.6 kg/ha with 20.7% damage in Andhra Pradesh. While regularly propped and detrashed fields resulted in totally erect crops, improperly maintained ones resulted in lodging of cane. Neglected fields had a staggered damage of 63%. Bindra and Sagar (1975) and Srivastava (1992) also reported similar damage patterns. *B. bengalensis* is the predominant rodent pest species in the crop. In Punjab, *Nesokia indica* also inhabits sugarcane fields. Rodents

Table 1. Extent of crop losses due to rodent pests, the pest species involved, and their distribution in India.

Crop	Extent of loss (%)	Rodent pest species	Habitat/distribution of species
Rice	1.1–44.5	*Bandicota bengalensis* *Millardia meltada* *Mus booduga* *Rattus nitidus* *Rattus rattus brunneusculus*	Irrigated fields Semi-irrigated fields Irrigated fields *Jhum* fields in the north-east *Jhum* fields in Mizoram
Wheat	2.7–21.3	*Bandicota bengalensis* *Millardia meltada* *Tatera indica* *Meriones hurrianae*	Irrigated fields Irrigated dry fields Rainfed fields Desertic soils in Indian desert
Sugarcane	2.1–31.0	*Bandicota bengalensis* *Nesokia indica* *Millardia meltada*	Irrigated fields Irrigated fields in Punjab Irrigated fields
Groundnut	2.9–7.3	*Tatera indica* *Millardia meltada* *Bandicota bengalensis*	Irrigated dry fields Irrigated dry fields Irrigated fields
Coconut	4.5–55.0	*Rattus rattus*	Throughout India
Cocoa	30.0–50.0	*Rattus rattus wroughtoni* *Funambulus palmarum* *Funambulus tristriatus*	Southern India Andhra Pradesh and Tamil Nadu Kerala and Karnataka
Oil palm	11.2–57.3	*Bandicota bengalensis* *Hystrix indica* *Tatera indica*	Fruits in southern India and Andaman Seedlings in nurseries
Vegetables	1.4–30.6	*Bandicota bengalensis* *Millardia meltada* *Tatera indica* *Meriones hurrianae* *Funambulus pennanti*	Irrigated fields Irrigated dry fields Dry fields Indian desert soils Northern India
Fruits	Varied	*Funambulus pennanti* *Funambulus palmarum*	Northern India Southern India
Storage	2.5	*Rattus rattus* *Mus musculus* *Bandicota bengalensis*	Residential premises and farm level storage

Source of damage data: Rao and Joshi (1986) and Parshad (1999).

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[1] '*jhum* cultivation' is shifting cultivation in which the forest is burnt periodically in different places.

colonise cane fields because they provide an undisturbed habitat for burrowing, feeding, breeding activities and protective cover from avian predators for most of the year. Further, the crop affords an alternative site for rodent activity during the inter-cropping period in surrounding fields, especially rice/wheat.

Pulse and oilseed crops

The high protein content of seeds results in moderate rodent damage to the pods of lentil, arhar, moong, soybean and Bengal gram. Changing patterns of agricultural practices, such as introduction of summer pulses between the *rabi* (winter crop) and ensuing *kharif* (rainy season crop) seasons, made availability of food continuous for rodents, increasing their population and rendering the area endemic for these pests. Awasthi and Agarwal (1991) reported a yield loss of 16.5 kg/ha in soybean crop at the green pod stage.

Groundnut is grown as an irrigated dry crop in most areas in the country. Rodents damage and remove the pods at sowing time and at maturity (4–7%) and hoard sometimes up to 320 g/burrow (Patel and Nayak 1987; Mittal and Vyas 1992). Indian gerbil, *Tatera indica*, and soft-furred field rat, *Millardia meltada*, along with *B. bengalensis*, cause the major damage in irrigated fields. During the rodent outbreaks in Gujarat in 1976 (Shah 1979) and 1988–89 (Vyas et al. 2000), rodents damaged up to 85.42% of the crop in the Saurashtra region.

The area under oil palm cultivation is increasing and there are reports of rodent damage in several parts of the country, although documentation of the damage was done only in the Andaman islands. Rodents damage the female flowers while feeding on the oil-bearing tissue. Subiah (1983) and Advani (1985) reported up to 57.3% damage to oil palm fruits.

Plantation crops

Coconut is one of the major plantation crops affected by rodents, with damage done at the point of attachment of the nuts and to the pulp. Most of the damaged nuts fall to the ground after 2–4 weeks of damage (Shamsuddin and Koya 1985; Rao 1995). Most coconut palms are infested by *Rattus rattus* and 10–32% damage often occurs to tender coconuts (Subiah and Shamsuddin 1992; Rao 1995; Gandhi 2001). The bunch size class with 6–10 nuts was reported to be more affected (36%), suggesting placement of baits at the base of such bunches (Gandhi 2001).

Rodents also affect the shrub plantations of cocoa and cardamom. Squirrels and rats make irregular holes in the cocoa pods (sometimes up to 50%) to feed on their contents (Bhat 1992). Injured pods are not fit for use due to black pod disease caused by a fungus, *Phytophthora palmivora.* Cardamom capsules are damaged by *B. bengalensis* and five-striped palm squirrel, *Funambulus palmarum*, at the ripening stage when they begin to emit the typical cardamom odour (Srihari and Chakravarthy 1992).

On-farm damage after harvest

Malhi and Parshad (1987) reported a loss of 4.31% panicles, equivalent to 1.11 quintals per hectare of wheat and 4.64% loss of rice panicles, equivalent to 1.72 quintals of coarse rice after harvest and before the produce was lifted from the field.

Post-harvest losses

Farmers retain 60–70% of their produce in storage. A committee constituted by the Government of India for assessment of storage losses in 1996 estimated a total loss

Table 2. Rodent outbreaks in India during the last 10 years

Year	State/Union territory	Area (and crops affected)	Estimated loss
1990–91	Gujarat	Saurashtra region (groundnut, wheat, gram and cotton)	Not available
1994	Pondicherry	Karaikal region (rice, gram and soyabean)	Not available
1994	Tamil Nadu	Cauvery Delta (rice and gram)	Not available
2001	Tamil Nadu	Cauveri Delta (rice)	Not available
1997–98	Andhra Pradesh	210,000 ha in Godavari Delta (rice)	3301.85 million t
2001	Andhra Pradesh	31,000 ha in East Godavari district (rice)	Not available
1999–2000	Arunachal Pradesh	7000 ha (rice and maize)	Not available
1999	Manipur	1000 ha (*jhum* rice)	Not available
2000	Manipur	1264 ha (*jhum* rice)	Not available
1999–2000	Mizoram	53,945 ha (rice, maize and vegetable crops)	Not available
1999–2000	Nagaland	1000 ha (rice)	Not available

Source of information: Directorate of Plant Protection, Quarantine and Storage, Department of Agriculture and Cooperation, Ministry of Agriculture, Government of India.

of 9.33% for food commodities, and rodents accounted for 2.5% of this. A national study made by the Indian Grain Storage Management and Research Institute (IGMRI) revealed a total post-harvest loss of 4.75% of wheat with rodents accounting for 0.59%. Rodents contaminate food with their hair, urine and faecal droppings, the level varying in different situations. The daily rate of defecation was reported as 22 pellets for *B. bengalensis* and 13 pellets for *M. musculus* (Nimbalkar 2000). Due to this, the Government of India stipulated that food commodities should not have hair and excreta in excess of five pieces per kg sample under *Prevention of Food Adulteration Rules 1956* and amended from time to time.

Public health

Rodent-related problems exist in public health due to their role as vectors and reservoirs for bacterial diseases such as leptospirosis, murine typhus and salmonellosis, in addition to plague. As humans and livestock are in regular contact with rodents, the potential for transmission of zoonotic diseases is high. Limited investigative work exists on the exact role that rodents play in the epidemiology and transmission of human and animal diseases.

Plague

Although plague has been present in India since the 16th century, the mortality attributed to it in British India from 1896 until 1994 was 12,657,077 lives (Viliminovic 1972; John 1996). During 1994, 54 fatalities were reported among 876 cases (WHO 2000a). During February 2002, a confirmed report of plague was received from Himachal Pradesh.

In India, sylvatic plague foci are recognised at the foothills of the Himalayas (Jammu and Kashmir, Himachal Pradesh, Uttaranchal and Bihar), in the watersheds of the Vindhyas (Madhya Pradesh) and in the Deccan Plateau covering Andhra Pradesh, Karnataka, Maharashtra and Tamil Nadu states (John 1996). Rodents are primary hosts of *Yersinia pestis* (the causal agent of plague), which is transmitted by the oriental flea, *Xenopsylla cheopis.* The primary species of wild rodent infected with *Y. pestis* in India is the Indian gerbil, *Tatera indica.* This gerbil is susceptible to infection, but resistant to disease and consequently acts as a permanent reservoir host. When gerbils frequent fields around human habitations, peri-domestic rodent species like *B. bengalensis* in these fields become infested with the plague-infected flea. This transmits in turn to *R. rattus* in ruderal habitats. Both *R. rattus* and *B. bengalensis* are susceptible to infection, disease, and rapid mortality. This can lead to increased incidence of human plague.

Leptospirosis

Leptospirosis is a zoonotic disease which occurs worldwide in warm humid tropical countries. The International Leptospirosis Society opined that greatly in excess of 100,000 severe cases of leptospirosis occur annually worldwide (WHO 1999). This survey and available information indicate human leptospirosis-infected areas in Andamans, Gujarat, Kerala, Maharashtra, and Tamil Nadu. The animal hosts for leptospirosis are cattle, rodents, pigs, dogs and cats. The common sero group is *icterohaemorrhagiae.* Pathogenic species of *Leptospira* survive for long periods in the convoluted tubules of the kidney in natural hosts, mostly rodents. The organisms multiply and up to 100 million leptospires/mL urine may be shed. The infectious bacillus is transmitted to man by skin contact, particularly contact with broken or abraded skin, in stagnant waters. Hence, rice and sugarcane field workers are particularly vulnerable to this disease because of their working conditions.

In India, three rodent species (*Rattus norvegicus*, *R. rattus* and *B. bengalensis*) are known to be associated with this disease (Gangadhar 1999), which is more common than ordinarily diagnosed—many so-called ‘fevers of unknown origin’ being caused by it (John 1996). Leptospirosis was reported in Orissa (WHO 2000b) after the 1999 cyclone and affected at least 14.1% of the population due to the closer interaction between humans and reservoir animals. Leptospirosis is often ignored or undiagnosed due to lack of awareness, misdiagnosis, and a lack of diagnostic services (WHO 2000b).

Other diseases

Since 1990, a variety of typhoid fever caused by *Salmonella typhi* and resistant to most of the existing antibiotics has been prevalent in many parts of India (John 1996). Human infections with the virus causing Kyasanur forest disease were reported in Karnataka state. The disease is transmitted by ticks belonging to the genus *Haemaphysalis* and is maintained in small mammals, such as *Suncus murinus* and *Rattus* spp., while monkeys in forest areas serve as amplifying hosts (Rajagopalan 1966).

Major rodent pest species

The rodent fauna of the Indian sub-continent is represented by 46 genera and 128 species (Roonwal 1987). Among them, 13 species are predominant pests requiring attention (Table 1). The lesser bandicoot rat, *B. bengalensis*, is predominant in irrigated crops throughout the country, including arable areas of the Thar Desert, but is not present on Lakshadweep and Andamans islands (Rao 1993). Due to its ferociousness, it replaced other species and became a major pest in storage situations and other premises in metropolitan cities like Mumbai, Calcutta and Delhi.

The Indian gerbil, *T. indica*, soft-furred field rat, *M. meltada*, and field mouse, *Mus booduga*, are widespread in both irrigated dryland and dryland crops in the country except in the north-eastern states. The Indian crested porcupine, *Hystrix indica*, is widely distributed in hillock or arid habitats, occasionally inflicting severe damage to crops, orchards and reforestation plantations.

Other rodent species have restricted distribution, namely: the desert gerbil, *Meriones hurrianae*, in desert areas; the Himalayan rat, *Rattus nitidus*, in the north-eastern region; the short-tail mole rat, *Nesokia indica*, in the north-western plains; the three-striped squirrel, *Funambulus palmarum,* on the southern peninsula; the five-striped squirrel, *F. pennanti*, on the northern peninsula; the western Ghat squirrel, *F. tristriatus*, on the west coast of the southern peninsula; and the Norway rat, *R. norvegicus*, in port areas.

The house rat, *R. rattus*, and the house mouse, *Mus musculus*, are the major commensal pests (Prasad and Rao 2000). At least 14 subspecies of *R. rattus* have been reported from India (Biswas and Tiwari 1969). Of these, *R. r. rufescens* Gray occurs in premises throughout the country, *R. r. wroughtoni*, Hinton and *R. r. blanfordi* Thomas are restricted to plantation crops like coconut, oil palm and cashew on the southern peninsula (Bhat 1992), *R. r. andamanensis* Blyth occurs on Andaman and Nicobar Island (Subiah and Mathur 1992) and *R. r. brunneusculus* occurs in Mizoram (Chauhan and Saxena 1985).

Existing technical know-how

Due to the research support extended by the Indian Council of Agricultural Research (ICAR) All India Network Research Project on Rodent Control, Jodhpur, adequate technology for effective rodent management exists (Rana and Tripathi 1999).

Environmental and cultural methods

Several agronomic measures used in raising crops in the country contribute indirectly to reduction of rodent populations. Deep ploughing, bund trimming and other land preparation measures reduce the carrying capacity of the habitat for rodents. Routine weed removal by farmers in crops also deprives rodents of shelter and alternative food sources. Sharma and Rao (1989) reported a decline in rodent infestation in rice fields with reduction in bund dimensions. Sabhlok and Pasahan (1985) also reported migration of gerbils from about 65–78 m away after removal of wild vegetation from the fields. Christopher et al. (1984) reported that periodic removal of garbage and nesting material in animal/human dwellings, stores and godowns discourages rodent habitation. Alley planting of rice also reduces rodent damage (Anon. 1959–69).

Physical elimination of field rats is in vogue with communities in Irulas of Tamil Nadu and Erukulas of Andhra Pradesh where rats are used for food. Rodents, especially *T. indica* and *B. bengalensis*, are caught physically by digging the burrows. Sometimes, fumigation of burrows using smoking straw is employed. However, this physical killing is done often around the time of ripening of the crop after maximum rat damage has already occurred. Staff at Acharya N.G. Ranga Agricultural University, Hyderabad, developed an improved smoke generator for effective control of burrowing rodents. Paddy straw is burned, leading to the generation of smoke, which is pushed into the burrow tunnel with the help of a blower (Rana and Tripathi 1999).

Trapping

Although trapping is one of the oldest methods, there is little proof in the scientific literature that it is an effective method of reducing rodent numbers (Reddy 1999). *Tanjor kitties* (bamboo palmyra traps) are effective in maintaining rodent numbers at a low level once they have been reduced by other methods. Indigenous bamboo snap-traps are laid on the periphery of *jhum* cultivated fields in the north-eastern states to trap rodents immigrating from adjoining forest areas and resemble the trap–barrier system of rodent management (Singleton et al. 1999).

Role of predators

Biological control existed in the country before the 1970s due to the presence of natural predators. Cats in domestic situations, and snakes and owls in field situations, are the predominant vertebrate predators. Whitaker and Dattatri (1986) reported that rodents constitute prey items for the cobra (75%), Russels viper (75%), krait (29%) and scaled viper (22%). However, the feeding rate of captive snakes is one rodent every three days. This predatory pressure on rodents is very low compared to the faster breeding propensity of rodents. Hence, snakes alone may not be able to control rodent populations in nature.

Kumar (1985) reported that 61% of the total estimated biomass of the pellets of spotted owlet was *R. rattus* and *M. musculus.* Neelanarayanan (1997) reported the consumption of 1–6 rodents/night by the barn owl, with an average of 1.58 rodents/day. *B. bengalensis* (40%) and *M. musculus* (33%) constituted the major prey items. Provision of nest boxes (91.4 × 45.7 × 53.3 cm) and T-shaped owl perches provided alternative sites for barn owls for predatory activity (Neelanarayanan 1997). However, declining rodent populations post-harvest resulted in predators leaving the area**.** The T-shaped owl perches are currently popular in cereal crops as one of the integrated pest management (IPM) practices. However, their use is not desirable after the flowering stage of crops because granivorous birds use the perches during their feeding activity in the grain crops.

Use of microbes

Salmonella and murine typhus bacteria were found to be ineffective against *R. rattus* and *B. bengalensis* in India (Deoras 1964). Bindra and Mann (1975) reported that the murine typhus bacterium cause <40% mortality of *M. musculus* and *T. indica*. Studies with the trichostrongloid nematode, *Hepatojarakus bandicoti*, are yet to explore the potential for rodent control. Studies on virally vectored immunocontraception (Hinds et al., this volume) are yet to be considered in India.

Ultrasound devices

The sense of hearing among rodents is above 20 kHz, thus extending well into the ultrasonic range. Ultrasound devices are being used as deterrents to rodent immigration but to date evidence has found them ineffective.

Chemical repellents

There is no effective chemical repellent to rodents available that is not also toxic to humans. Field rodents often damage the imported rodent-repellent cables installed in telecommunication networks. Although pheromones appear to be promising, scientific work is lacking to identify, isolate and introduce pheromones for extension purposes.

Rodenticides

The use of rodenticides is the most common approach to tackle the rodent problem in the country. Among the seven rodenticides registered under the *Insecticides Act 1976*, those able to be marketed and used commonly include aluminium phosphide, zinc phosphide, bromadiolone and coumatetralyl.

Zinc phosphide is the most commonly used acute rodenticide. Used at 2% in cereal baits, it detoxifies rapidly in carcasses and baits, and thus is relatively safe and economical (Prakash and Mathur 1992). Development of bait shyness and the lack of an effective antidote are limitations to its use. The control success that can be achieved is usually around 60% (Rao et al. 1998). ICAR recommends use of zinc phosphide in rice, wheat, jowar, millets, sugarcane, pulses, oilseeds and vegetable crops. However, due to toxicity problems in non-target species, its use is advocated primarily in situations where rodent infestations are at high levels, i.e. 50 active burrows per hectare. Efforts are in progress to develop a ready-to-use formulation of this rodenticide for effective application in different situations.

Among first-generation anticoagulants, coumatetralyl is used in cereal-mixed baits at 0.0375%, mostly in storage/domestic situations. Low toxicity level, chronic action and availability of vitamin K_1 as an antidote make it an effective anticoagulant. It is also recommended in controlling *B. bengalensis* in crops of Punjab (Rana and Tripathi 1999).

The second-generation anticoagulant bromadiolone has been available commercially in ready-to-use formulation since 1988 for use in crops and storage/domestic situations. It is recommended as a component of the IPM packages for rodent control in crops with moderate levels of rodent infestation. It is used in cereal bait at 0.005% and applied inside burrows at 15 g per burrow. It is advocated for use in bamboo bait stations in *jhum* fields of the north-eastern states. Bait shyness does not exist with this chemical, hence a second application is recommended after 15 days to address the residual rodent infestation (Rana and Tripathi 1999).

Application of aluminium phosphide pellets at two per active burrow is recommended for effective field rodent control. Due to easy handling, application and immediate kill of rats inside burrows, the farming community prefers this fumigant rodenticide. However, because of the higher toxicity of the chemical to non-target species and the absence of an antidote, the Government of India has restricted the use of this rodenticide.

Timing of rodent control

Farmers normally resort to symptomatic treatments, i.e. controlling rodents after damage is seen in their crop. Mostly, these measures lead to partial success due to poor bait intake in the presence of food crops in the fields. Most of the states of the country adopt prophylactic or lean-period rodent control. It is presumed that bait intake will be high during the interval between two crop seasons and farmers will have free time to participate in the control operations on a community basis. However, analysis of implementation of this approach showed that farmers were not keen on rat control in this period due to the absence of rodent infestation in their fields (Rao et al. 1998).

Cereal crops exhibit compensatory growth if pests inflict damage in the initial stages, but not if damage occurs after the vegetative stage (Rao 1992). Hence, rodent control is advocated during the vegetative stage of cereal crops when rodents immigrate to and try to establish in the crop. Treatment during this stage resulted in effective rat control (Rao et al. 1998).

Strategies for rodent management

National Programme on Rodent Pest Management

Recognising the increasing rodent problems, ICAR launched a National Programme on Rodent Pest Management (Anon. 1976) from 1976 in collaboration with the Directorate of Plant Protection, Quarantine and Storage (DPPQ&S) and Union Department of Food. The program has four components: preparation of the community, training of personnel, control operations, and prophylactic strategies. The primary aim is to undertake rodent control at the community level on a continuous basis.

In view of the dearth of qualified extension personnel in rodent management, training of trainers (ToTs) through Apex Level Training programs was given priority. The Central Arid Zone Research Institute, Jodhpur, IGMRI, Hapur and National Plant Protection Training Institute (NPPTI)/Acharya N.G. Ranga Agricultural University, Hyderabad to date have trained about 4000 extension personnel and university scientists. In addition, the NPPTI, a training wing of DPPQ&S, organises All India training programs for extension personnel of states/union territories (UTs)/other organisations. To date, 305 extension personnel from the states have been trained in 17 programs in the institute. This institute also organised *in situ* training programs in the states/UTs of Andhra Pradesh, Arunachal Pradesh, Assam, Goa, Karnataka, Lakshadweep, Manipur, Meghalaya, Mizoram, Nagaland, Pondicherry, Uttar Pradesh, Tamil Nadu and Tripura as needed.

A ‘rodent control week’ was observed by the states/UTs every year until the early 1990s to expose large areas to the control of rodents through a community approach. This was discontinued because rodent control was incorporated as an integral component of the IPM activity of the states/UTs.

Inputs for rodent management

To encourage rodent control by states/UTs, the Government of India formulated a centrally sponsored scheme for control of special pests of agricultural importance from 1976–77 with a subsidy of 50% on the cost of rodenticides. Until 1992, the scheme provided an assistance of Rs20.4 million for rat control, covering an area of 13.76 million ha. After 1992, central assistance was provided through identified crop-based central sector schemes. During 2000, with the amalgamation of the crop-based central sector schemes into a Macro Management in Agriculture Scheme, states/UTs were given flexibility to incorporate the rodent control component under the crop-based central sector schemes. There is an increasing trend in the country to use anticoagulant rodenticides (Table 3).

Rodent management in the post-harvest situation

To protect food grains in storage at the farm level, the Ministry of Consumer Affairs, Food and Public Distribution, Department of Food and Public Distribution (erstwhile Department of Food under Ministry of Food and Agriculture) launched the Save Grain Campaign (SGC) scheme with 14 regional and 3 sub-regional SGC offices. Training, demonstration and publicity programs in scientific preservation of food grains and pest control techniques were given by these units (Anon. 2002). The research support was extended by IGMRI, Hapur.

Research support and documentation

ICAR extended research support initially with a project, All India Coordinated Scheme for Research on the Study of Field Rats, from 1959 until 1969 with four centres in the country. Subsequently, ICAR launched a major scheme All India Coordinated Research Project (renamed as Network Project) on Rodent Control from 1977. It has 10 centres covering the major agro-climatic zones of the country. The project scientists developed new information on different aspects of ecology and management of major rodent pest species of crops, and also suitable location-specific packages of practices. The research information in the country is being disseminated periodically by the ICAR bulletin *Rodent Newsletter.* Effective interactions among rodent researchers are also organised through biennial workshops/group meetings.

To fine-tune the field-based extension technology for rodent management, the DPPQ&S organises national workshops at NPPTI, Hyderabad, bringing together senior extension personnel of the states/UTs, ICAR project and agricultural university scientists, and representatives of the rodenticide industry. The extension-based recommendations finalised in these workshops are circulated to all states/UTs for their adoption. Four workshops have been conducted to date. NPPTI also undertakes limited research activities to fine-tune the research results produced by various research organisations.

Planning for rodent pest management

During 2001, the Government of India formulated planning for IPM with rodent control as one of the components for implementation by all relevant extension agencies. The available technology is being advocated to the states/UTs. In addition, challenges were identified, critical suggestions to address them were developed, and a strategy planned by relevant technical organisations.

Challenges for integrated rodent management

Intensive cropping due to increased irrigation fosters invasion by rodent pests and causes increased problems.

Table 3. Amounts of rodenticides (technical grade) used (t) in India.

Year	Rodenticide consumption (t)		
	Aluminium phosphide	Bromadiolone[a]	Zinc phosphide
1990–91	700	–	300
1991–92	650	–	250
1992–93	600	–	300
1993–94	850	116	300
1994–95	875	158	300
1995–96	900	195	300
1996–97	1050	223	250
1997–98	865	284	230
1998–99	955	266	250
1999–2000	1400	489	285
2000–01	2000	697	330

[a] Amount of formulated product.

Source of information: Pesticide Information (magazine issues in different years).

These changing agricultural practices also influence the density of rodent populations. The Indira Gandhi Canal in desert tracts brought more cultivable land under irrigation, but also increased rodent problems due to replacement of desert rodents with the lesser bandicoot rat, a dominant rodent pest. Similarly, failure to follow proper spacing in increased coconut cultivation has led to significant rodent damage to the nuts. Cultivation of oil palms in rodent-endemic areas also naturally decreases the productivity of oil palms due to their vulnerability to these pests in the initial bearing years. Natural calamities like flash floods and drought spells followed by heavy rains etc. also foster irruption of rodent populations in these areas, contributing to significant crop losses. However, monitoring the rodent situation in the regular pest monitoring systems of the states is lacking in the country. A survey of sporadic bamboo-flowering areas, rodent surveillance in the flowering areas, training of trainers, creation of awareness among the farming community, and rodent control measures are in progress to arrest major outbreaks in the north-eastern states anticipated from 2005 to 2007. However, actual causal factors responsible for such rodent outbreaks in this region are not known. There are endemic areas for rodent pests due to continuous availability of food and shelter in irrigated crops. Intensified monitoring efforts are not occurring after prolonged drought/dry spells and subsequent floods. As a consequence, early signs of irruptive rodent populations are not detected and the opportunity for timely action is missed. The existing linkage of extension and rodent research is inadequate for proper translation of research recommendations to the farm level.

Reports of an increased incidence of leptospirosis and the reappearance of plague are of major public health concern. Epidemiological surveys and studies on the biology of ecto-parasite populations in different areas are lacking. Such studies would indicate the actual reservoir/vector species responsible for disease transmission, indicate factors responsible for arthropod propagation in the rodent burrow, and may lead to appropriate management of the vector species.

Conclusion: critical suggestions for avoiding rodent-related problems

The states/UTs need to: popularise a non-chemical and community approach among the farming community; include rodents in pest/disease surveillance activities; train more personnel in rodent pest management; create awareness through the media; make available safer rodenticides in vulnerable places; liaise with public health authorities for coordinated action; and ensure quality control. The activities in the central sector include extending timely guidance to the states/UTs on appropriate control operations. The pesticide industry may supply rodenticides in a more timely manner in vulnerable places and develop safer formulations through research and development.

Revitalising research activities is the prime requirement in the development of rodent surveillance and ecologically based rodent management strategies. Microbiological expertise and epidemiological surveillance require updating in public health systems in India. Simultaneous toxicological studies of both rodent and flea populations should be undertaken.

A species-based approach to rodent management is desirable. During plague prevention activities, the main reservoir species, *T. indica*, is not targeted because it lives far away from human habitation. In view of this, planning of rodent vector management is desirable for preventing human disease. Even a small residual rodent population may lead to propagation of the bacteria and transmission of the disease to more animals/people. Hence, with the linkage between various extension agencies and central IPM centres, and the technical expertise of IGMRI, the ICAR project should be strengthened. More technical personnel must be trained to undertake management of the rodent pests and their plague vectors more effectively.

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Habitat manipulation and rodent damage control: reducing rodent damage in Australian macadamia orchards

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Abstract. This paper examines the relationship between adjacent non-crop vegetation and rodent (*Rattus rattus*) damage in Australian macadamia (*Macadamia integrifolia*) orchard systems. Orchards adjacent to structurally diverse, non-crop vegetation dominated by woody weeds exhibited significantly higher damage when compared to orchards adjacent to managed grasslands. This relationship formed the basis for a rodent damage reduction strategy utilising habitat manipulation. Structurally diverse, non-crop habitats were modified to grasslands leading to a reduction in rodent damage of 65%. This strategy was cost-effective and has the potential to be long-term with minimal effort needed to maintain sites in a modified state. Habitat manipulation is a process whereby the resource load in a system is reduced and hence rodent densities cannot reach levels where they cause significant crop damage. This paper provides empirical evidence to support habitat manipulation as a practical, cost-effective control strategy for rodent pests.

Introduction

Rodents cause significant damage to crops throughout the world and hence have been a target for control for most of our modern history. Rodent control methods have largely focused on manipulating the mortality of a population in order to suppress the population to a point where damage is acceptable. Unfortunately, mortality-based control often does not address the cause of high rodent densities and hence high damage to crops. When populations are reduced through mortality-based control, the remaining animals are exposed to increased resource levels and may in fact compensate for reductions in population size with an increase in reproductive output. This is ultimately expressed as the population ‘bouncing back’ post control. Caughley and Sinclair (1994) suggest that such control can be likened to a sustained-yield harvesting exercise where the off-take is never utilised.

In more recent times, the reliance on mortality-based control has been questioned. New methods of control are being sought that address the cause of rodent populations reaching high densities in crop systems. These new methods of control are conceptually different, with research directed towards: (1) reducing the fecundity of populations and hence reducing the populations’ ability to respond to high resource availability (Chambers et al. 1999); and (2) reducing the resource availability (e.g. shelter and alternative food) in crop systems so that populations cannot build to high densities (habitat manipulation). Both these approaches aim to prevent populations from reaching densities where they have the potential to cause significant damage, as opposed to conventional, mortality-based methods where control is often not initiated until damage has occurred.

This paper examines the potential for habitat manipulation as a rodent damage mitigation strategy. A case study of rodent damage in Australian macadamia orchard systems is provided to highlight the approach to developing such a strategy. A more detailed analysis of the approach can be found in Horskins et al. (1998) and White et al. (1997, 1998).

Materials and methods

These studies were conducted on the Sunshine Coast in south-eastern Queensland, Australia. All orchard sites were at least 20 years old, were dominated by two macadamia varieties (HAES508 and HAES246) and were spaced at 5 m × 10 m intervals.

Twenty-one orchard sites were chosen on the basis of the type of adjacent non-crop habitats:

- six large, temporally stable sites (at least 10 m wide and consisting of a thick ground layer with a dense cover of woody vegetation);
- five small, temporally stable sites (less than 3 m wide and consisting of dense woody vegetation);

- four modified sites (grassland sites which were intermittently slashed when machinery access was possible);
- three highly modified sites (grassland sites routinely slashed throughout the year); and
- three sites which were surrounded by macadamia orchards.

To determine the spatial pattern of damage, tree selection for damage assessments was based on distance from the adjacent habitat. Five trees were randomly selected every two rows into the orchard (20 m), from the front row to the ninth row (80 m into the orchard). Five second-row trees were sampled also. All nuts that fell within a 2.5 m radius from the base of each tree were collected by hand and the numbers of both potentially harvestable mature nuts and mature nuts damaged by rodents were recorded, thus providing an estimate of economic loss for each tree.

Trapping

Of the 21 sites used for the analysis of damage, seven sites were randomly selected for kill-trapping of rats. Four sites were adjacent to large, temporally stable habitats and three sites were adjacent to temporally unstable sites (two modified and one highly modified). Each trapping site consisted of a block of 63 trees (seven rows by nine trees per row). Sixty large traps (Supreme rat snap traps) were placed at each site on a 10 m × 20 m trapping grid, with 40 traps in the orchard (20 ground layer and 20 tree layer) and 20 traps in the adjacent habitat (trapping was conducted at least 50 m away from damage estimation sites). All traps were baited with a mixture of rolled oats, peanut butter and linseed oil. Trapping was conducted over a 12-month period, with three consecutive nights of trapping at each site per month. The location of each animal was recorded and the animals' stomachs were removed for dietary analysis.

Habitat manipulation

Eight sites from the damage distribution study were selected for a trial of habitat manipulation—five with temporally stable (large) adjacent habitats and three with highly modified adjacent habitats. Three of the five large, temporally stable adjacent habitats were cleared of all vegetation greater than 10 cm in height. The area manipulated at each site had an orchard frontage of 125 m (25 tree frontage) and extended 20 m into the adjacent habitat. The adjacent habitats were sprayed with Grazon™ (the active ingredient of which is picloram), a dicotyledon-specific herbicide, during the growing season to minimise regeneration of shrubs and trees.

To determine the effect of habitat manipulation, damage estimates were conducted at all sites using the methodology outlined in the damage distribution study. Damage estimates from the previous year were compared to assess the success of habitat manipulation.

Results and discussion

Distribution of damage

The mean number of damaged nuts per tree across all study sites was 93 (5% of mean yield), however damage per tree ranged from 0 to 1522 nuts (0% to 83.4% of mean yield). The distribution of damage was skewed with the majority of trees (98.5%) sustaining some damage and the median damage was 40 nuts per tree (2.2% of mean yield).

Damage varied with the type and size of adjacent habitat ($F_{(4,543)} = 110.96$, $p < 0.001$)(Figure 1). Damage was significantly higher in orchards adjacent to large, temporally stable habitats (mean damage per tree 9.9%). Orchards adjacent to small, temporally stable habitats and modified habitats sustained significantly less rodent

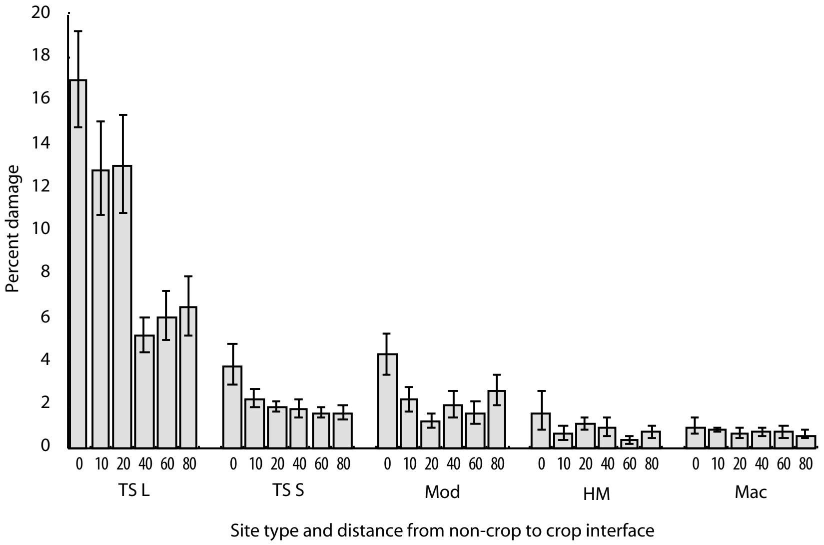

Figure 1. Percentage (1 se) of macadamia nuts damaged in association with adjacent habitat types and the distance (m) from the crop/non-crop interface, where: TS L = temporally stable (large); TS S = temporally stable (small); Mod = modified; HM = highly modified; and Mac = other macadamia orchards (after White et al. 1997).

damage (mean damage per tree 2.2%). The lowest level of damage was associated with orchards adjacent to highly modified and macadamia habitats (mean damage per tree 0.8%).

Distribution of damage within the site was associated with the distance from and the type of adjacent non-crop habitat ($F_{\text{Habitat (4,532)}} = 100.49$, $p < 0.001$; $F_{\text{Distance (5,532)}} = 7.19$, $p < 0.001$; $F_{\text{Interaction (20,532)}} = 2.39$, $p < 0.001$) (Figure 1). Sites adjacent to temporally stable habitats (large and small) sustained higher front-row damage (LSD < 0.05). Sites adjacent to large, temporally stable non-crop habitats sustained high levels of damage for the first three rows, whilst damage in orchards adjacent to small, temporally stable habitats was only high in the first row. This trend was not observed in orchards adjacent to temporally unstable (modified and highly modified) or macadamia habitats, with damage being evenly distributed throughout the orchard. Ultimately, the level of damage in a crop was directly related to the size, structure and temporal stability of the non-crop habitat.

Rodent distribution and diet

A total of 696 *Rattus rattus* was captured. Rodent captures were not uniformly distributed throughout the orchard system. Highest trap success occurred in large, temporally stable adjacent habitats. Trap success in temporally unstable adjacent habitats (mean = 1.4%) was significantly lower than trap success in temporally stable adjacent habitats (mean = 12.9%) ($t = 4.66$, df = 5, $p = 0.006$). Orchard trap success (mean = 2.2%) was similar regardless of the temporal stability of the adjacent habitat ($t = -0.65$, df = 5, $p = 0.542$). Damage levels in orchards were positively correlated with the number of rodent captures in the adjacent non-crop habitats ($r = 0.794$, $p = 0.033$, $n = 7$).

Of the 363 rodents captured within the adjacent habitat, 218 (60.1%) had consumed macadamia nuts along with 94.1% of the 204 rats caught within the orchard. These results suggest that a large rodent population utilises the temporally stable adjacent non-crop habitats and move into the orchard to feed. This supports the damage distribution studies, which suggest that the majority of damage occurs in the first few rows of crops adjacent to large, temporally stable adjacent habitats. These results also indicate that there may be a second, smaller population that lives within the orchard component of the system causing the low baseline damage that is seen in all orchards, regardless of adjacent habitat type.

Habitat modification

The damage and dietary results confirm that adjacent non-crop habitats play an important role in crop damage in macadamia orchards. The large difference between damage in orchards adjacent to large, temporally stable non-crop habitats and those adjacent to highly modified non-crop habitats suggested that a habitat manipulation strategy could be appropriate for reducing rodent damage. The process used involved simplification of the large, temporally stable adjacent non-crop habitats, from largely dense weedy vegetation providing high vertical structure, to large, highly modified grasslands, providing limited structure.

There was no significant difference in the level of damage between years in orchards adjacent to highly modified habitats ($F_{(1,166)} = 2.301$, $p = 0.131$) or unmanipulated sites adjacent to temporally stable adjacent habitats ($F_{(1,110)} = 0.101$, $p = 0.751$). Before habitat manipulation, there was no significant difference in damage levels between the temporally stable sites that were manipulated and those that were to remain unmanipulated ($F_{(1,93)} = 0.534$, $p = 0.467$). However, orchards adjacent to habitats that were manipulated showed a significant reduction in damage compared to unmanipulated, temporally stable sites ($F_{(1,178)} = 38.04$, $p < 0.001$) (Figure 2). Manipulation of the adjacent habitat reduced damage from 13% (±1.8%) to 4.6% (±0.4%), a reduction of 64.6%.

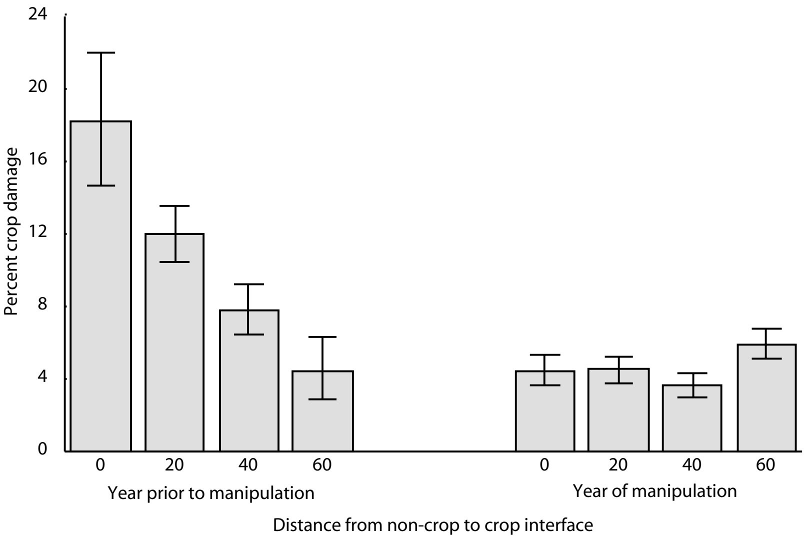

Figure 2. The effect of manipulating large, temporally stable, structurally complex non-crop habitats on the distribution of macadamia nut damage (mean, ±1 se) in adjacent orchards (after White et al. 1997).

The high edge damage associated with temporally stable non-crop habitats was significantly reduced by the manipulation of the non-crop habitat. This effect was most likely the result of the non-crop population of rodents significantly declining in number due to reduced availability of structural resources. The resultant damage in the orchard was likely associated with the small component of the population that lived within the orchard itself.

The cost of manipulating the adjacent habitat along an orchard frontage of 25 trees (120 m) was calculated at US$164 in the initial year. This figure represents the estimated cost of clearing the vegetation (US$54) and applying two rounds of herbicide to control regrowth (US$105). The average tree yield of the orchards examined in this study was 20.5 kg of nut in shell (NIS). At the time of this study, NIS sold for US$1.65/kg. The losses due to rodent damage were calculated on the basis of a frontage of 25 trees and extending 7 rows into the orchard. The losses due to rodent damage in the year before manipulation at sites adjacent to temporally stable habitats was US$820 (±$170). At sites which had been manipulated, the losses were US$271 (±$23). Habitat manipulation reduced crop losses by US$549 at a cost of US$164, resulting in a saving of US$385/site to the grower. The profit associated with control should increase in subsequent years due to reduced costs in maintaining previously manipulated adjacent habitats.

Conclusions

Habitat manipulation operates by removing or altering the critical resources that give rise to high reproductive success and/or survival. The method has been described as one of the few control methods that does not operate against a negative feedback loop (Caughley and Sinclair 1994). This method of control has the potential to be implemented in many crop–rodent systems, but requires a sound understanding of the system in which control is to be implemented. The main aspect of habitat manipulation is determining the habitat features that give rise to high damage levels and also identifying habitat features that lead to limited damage levels. Ultimately, reducing the size of habitats and replacing them with habitats that lead to low damage is the objective of such control.

Habitat manipulation is one of the few rodent damage control strategies that has been shown to be cost-effective. The other main advantage of such a strategy is that it is not technically challenging to conduct and does not require access to rodenticides that are often expensive. A difficulty associated with habitat manipulation is that environmental damage may occur as part of the strategy. Habitat manipulation may also impinge upon biodiversity values of the areas in which they are implemented. These issues should be examined in subsequent research examining habitat manipulation.

Acknowledgments

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Patterns of rodent pest distribution in a maize cropping system in the Kenyan Rift Valley

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Abstract. We studied the small mammal community structure in a maize cropping system in the Kenyan Rift Valley. Using the capture–mark–recapture (CMR) method, we set in maize fields four permanent trapping grids each with 100 box-traps. Traps were opened for three consecutive days every 4 weeks for 20 months. Eight hundred and thirty-seven individual small mammals were captured 1240 times in 20,100 trap-nights. The rodents included six murids (*Aethomys* cf. *kaiseri*, *Arvicanthis* cf. *neumanni*, *Lemniscomys striatus*, *Mastomys* cf. *erythroleucus*, *Mus minutoides* and *Rattus rattus*) and a cricetid (*Tatera* cf. *robusta*), while the shrews were all soricids (*Crocidura* species). *Mastomys* was the most dominant species within and across the entire grids, accounting for 71.0% of all captures. Other common rodents were *Arvicanthis* (14.1%) and *Mus* (8.0%). *Aethomys* and *Rattus* were rare, being captured only at the highest altitude (1922 m) while *Tatera* was restricted to the lowest altitude (1712 m). Rodent pests were not uniformly distributed in maize fields even though the maize cropping agro-ecosystem was continuous here. *Mastomys* remains the most important pest species due to its distribution and abundance in the study area.

Introduction

In Kenya, almost half the acreage used for food crops in the small farm sector is planted to maize (Rundquist 1984). More than 1 million ha of maize, with a production of between 1.4 and 3 million t, are cultivated. Large-scale farms produce 13% of the total production on 10% of the area and supply 45% of the maize sold in local markets. The remaining 87% of the Kenyan maize production is subsistence for the farming population and only a small surplus is marketed for profit (Dissemond and Hindorf 1990), yet it is the basic foodstuff for about 90% of the population (Gerhart 1975).

Reports of rodent damage are recorded annually in Kenya with serious outbreaks every few years and some areas experiencing up to 90% loss. In April 2001, 2833 ha of land under maize was reported destroyed by rodents in Kwale district of Kenya. This constituted 30% of the total area under maize in the district. With a population of 28.8 million (Goliber 1997), likely to double by the year 2020, a steady loss of even few per cent of production must be checked. Moreover, the region has 70 million inhabitants requiring food aid (FAO 2000).

Although rodents have received relatively little attention in Africa as vertebrate pests (Fiedler 1994; Bekele and Leirs 1997), their capacity for crop depredation and transmission of diseases introduces an applied aspect of rodent ecology. Where rodent outbreaks have been reported, control measures have favoured application of toxic chemicals often at a time too late to be effective. The contemporary approach to rodent problems is that of ecologically based management. This has received fewer considerations due to insufficient basic field and experimental data in support of their efficacy (Makundi et al. 1999). Thus, strategies in management of rodents both in the field and in stores are poorly developed. Effective control needs information on accurate pest identity, ecological theory and field data to provide vital ingredients in the design of sustainable management strategies (Singleton et al. 1999). Our knowledge of rodent pests in Kenya is inadequate, while issues on pest problems remain anecdotal. Thus, we developed a study to provide information towards breaching this gap.

Materials and methods

The study was carried out in Nakuru district in the Kenyan Rift Valley at latitudes 35°28'–35°36'E, longitudes 0°13'–1°10'S, and altitudes of between 1720 and 1800 m above sea level. The climate in this area falls between semi-arid (annual rainfall less than 760 mm) in the lower areas and dry subhumid (annual rainfall of 1270 mm) regions at the higher altitudes. Rainfall is bimodal with peak precipitation (70–80%) in March to May and late August to October, although great variations may occur from year to year. The maximum temperature is about 30°C, with December to March being hottest and July being coolest at an average of 23.9°C.

Trapping was done on four permanent grids (1 ha each) in maize crop fields along an altitudinal gradient: (i) Mugo (1922 m); (ii) Beth (1895 m); (iii) Kurt (1823 m); and (iv) Moto (1712 m). The capture–mark–recapture (CMR) technique was used in sampling small mammal populations. Rodents were live-trapped using Sherman's LFA traps measuring 23 × 8 × 9 cm, between May 2000 and December 2001. Each grid consisted of trapping stations laid at 10 m within and between rows, giving 100 traps per grid. Trapping in Mugo and Beth grids commenced in May 2000, at Moto grid in July 2000, and at Kurt grid in April 2001. Primary trapping was made every 28 days and secondary trapping for three consecutive days and nights during each primary trapping session. Traps were baited with a mixture of peanut butter, corn oil and fried coconut cubes.

Results and discussion

A total of 1240 captures of 837 individuals were made of seven rodent and undetermined shrew species in 20,100 trap-nights. This gave a trap success of 6.2%. The low capture rates were attributable to prolonged drought before the study and inconsistent precipitation during the work. Rodents captured included six murids (*Aethomys cf. kaiseri* (Noack 1887), *Arvicanthis cf. neumanni* (Matschie 1894), *Lemniscomys striatus* (Linnaeus 1758), *Mastomys* cf. *erythroleucus* (Temminck 1853), *Rattus rattus* (Linnaeus 1758), *and Mus minutoides* Smith 1834) and a cricetid (*Tatera* cf. *robusta* Cretzschmar 1826), while the shrews were all soricids (*Crocidura* species) (Table 1).

The most dominant species in all the trapping grids was *Mastomys*, accounting for 71% of all captures. Reasonably common were *Arvicanthis* (14.1%) and *Mus* (8.0%). The distribution of *Mastomys* was uniform (χ^2 = 4.855, P = 0.182, n = 594) in all the grids. Distribution of other species varied significantly among the four grids: *Arvicanthis* (χ^2 = 28.529, P = 0.000003, n = 119), *Mus* (χ^2 = 64.632, P < 0.00001, n = 67), *Lemniscomys* (χ^2 = 20.538, P = 0.0001, n = 13), *Tatera* (χ^2 = 81.000, P < 0.00001, n = 27) and *Crocidura species* (χ^2 = 15.000, P = 0.0001, n = 13) (Table 1). Three and one individuals represented *Aethomys* and *Rattus*, respectively.

The importance of *M. erythroleucus* in eastern African agriculture has been documented previously in maize fields of Ethiopia (Bekele and Leirs 1997). Although it was not reported in the early rodent outbreaks in the Kenyan Rift Valley (Taylor 1962, 1968; Taylor and Green 1972), this may have been due to misidentification. Moreover, the multimummate rats—especially *Mastomys natalensis*—are the most important murid pests in eastern Africa (Fiedler 1994; Martin et al. 1989; Leirs et al. 1996). Other important murid pests previously recorded in our study sites include *Arvicanthis*, *Lemniscomys* and *Rhabdomys pumilio* (Sparrman 1784) (Taylor 1962, 1968; Taylor and Green 1976). During our study, *Arvicanthis* was captured in fair numbers (14%), *Lemniscomys* was recorded only at the higher altitudes in low numbers, while *Rhabdomys* was not recorded in over 20,000 trap-nights. Despite its pest status elsewhere, *Tatera* has never been reported as a pest in this area where it was restricted to the drier, lower altitude (the Moto grid).

Conclusions

Our study has shown that rodent pests are not uniformly distributed in maize fields, even within a continuous maize cropping agro-ecosystem in Kenya. Patterns in rodent pest distribution may be attributed proximally to

Table 1. The community structure, number of individuals, and distribution of rodents and *Crocidura* captured in four trapping grids in maize fields in the Kenyan Rift Valley between May 2000 and December 2001.

Species	Study grids				
	Mugo	Beth	Kurt	Moto	Total
	Trap nights				
	6000	6000	2700	5400	20,100
(a) Rodentia					
Mastomys cf. *erythroleucus*	151	152	164	127	594
Arvicanthis cf. *neumanni*	32	8	30	49	119
Mus minutoides	45	4	8	10	67
Tatera cf. *robusta*	0	0	0	27	27
Lemniscomys striatus	10	3	0	0	13
Aethomys cf. *kaiseri*	3	0	0	0	3
Rattus rattus	1	0	0	0	1
(b) Insectivora					
Crocidura species	3	9	1	0	13
Total	245	176	203	213	837
Trap success (%)	6.0	5.8	11.2	5.1	6.2

localised conditions driven by land use and altitude. Since rainfall here varies with altitude, climate is perhaps of ultimate importance in determining the distribution of the pest species. Due to ease of capture of *Rhabdomys*, its absence during this study was surprising given it had been a major pest here previously. It would appear that the species is locally extinct for reasons beyond the scope of current findings. *Mastomys* is the most important pest species with uniform distribution in all maize fields.

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Prey selection by barn owls in rice fields in Malaysia

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Abstract. Prey selection of the barn owl, *Tyto alba,* in rice fields in Malaysia was measured using feeding pellets collected in and around nest boxes and perching sites from September 2001 to February 2002. Analysis of the feeding pellets showed that rats constitute 94.7% of the barn owls' food (*n* = 160), while shrews (6.3%, *n* = 5) and birds (7.4%, *n* = 4) constitute the remainder. The rice-field rat, *Rattus argentiventer,* constitutes 85.7% of the identifiable rat prey species and the remainder (14.3%) is the wood rat, *Rattus tiomanicus*. Pellets collected in January showed that 61.1% of the prey consist of juvenile rats, compared with 12.2%, 25.8% and 42.8% in the preceding months of October, November and December, respectively. The higher percentage of juvenile rats in the prey can be associated with the rice-field rat's reproductive cycle, which in turn is influenced by the phenology of the rice paddy plant. Pellets collected in October, November and December showed a high proportion of headless prey, i.e. 51.2%, 54.8% and 76.2%, respectively. Fewer pellets were collected in January and February, with a relatively lower proportion of headless prey, i.e. 22.2% and 50%, respectively. These findings can be explained by association with the owl's breeding period that lasts from October to December, during which male barn owls usually decapitate and consume the head and bring home headless rat carcasses to the females and their young.

Introduction

The barn owl, *Tyto alba*, is a cosmopolitan species occurring on all continents and in a wide range of habitats, except Antarctica and the smaller Pacific islands (Smith and Cole 1989). In recent years, there has been increasing public interest in the potential for owl predation to control rats. In Peninsular Malaysia, the first confirmed breeding of the barn owl was recorded on Fraser Estate, Kulai, Johore, in 1969 (Wells 1972), and these owls are believed to have originated from Java and Sumatra (Lenton 1985). The spread of *T. alba* in Malaysia was closely associated with extensive oil palm cultivation, as these plantations harbour a bounteous supply of rats. The provision of artificial nest boxes in oil palm plantations has succeeded in boosting local *T. alba* populations to effectively reduce rat infestations (Smal 1988). The barn owl feeds exclusively on live prey, preferring small rodents and birds, which it swallows whole or in parts (Harrison 1991). After digesting the softer tissues, it regurgitates the remains in compact oral pellets, which usually contain bones, claws, teeth, fur and feathers.

Several studies on the food selection of *T. alba* in oil palm plantations show that rats constitute a major prey. Lenton (1980) and Smal (1988) found, from analysis of oral pellets, that rats comprised more than 98% of the owls' food. The objective of this study was to evaluate prey selection of *T. alba* in rice-field areas. Monthly variations in prey items, with particular reference to adult versus juvenile rats and the presence or absence of skulls in pellets, were also recorded to determine whether feeding behaviour is influenced by the owl's breeding cycle and the rat's reproductive cycle.

Materials and methods

Pellets were collected from September 2001 to February 2002 in and around nest boxes and perching sites in a paddy-field area in Sawah Sempadan, Tanjung Karang, Selangor, and pooled into monthly samples. Individual pellets were dried at 60°C for at least 48 h, then soaked in 0.5 M NaOH. The pellets were than teased apart and the contents recorded. If a skull was present, the following measurements were made to 0.1 mm using a caliper (Mitutoyo Series 505): (1) skull length (from the posterior-most point of the supraoccipitals to the anterior tip of the upper incisor socket, (2) upper tooth row, and the length of the (3) palatine foramen, (4) lower jaw (mandible), (5) femur, and (6) humerus. The identification of *Rattus argentiventer* and *Rattus rattus diardii* follows Harrison (1962). For *R. argentiventer,* the anterior palatine foramine is longer than the upper tooth row and extends between the cheek teeth, while that for *R. r. diardii* is usually variable (Figure 1). *Rattus tiomanicus* is identified by the presence of anterolabial stylid on the second lower molar (Lekagul and McNeely 1977). Smaller skulls were designated as juveniles. If a skull was lacking, measurements of the femur and humerus were used to distinguish juveniles from adults.

Results and discussion

Prey items

A total of 169 prey items were identified from 160 pellets (nine pellets had two prey items in them) collected during this study. Of these, 160 or 94.7% contained rats. The other prey identified from the pellets were the common shrew, *Suncus murinus* (2.9%, *n* = 5) and birds (2.4%, *n* = 4). Lenton (1980) analysed 2839 pellets from oil palm plantations and determined that 99.1% of the prey items were rats. He also determined that shrews were the most common non-rat prey in the plantations but from a much wider range of prey, which included birds as well as arthropods and amphibians. The far fewer pellets analysed in this study may explain the lower range of prey items. The overwhelming dominance of rats in the diet of the owls nonetheless was striking.

Rat species were determined from pellets in which skulls were present. Only two species, *R. argentiventer* and *R. tiomanicus*, were identified based on the measurements and designated features of the skull. *R. argentiventer* formed the primary diet with 85.7% of the identifiable rat prey (*n* = 77) as compared to *R. tiomanicus* with 14.3%. In oil palm plantations, Lenton (1980) determined *R. tiomanicus* as the most common rat species, accounting for 89.78% of the prey items, whereas *R. argentiventer* was only 6.22%; the rest being occasional *Rattus exulans*, *R. annandalei*, *R. rajah* and *R. surifer*. The rat species composition from both Lenton's and this study suggests that the diet of *T. alba* is influenced by the rat species' composition, although this needs to be substantiated with live trappings. However, it is fairly well established that *R. tiomanicus* is more common in oil palm plantations (Han and Bose 1978; Wood and Liau 1984) and *R. argentiventer* is more common in rice fields (Lam 1982, 1988). The presence of *R. tiomanicus* in the owls' diet in the present study can be attributed to owls hunting in oil palm plantations adjacent to the rice-field area (Figure 2).

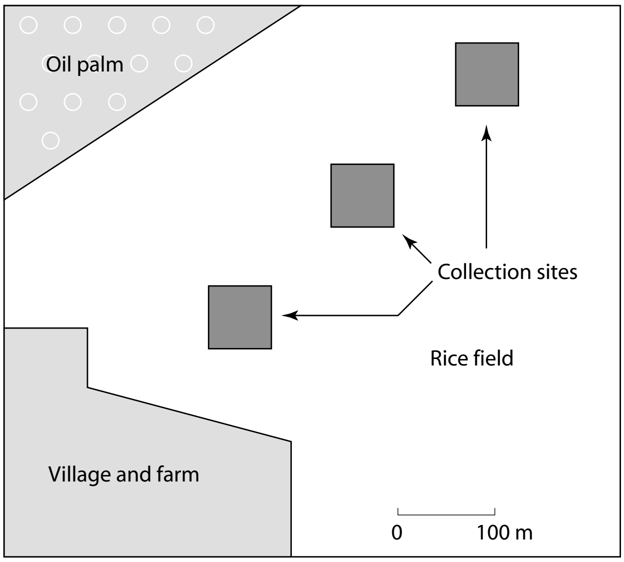

Figure 2. Sites for the collection of oral pellets around nest boxes and perching poles.

Analysis of a higher number of pellets should give a better picture of the rat species' composition in the diet of *T. alba* in rice fields. Occasional trappings in the area, especially near farmers' houses and other buildings,

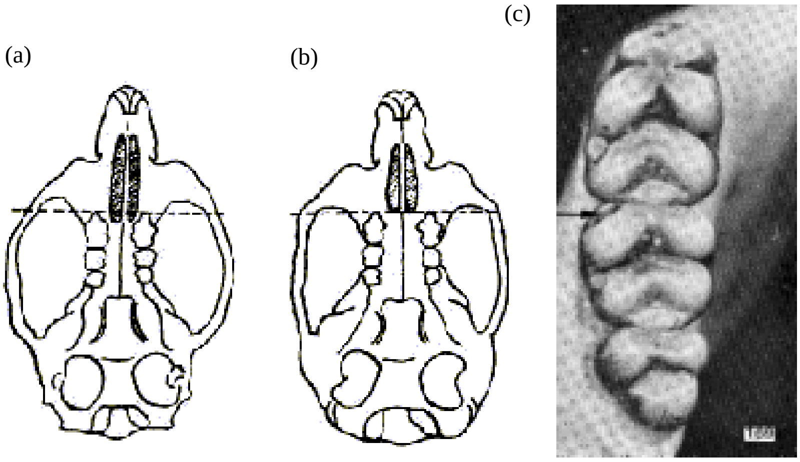

Figure 1. The anterior palatine foramina (dark shaded) is longer than the upper tooth row and extends between the cheek teeth in *Rattus argentiventer* (a); while that of *Rattus rattus diardii* (b) is variable. *Rattus tiomanicus* (c) possesses an anterolabial stylid on the second lower molar.

revealed that *R. r. diardii* is quite common and it may also constitute an occasional prey of *T. alba*. Lam (1988) conducted a trapping study in another rice-field area in Malaysia at Bumbung Lima, Perak, and caught a small number of *R. r. diardii* among the predominantly *R. argentiventer* rodent population.

As an oligophagous predator with a narrow prey range (Lim 1999), this study reaffirms the suitability of the barn owl as a natural predator in a rice agro-ecosystem as it is unlikely to prey on poultry or other non-target species.

Rat prey selection of barn owls

Barn owls in this study took both adult and juvenile rats. On average, juvenile rats constituted only 28.1% of the total rat prey (Table 1). However, the proportion of juveniles varied from month to month. The highest proportion of juveniles occurred in December and January, comprising 42.8% and 61.1% of the total number of pellets with rats, respectively. The largest number of pellets collected was in November, but juveniles comprised only 25.8% of that month's uptake. These figures suggest that the prey composition is influenced by the rice-field rat's reproductive cycle, which peaks around harvesting time (Lam 1983), the period when new cohorts join the above-ground population. At Tanjung Karang, rice is harvested in December and January, and this explains the higher proportion of juveniles in the diet during those months. Although *T. alba* prefers to take smaller rats (Harrison 1991), this preference is largely influenced by the availability of the range of prey sizes. This study did not attempt to estimate the relative availability of each size class of rats, but the data suggest that *T. alba* takes mostly adults rats, varying juvenile prey uptake according to their availability.

Table 1. Monthly percentage of *Tylo alba* pellets containing juvenile rats and rats without heads.

Month	% juvenile	% rat prey without head	Total number of pellets containing rats
September	0	33.3	6
October	12.2	51.2	41
November	25.8	54.8	62
December	42.8	76.2	21
January	61.1	22.2	18
February	33.3	50.0	12

Proportion of pellets without skulls

Pellets were categorised according to whether or not they contained a skull. The highest proportion of pellets not containing skulls was collected in December (76.2%, *n* = 21). The proportion was also high in October and November (51.2%, *n* = 41; and 54.8%, *n* = 62, respectively), but substantially lower in January (22.2%, *n* = 18). In February, the percentage was 50% but this could be due to the small sample size (*n* = 12) (Table 1). The presence or absence of skulls in pellets can be associated with the owl's breeding cycle. In Tanjung Karang, *T. alba* starts to breed in October. Most of the chicks hatch in November and December. Male barn owls have been observed to decapitate their prey and bring the headless carcasses to feed the females and her chicks (Lenton 1984). During the time that chicks are in the nest, female barn owls rarely leave their nest. Therefore, the higher percentage of skull-less pellets in the nest box during the breeding period is the consequence of males taking home headless meals for the chicks. In January, most of the owlets have fledged, and therefore males take less food home, resulting in a lower percentage of skull-less pellets.

Conclusion

The food of the barn owl in the rice-growing area of Tanjung Karang is mainly *R. argentiventer.* Other rat species may also be taken subject to availability, particularly *R. tiomanicus*. Shrews and birds were also preyed upon but comprised little of the prey eaten. Prey preference is associated with the rice-field rat's reproductive cycle as reflected by the higher proportion of juvenile rats in the diet as these become available. The proportion of pellets without skulls was higher during the owl's breeding season because males usually feed on the head and bring home the headless portion to feed the females and chicks.

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Robustness of techniques for estimating rat damage and yield loss in maize fields

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Abstract. Four sampling techniques for estimation of maize damage and yield losses due to rodents were compared. We determined the actual rodent damage in 15 maize fields in Tanzania by counting damaged and undamaged maize plants and calculated the actual yield loss. The techniques of (a) non-stratified systematic row sampling, (b) non-stratified systematic Z-sampling, (c) stratified random square sampling, and (d) non-stratified simple random sampling were compared for robustness in terms of precision and accuracy, and time spent on damage and loss estimations. Our results showed clearly that non-stratified systematic row sampling is the most robust technique for assessing rodent damage and yield loss in the study fields. We provide a standard curve for sampling density and precision for this technique.

Introduction

Rodent damage is a serious impediment for agriculture (Fiedler 1988; Singleton et al. 1999). Survey reports in Tanzania, relying on data from questionnaires, have shown that, on average, rodents cause about 15% loss of maize crop annually (Makundi et al. 1991). Precise estimates are rarely available though obviously needed (Judenko 1973; Mwanjabe and Leirs 1997). There are many reasons for making more precise assessments, including: to establish the economic status of specific pests; to justify expenditure on control; to estimate the effectiveness of control measures; to measure the effects of environmental factors on the loss of yield caused by pest attack; to give information to manufacturers and distributors of pesticides to enable them to decide what action should be taken; and to give a basis for directing future research and agricultural planning (Judenko 1973; Buckle 1994). Clearly, many of these requirements are important in planning a strategy for field rodent control.

Unlike insects, rodents are secretive and not easily observed; many are nocturnal. Often, the investigator must rely on various signs such as tooth marks, missing plants parts and characteristics of the damage, burrows, and traps to identify rodent species (Fiedler 1988). Also, to assess rodent damage, a larger area must be investigated than is the case with insects, since rodents are more mobile, far from homogeneously distributed in the crop, and a single individual typically can cause damage to several plants in one night. Estimation techniques for insect damage, therefore, would be not be adequate for assessing rodent damage.

Several sampling techniques for estimating rice damage and yield loss caused by rodents have been evaluated in southern Asia, and this research has suggested that a stratified or clustered approach is the most reliable (Benigno 1979; Rennison and Buckle 1988). Hoque et al. (1986) evaluated three damage-estimation sampling techniques in maize fields one week before harvest and found that they gave similar results but differed considerably in efficiency. Benigno (1980) reported that stratified, random quadrat sampling is suitable for maize-damage evaluation. In Africa, Mwanjabe and Leirs (1997) used a systematic row sampling approach in their study in Tanzania to estimate rodent maize damage at planting, while Key (1990) used transects of 50 planted points within a maize plot to estimate rodent damage at the seedling stage and rodent cob damage at the maturity stage.

In the present study, we compared the actual rodent damage and yield loss in maize fields with four different estimation techniques. We investigate which technique is most robust in terms of precision and accuracy and most efficient in terms of technical complexity and time. This research aims to provide a sound basis for future work, which requires damage and yield loss estimation for pest monitoring, surveillance and forecasting and management evaluations.

Materials and methods

Locations and seasons

Field experiments were carried out during the cropping seasons in 1999 and 2000, in two farms at Sokoine University of Agriculture, Morogoro, Tanzania. The farms are located at 6°50'S, 37°38'E at an altitude of 510 m above sea level (asl) and 6°46'S, 37°37'E at 480 m asl, respectively. The area has a bimodal rainfall pattern and the study was conducted during the long rains maize-growing season each year. The seeds were sown in March, although the exact timing depends on rainfall, while the harvesting was done at the end of July.

Treatments

The study was carried out in 15 plots for damage assessment at the seedling stage and 8 plots for assessment of cob damage at maturity, 70 × 70 m each. Actual damage was assessed for comparison with estimations made using the sampling techniques described below. Rodent densities during the damage assessments ranged from 0 to 140 animals per ha (L.S. Mulungu et al., unpublished data). All fields received similar standard agronomic treatments, i.e. early ploughing, application of triple superphosphate (TSP) fertiliser (20 kg P_2O_5/ha) before planting, and nitrogen fertiliser (40 kg N/ha) twice as a top dressing, three weeks after the sowing and booting stages. Three seeds of maize (variety Staha) were planted per hole, at a planting space of 90 × 60 cm. Weeding was carried out twice. Harvesting was carried out by hand picking of the cobs when all cob silks were dry.

Sampling procedures

Crop damage assessment was carried out at the seedling stage, 10 days after planting, and at maturity, 1 week before harvesting. At the seedling stage, the number of seedlings was recorded at each sampled planting hole (since three seeds were planted per hole, damage was expressed as the proportion of missing seedlings). At maturity, the damaged proportion of each sampled cob was estimated. We used four different sampling methods, based on Mwanjabe and Leirs (1997), Rennison and Buckle (1988), Hoque et al. (1986), Benigno (1979, 1980):

- (a) *Non-stratified systematic row sampling*, where the sampling unit is a maize row; four rows apart and leaving out the two outer rows in order to reduce inter-field effects and prevent sampling of abnormal rodent movement behaviour in relation to barriers (Kaukeinen 1984). The assessor walks along maize rows across the field, recording damage at each plant hole in the row. In our fields, 15 rows were sampled per field.
- (b) *Stratified random square sampling*, in which the fields first are surveyed superficially in order to determine the distribution of rodent damage. Parts of the field with relatively similar damage intensity are then grouped in strata as low, medium, and high damage. Within each stratum, three squares of 5 × 5 holes are selected randomly in an area of similar damage intensity. From there, mean percentage damage is calculated for the whole field on the basis of the proportion of the different strata in the field.
- (c) *Non-stratified systematic Z-sampling*, in which the samples are systematically taken from nine points (2 × 5 holes) at fixed distances along a zigzag line in the maize field, running along two sides of the fields, connected by a diagonal line. Thus, a total of 90 holes (270 plants) are examined per field. In our fields, the distance between any two sampling points in the parallel lines was 27.5 m apart, while that between points on the diagonal line was 21.0 m.
- (d) *Non-stratified simple random sampling*, in which each individual sample unit (a planting hole) is drawn independently and with equal probability using the random-pair technique (Gomez and Gomez 1984). We selected the holes as follows: the total number of rows per field and holes per row was determined leaving two rows out around each field (e.g. 75 rows per field and 114 holes per row); then 120 pairs of random numbers was selected, each with a random row number and an independent random hole number in that row. These pairs formed the coordinates of the sampling points and were located and inspected in the field.

We also measured the actual damage by sampling every planting hole in a number of fields at the seedling stage (15 fields: 2 fields in 1999 and 13 fields in 2000) and at maturity (8 fields) to compare the robustness of the sampling methods. Cob damage at maturity was not observed at the first farm. In eight plots at the second farm in both years, only non-stratified systematic row sampling was used at seedling stage but the four sampling techniques and the actual counting of all plants were employed at maturity because maize cobs in this farm were damaged by rodents.

Yield loss

After harvest, the maize was threshed, cleaned by hand winnowing, and sun dried. The grain was weighed and the weight, adjusted to a common moisture level of 15.5% (Moyal 1998), was taken as the actual yield for the plot. The potential yield for the plot was calculated as the product of the total number of seeds planted times the mean actual yield per unattacked plant (surrounded by other unattacked plants), assuming no compensation. The total yield loss for each plot (Y_t) was calculated as the difference between potential and actual yield. The yield loss during the maturation period (Y_m) was calculated by using a difference between mean actual yield per unattacked plant and mean yield per attacked cobs. The yield loss due to damage at planting was then $Y_t – Y_m$.

Evaluation of techniques

The four sampling techniques were compared with regard to time use (time spent for completing the estimate for a plot), complexity for the observer, and reliability (correlation between estimated damage versus actual damage and yield loss, at planting as well as at maturity).

Sampling intensity

Since the non-stratified systematic sampling technique turned out to perform best (see Results), we investigated which sampling row interval at planting time would give an optimal balance between effort and accuracy. Using a computer, we simulated sampling intensities, re-sampling data from the 15 plots for which actual damage was recorded for all plants. Different sampling intervals (every 2nd, 3rd, 4th, 5th, ...20th row) were chosen and, for each sampling interval, we ran all possible simulations by choosing a different starting line every time. Simulated sample size decreased with increasing interval between sample rows. Obviously, choosing every single line corresponds to counting all plants, i.e. the actual damage. The variation between estimates was plotted against sampling interval.

Results and discussion

Comparison of sampling techniques

The average time spent per plot for each sampling technique is shown in Table 1. Non-stratified systematic row sampling was the fastest method, while non-stratified simple random sampling required the most time. In terms of complexity, the non-stratified systematic row sampling technique was the easiest. Previous studies in maize and rice in Asia also indicated a preference for similar methods, mainly because of the technical complexities of random sampling (Hoque et al. 1986; Rennison and Buckle 1988; Bailey 1994).

The correlation analyses between estimated and actual damage during seedling stage and harvest period show that for all sampling techniques, estimates and actual damage were highly correlated (Table 2). The non-stratified systematic row sampling technique had the highest correlation values both at the seedling stage and at maturity (r = 0.99 and r = 0.98, respectively). The non-stratified simple random technique had relatively lower correlation values (r = 0.95, r = 0.88) in all crop growth stages. In theory, stratified sampling should give at least as good an estimate as a non-stratified one. That was not the case, and probably is an indication that it is difficult to keep track of the boundaries of the strata and estimating their relative proportion of the field (Hoque et al. 1986).

Our study also showed that the four tested techniques gave good predictions of yield loss due to rodent damage at crop seedling and maturity growth stages. However, at maturity, stratified random square sampling again provided the weakest relationship (Table 2). This suggests that this sampling technique is not robust at this crop growth stage. Non-stratified systematic row sampling gave the highest correlation of crop damage and yield loss at both seedling and maturity stages of the crop. At the seedling stage, the regression coefficient (r^2) is lower than that at maturity, probably because many things can happen in the period between seedling and maturity stages, such as attack by other pests, disease, effects of weeds, and change in weather conditions. Buckle (1994) and Judenko (1973) pointed out that crop damage at the planting stage is compensated from better growth caused by reduced competition for growth resources following the death of neighbouring plants. However, Myllymäki (1987) pointed out that, in maize, compensation was minimal. Maize damage at the ripening stage is not compensated for, since kernels have completed growth by then.

Our computer simulations for different sampling intensities allowed us to quantitatively describe the intuitively assumed relationship between sampling intensity and estimate accuracy for the systematic row sampling. The standardised variance, which is the ratio of variance of the estimated damage values to the actual damage, gives a measure of the proportional variance of the estimates. An increase of estimate variation is observed when the interval between rows becomes larger (Figure 1). In other words, estimates become less reliable.

Table 1. Average time used to collect samples and degree of complexity for each sampling technique.

Sampling technique	Time (h) spent per plot (mean ± sd)	Complexity
Non-stratified systematic row sampling	1.09 ± 0.05	Simple, little training required on how to count and select rows, no special equipment required
Stratified random square sampling	1.37 ± 0.19	Complex, requires training to identify and weigh strata
Non-stratified Z-sampling	1.99 ± 0.08	Complex, requires measuring quadrats and distance between sample points
Non-stratified simple random sampling	3.34 ± 0.07	Very complex, requires understanding of the concept of randomness and availability of random tables or something similar

Table 2. Linear relationship between estimated damage at different crop growth stages and the actual damage or yield loss.

Sampling technique	Actual damage (%)			Yield loss (kg)			Sample size (n)
	Regression equation	R^2	p	Regression equation	R^2	p	
Seedling stage							
Non-stratified systematic row sampling	$0.957x + 3.436$	0.99	0.001	$12.20x + 38.46$	0.73	0.001	15
Stratified random square sampling	$1.132x – 7.149$	0.94	0.001	$12.731x + 11.204$	0.69	0.001	15
Non-stratified Z-sampling	$1.082x + 1.992$	0.93	0.001	$11.997x + 57.109$	0.60	0.001	15
Non-stratified simple random sampling	$0.851x + 9.201$	0.90	0.001	$12.041x + 48.598$	0.69	0.001	15
Maturity stage							
Non-stratified systematic row sampling	$1.505x – 0.005$	0.95	0.001	$1.1696x + 0.1728$	0.91	0.001	8
Stratified random square sampling	$1.789x – 0.269$	0.90	0.001	$31.358x + 174.23$	0.10	0.440	8
Non-stratified Z-sampling	$1.654x – 0.652$	0.90	0.001	$94.068x + 23.094$	0.90	0.001	8
Non-stratified simple random sampling	$3.556x + 0.180$	0.78	0.001	$49.301x + 62.711$	0.76	0.01	8

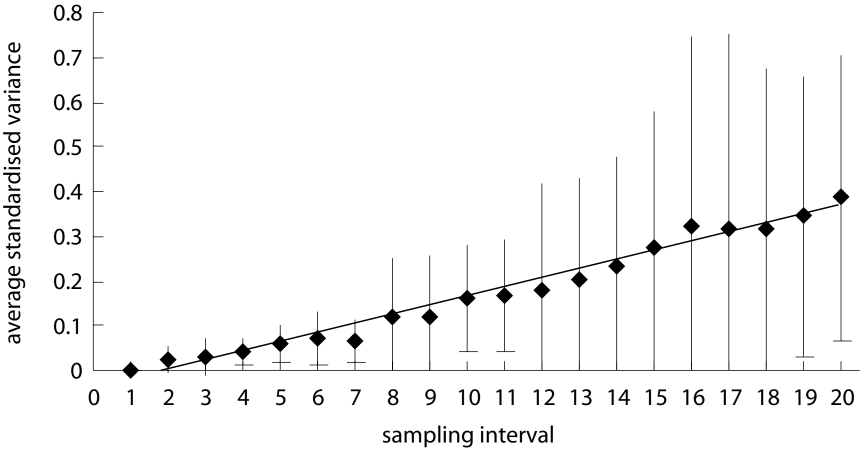

Figure 1. Average standardised variance for each simulation of 15 plots versus sampling interval for each plot.

On some plots, this effect was more dramatic than others, illustrating that damage is not equally distributed in all fields. When a sampling interval of less than six rows is used, the variation of an estimate stays below 10% of the actual damage (Figure 1). Therefore, the curve can actually be used as a standard curve for future studies to decide what sampling row interval should be chosen for obtaining a desired accuracy, or what kind of accuracy can be expected for a given sampling row interval. To sample each 5th row in the maize field, as used by Mwanjabe and Leirs (1997), seems to be a reasonable balance.

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Effect of land preparation methods on spatial distribution of rodents in crop fields

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Abstract. A mark–capture–release (CMR) study was carried out in Morogoro, Tanzania, from April 1999 to August 2000 to investigate the effect of slashing and burning versus tractor ploughing on the population of rodents in agricultural fields. We found that the spatial distribution of individuals was significantly affected by the land preparation method. The coefficient of dispersion values (based on variance-to-mean ratio calculations) indicated that more animals clustered around the edges in tractor-ploughed fields whereas in the slashed-and-burnt fields, animals were randomly distributed. Before land preparation, animals were randomly distributed everywhere. This suggests that the slashing-and-burning practice does not affect the rodent population distribution in crop fields while tractor ploughing does affect rodents, probably by reducing cover and food availability or even by killing some individuals. Yet, it seems useful as a management tool when it is practised over a large area and if the surrounding fallow lands, which act as donor habitat, are cleared.

Introduction

Rodents are responsible for substantial damage to food and cash crops and play an important role as reservoirs and carriers of zoonotic diseases in East Africa (Fiedler 1988). A mosaic of small plots of various crops, intermingled with patches of fallow and permanent grassland, combined with minimum land preparation and subsequent flourishing of weeds, creates favourable conditions for opportunistic and prolific species such as *Mastomys natalensis* and results in a high degree of damage to crops (Taylor 1968; Myllymaki 1989; Mwanjabe 1993).

Various studies have been carried out in Tanzania to establish the relationship between ecological parameters and rodent population dynamics. Most studies have largely involved research in areas with natural and semi-natural vegetation (Leirs et al. 1989, 1996; Telford 1989; Leirs 1994; Makundi 1995).

An understanding of factors that influence the population dynamics of rodent pests can provide an indication of the type of strategy that should be employed in their management. This study aimed to establish how cropping systems and land preparation methods influence the abundance and spatial distribution of *M. natalensis.* Here we discuss the effects on spatial distribution.

Materials and methods

The study area is located at 6°46'S, 37°37'E and 480 m above sea level at Solomon Mahlangu Campus (Mazimbu), Sokoine University of Agriculture, Morogoro, Tanzania. The area has a bimodal rainfall pattern with short rains between October and January and long rains between March and May. Two crops per year, depending on the amount and distribution of rainfall, are cultivated.

A capture–mark–recapture (CMR) study was conducted during the 1999–2000 cropping seasons. Eight 70 × 70 m grids were prepared, consisting of seven parallel lines, 10 m apart, and seven trapping stations per line (total of 49 trapping stations/grid), also 10 m apart. One Sherman live-trap (7.5 × 9.0 × 23.0 cm, HB Sherman Trap Inc, Tallahassee, USA) was placed on each trapping station. A 200–300 m wide zone of fallow land separated the grids from each other. The grids were subjected to two types of cropping systems (mono-cropping, inter-cropping) and two land preparation methods (tractor ploughing, slashing and burning). The mono-cropping system consisted of a monoculture of maize and the inter-crop consisted of a mixture of maize and beans. The experimental design was a completely randomised design (CRD) with 2 × 2 factors replicated twice. The grids were ploughed in November 1999 and February 2000 during the short and long rain seasons, respectively. Tractor ploughing was done using a disc plow at a depth of 30 cm—a normal rooting depth for most annual crops. Slashing was done manually close to the surface of the soil and the weeds were left to dry for one or two days, depending on weather conditions, after which they were burned. Maize sowing followed a standard procedure (planting lines 90 cm apart, plant holes 60 cm apart, and three seeds per planting hole). The bean crop was sown 3 weeks after the maize, at a spacing of 50 cm × 10 cm. All necessary agronomic practices such as fertiliser application and weeding were carried out equally on all the plots. Triple superphosphate (20 kg/ha) and nitrogen (40 kg N/ha) were applied before sowing and 3–4 weeks after sowing, respectively.

Trapping was conducted in each grid for three consecutive nights at intervals of 4 weeks. Additionally, trapping was conducted before land preparation (tractor ploughing or slashing and burning), after land preparation, and after seed emergence. Traps were baited with peanut butter mixed with maize bran and were inspected early in the morning. Animals were marked by toe-clipping. The trapping station, sex, weight, and reproductive status of captured animals were recorded. Animals were later released at the station of capture.

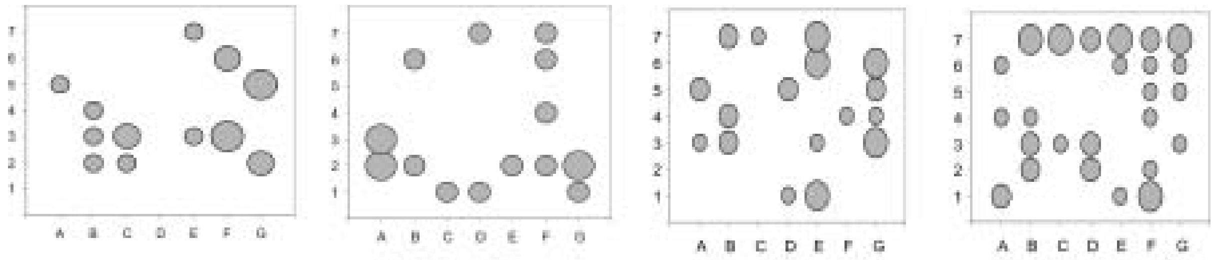
Population size was estimated for each 3-day trapping session using the M(h) estimator of the program CAPTURE for a closed population, which allows for individual variations in trapping probability (White et al. 1982). Spatial distribution of animals was established by means of capture maps showing the intensity of captures at different trapping stations. The pattern of distribution of individuals over the different trapping stations was established by determining the coefficient of dispersion (CD) by calculating the variance-to-mean ratio. These ratios indicate whether animals are aggregated, random or regular in their distribution (Kranz 1993). The distribution was considered random when the CD values were 0.7–1.3, aggregated (clustered) when CD values were >1.3, and regular when CD values were <0.7.

Using the established maps, the percentage of animals captured at the centre grids (40 × 40 m from lines 2–6 and trapping stations B–F) was compared between treatments. Since the central grid consisted of 5 × 5 of the 7 × 7 traps of the whole grid, we expected a proportion of 25/49 if animals were evenly distributed throughout the field. Statistical analysis using GLM Factorial ANOVA (analysis of variance) was performed in STATISTICA to compare the effect of the different land preparation methods and the cropping systems on the distribution of animals.

Results and discussion

The population abundance of rodents was influenced by the land preparation method and, to some extent, the cropping system. Trapping after land preparation showed a drop in population size in the slashed-and-burnt fields, but not in the tractor-ploughed fields (data not shown here). After seed emergence, the rodent population increased in all the grids, but a greater increase occurred in the slashed-and-burnt fields than the tractor-ploughed fields. During the long rain season, very few animals were captured and there was no clear pattern in the population trend.

The immediate effect of slashing and burning and tractor ploughing was a drastic drop in the rodent population, but it increased fast in the slashed-and-burnt fields after germination and emergence of weed and maize seedlings. The increased population size was probably due to recolonisation from the surrounding fallow land, but this needs to be investigated further. Figures 1 and 2 show typical examples of the spatial distribution of individuals in tractor-ploughed and slashed-and-burnt fields, respectively, during various growth stages of maize. The animals were randomly distributed in both the treatments before land preparation (Table 1). However, at the seed emergence and vegetative stages of the maize crop, animals occurred in clusters in the tractor-ploughed fields in both the short and long rainy seasons, while they remained randomly distributed in the slashed-and-burnt fields (variance-to-mean ratio, Table 1); the clusters in the ploughed fields were situated near the field edges. The land preparation methods, cropping systems and the season significantly affected the distances occupied by individuals from the centre of the grids. The mean distances were 27.8 m and 21.6 m for tractor-ploughed and slashed-and-burnt fields, respectively, and were significantly different (Tukey HSD test; $p < 0.001$).



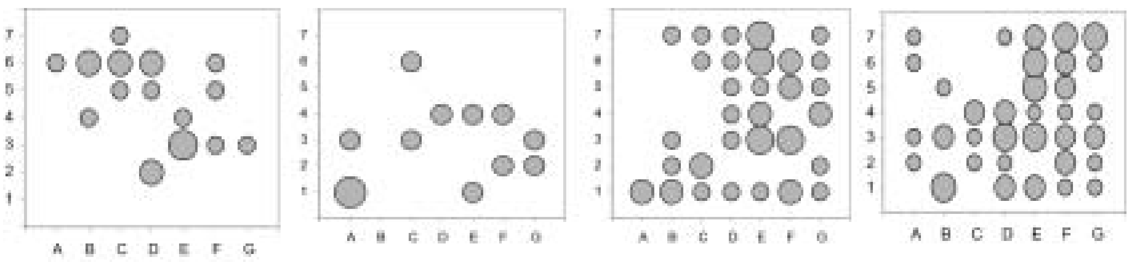
Before ploughing (November, 2)

After ploughing (November, 30)

After seed emergence (December, 10)

Vegetative stage (December, 28)

Figure 1. Distribution of trapped individuals over the different trapping stations in the tractor-ploughed fields (mono-crop) during the short rainy season 1999. Dot size increases with number of captures (1–3). Scale: trapping stations A–G and trapping lines 1–7 were 10 m apart. Lines with trapping stations were 10 m apart; the field extended 5 m beyond the outer trap lines; the fields were surrounded by fallow land.



Before slash and burning (November, 2)
After slash and burning (November, 30)
After seed emergence (December, 10)
Vegetative stage (December, 28)

Figure 2. Distribution of trapped individuals over the different trapping stations in the slashed-and-burnt fields (mono-crop) during the short rainy season 1999. Dot size increases with number of captures (1–3). Scale: trapping stations A–G and trapping lines 1–7 were 10 m apart. Lines with trapping stations were 10 m apart; the field extended 5 m beyond the outer trap lines; the fields were surrounded by fallow land.

Table 1. Coefficient of dispersion (CD) values (variance (s^2) to mean ratio calculations) and pattern of spatial distribution of rodents before and after land preparation and during growth of maize.

Cropping stage	Tractor-ploughed				Slashed-and-burnt			
	Mean	s^2	CD	Distribution[a]	Mean	s^2	CD	Distribution[a]
Before land preparation	0.65	0.65	0.99	Random	0.24	0.23	0.94	Random
After land preparation	0.51	0.75	1.48	Clustered	0.42	0.54	1.20	Random
After seed emergence	0.67	1.09	1.63	Clustered	0.95	0.87	0.91	Random
At vegetative stage	0.61	1.04	1.58	Clustered	1.20	1.08	0.89	Random

[a] Coefficient of dispersion scale: random distribution = 0.7–1.3; aggregated (clustered) distribution = >1.3; regular distribution = <0.7.

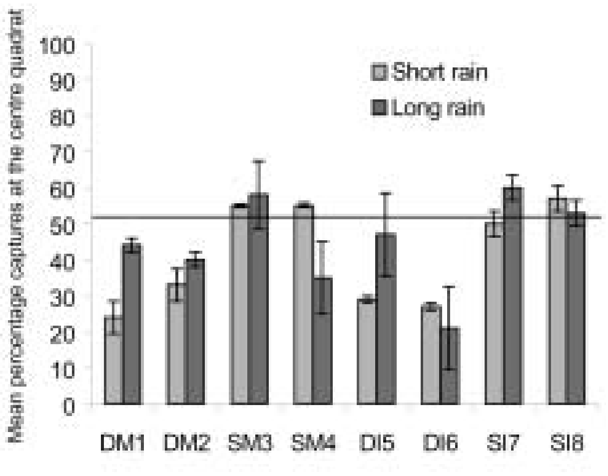


Figure 3. Mean percentage (± se) captures at the centre grid during the short (1999) and long (2000) rain seasons (the mean percentages are for the sum of captures before ploughing, after ploughing, after seed emergence and at vegetative stage). Abbreviations on the X-axis refer to land preparation (D = tractor ploughing; S = slashing and burning) and cropping system (M = mono-cropping; I = inter-cropping). Numbers refer to different replicates. The horizontal line at 51% indicates the expected value if animals were evenly distributed over the grid and the periphery.

For the two cropping systems, the mean distances were 26.0 m and 23.4 m for mono-cropped and inter-cropped fields, respectively, and also varied significantly (Tukey HSD test; $p = 0.007$). In the short and long rain seasons, the distances also differed significantly (Tukey HSD test; $p = 0.041$) (25 m for short rains and 23.8 m for long rains). The concentration of the animals along the edge of the tractor-ploughed grids is probably due to a combination of mortality in the ploughed grid, movement from the centre to the edges, and possibly recolonisation from the surrounding fallow land. Survival analyses, which can elucidate this, will be presented elsewhere. Deep ploughing using a tractor most likely reduces survival within the fields, because weed seeds, which are consumed by rodents, are ploughed under, while the nesting sites and burrow systems are destroyed. Ploughing may also have caused direct mortality of some individuals. Studies in China also showed that ploughing reduced the population of *Cricetulus triton* (Zhang et al. 1999).

Significantly, more animals were captured in the centre (40 × 40 m) grid in the slashed-and-burnt fields than in the tractor-ploughed fields during the two cropping seasons (Tukey HSD test; means, tractor-ploughed = 36.25%, slashed-and-burnt = 51.00%, $p = 0.03$) (Figure 3). The percentage of animals captured at the centre grid in the tractor-ploughed fields was significantly different from the expected value of 51% (equivalent to the ratio of 25/49 traps at the centre) ($\chi^2 = 8.5$; df = 1). In the slashed-and-burnt fields, the centre grid had 51% of the captures which corresponds to the expected proportion of captures for 25/49 traps. This suggests that in the slashed-and-burnt fields there were no differences in the distribution of animals between the centre and the periphery, while in the tractor-ploughed fields there was a tendency for more animals in the periphery than would be expected by chance. Cropping system and season had no significant effect on captures at the centre grid and there was no interaction between ploughing, cropping system and season on the distribution of animals. The observed distribution of animals in the different fields suggests that the slashed-and-burnt fields provided better protection and more resources than the tractor-ploughed fields. It could also be argued that the maize seeds provided more favourable food than weed seeds in the adjacent fallow land. This is consistent with Taylor and Green's (1976) observations that, when there were no cereal crops in the fields, rodents depended on weed seeds and the leaves of dicotyledonous plants, but as soon as the cereals became available, they formed a major part of the diet of *M. natalensis.*

The influence of cropping system on spatial distribution and population abundance of *M. natalensis* is not quite clear in the current study. However, it is plausible that there was increased activity of rodents in both types of cropping system because the weed density increased in the fields. It is also apparent that the population density within the inter-cropped fields increased, which could be attributed to better cover, or an alternative food was available when maize crop was not very attractive for the rodents. Therefore, it will be interesting to investigate how repeated weed control in both types of cropping system, and how the method of land preparation will affect the distribution pattern and population abundance of rodents and whether this could be part of an integrated approach for management of *M. natalensis*.

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Current approaches towards environmentally benign prevention of vole damage in Europe

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Abstract. Voles are the most important field rodent pest in Europe and farmers need benign means of reducing damage to crops. In this paper, I review ideas discussed during a recent meeting in Braunschweig, Germany, on *Prevention of vole damage in organic farming*. Measures suggested include the installation of migration barriers, the use of secondary plant compounds specifically acting against voles, support of vole predators, diversionary feeding, and physical devices for early detection of vole infestations. These approaches show some potential but require further investigation before they can be recommended for practical use. A successful strategy for the prevention of vole damage will probably have to integrate several of the suggested methods.

Introduction

Prevention of vole damage is still one of the prominent challenges facing European rodent control officers. Cyclic vole species like *Microtus agrestis, M. arvalis, M. subterraneus* and *Arvicola terrestris* cause significant damage throughout their wide geographical range during peak years of abundance. Besides taking grain from fields, voles debark trunks of young trees and destroy their root system by gnawing. Fruit trees in orchards and afforestations in forestry mostly suffer this type of damage. In 1998/99, damage by *Arvicola terrestris* in German forests occurred on more than 1000 ha with losses of up to 50% of trees and an estimated cost of 1.5 million Euro (Schneider 2001). In the same years, *M. agrestis* and *Clethrionomys glareolus* accounted for further damage on up to 9900 ha per year (Müller and Heidecke 2002). Furthermore, huge areas of grassland may be devastated when voles occur in high numbers (more than 1000 per ha in *A. terrestris* and up to 5000 in *Microtus* species) (Meylan 1977; Lauenstein 1979).

In conventional agriculture and forestry, voles are usually controlled by distributing anticoagulant or zinc phosphide baits. Due to restrictions in the use of pesticides, however, these poison baits cannot always be applied. These pesticides are mostly non-specific and effects on non-target species cannot be completely ruled out (Zahner 1996; Saucy et al. 2001). In organic farming, synthetic pesticides are not allowed, thus trapping and gassing remain the only applicable measures, requiring a lot of time and personnel skills (Malevez 2002; Popow 2002).

Here, I review the ideas presented during a meeting organised by the Federal Biological Research Centre for Agriculture and Forestry in Braunschweig, Germany, in June 2001 on *Prevention of vole damage in organic farming* in the context of *Plant protection in organic farming—problems and solutions*. The presentations of the meeting are documented in Federal Biological Research Centre for Agriculture and Forestry (2002). I refer to the papers contained therein by Gago (2002), Müller and Heidecke (2002), Pelz (2002), Saucy (2002), Sommer (2002), Wieland (2002) and Wink (2002).

Suggested approaches

Migration barriers (fencing) and trapping

Dispersal constitutes an important element in the population dynamics of small mammals. It is assumed that immigration and emigration will usually level out unequal population densities in uniform habitats, with juveniles dispersing after weaning in order to establish their own territories. This dispersal behaviour has the potential to limit the success of vole management strategies.

Control measures targeting rodent populations usually cover restricted areas and thus result in vacancies that will quickly be re-colonised from neighbouring populations, especially if the overall population density is high. Saucy (2002) and Wieland (2002) suggest the use of migration barriers to protect valuable crops from vole immigration.

Saucy and Schneiter (1997) observed extensive above-ground dispersal of young water voles during rainy nights. Based on this experience, Saucy (2002) recommends semi-permeable fences equipped with one-way exit doors that allow voles to leave the plots, but prevent them from re-colonisation. In connection with other control measures, like frequent grass mowing, traditional trapping and measures favouring natural enemies, Saucy thinks semi-permeable fences are likely to provide long-term protection against vole damage.

Wieland (2002) demonstrated in a field experiment that immigration of the field vole, *M. arvalis*, into a carrot field was totally stopped using a 4 mm plastic fence, 16 cm above-ground and 8 cm below-ground in combination with poison bait stations along the fence. Even a ploughing furrow equipped with poison bait stations blocked migration considerably, achieving an 80% reduction of immigration.

Potential significance of secondary plant compounds

More than 360,000 plant species, forming the base of the food chain, produce in addition to primary compounds (e.g. amino acids, carbohydrates, fatty acids) a large number of secondary compounds. About 80,000 of those secondary metabolites are already known from plants, although no more than about 20% of all plants have been investigated to date, and most of these investigations have been incomplete. Secondary compounds play an important role in the chemical defence of plants against herbivores. During evolution, plants have succeeded in developing specific substances targeting important organ systems of herbivores (e.g. the central nervous system, the digestive system, heart and blood circulation, respiration, muscle contraction or reproduction). Among the mechanisms underlying the toxic effects are the inhibition or modification of cell structures including deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), and the functional processes during protein biosynthesis (for an overview, see Wink 1993, 2000).

Polyphagous herbivores are capable of evaluating the quality of potential food plants and to detect and avoid secondary substances and the plants containing them (Bernays and Chapman 1994). They prefer plants with low content of or harmless secondary substances, like our cultivated plants that have lost most of their poisonous secondary substances. Most of the polyphagous species also use mechanisms for a fast detoxification and elimination of secondary substances. Mono- and oligophagous herbivores, on the contrary, are adapted to specific secondary substances that stimulate consumption by these species. They often store the poisonous secondary substances and utilise them for their own defence against predators.

Several secondary compounds are already known to have an effect on voles (Lindroth and Batzli 1984; Bucyanayandi et al. 1990). Wink (2002) suggests locating potential compounds by a systematic screening of the biological effects of secondary compounds on voles. Additional experiments would then be required to find a practicable way to apply these substances on cultivated plants to protect them. If these secondary compounds cannot be used as a repellent, there might also be a chance to find a more vole-specific poison in contrast to the non-specific rodenticides used today.

Tree species differ greatly in their palatability or repellence and even varieties vary in their palatability to voles. However, in years of high vole abundance, these properties seem to be insufficient to keep voles completely away from trees (Rousi 1989).

Müller and Heidecke (2002) report promising preliminary results using extracts from *Echinops sphaerocephalus* as a repellent. This plant contains echinorin, an alkaloid with a bitter taste but of low toxicity. In laboratory and field trials to protect shoots of apple twigs from gnawing damage by *M. agrestis*, the repellence of the echinops extract was on the same level as the standard thiram repellent used for comparison (HaTe-PELLACOL®). In the field trials, after 80 days the bark area gnawed in echinops-treated twigs was still less than 25% compared to the untreated (control) twigs. Investigations to further strengthen the effectiveness of the echinops extract are currently in progress.

Supporting vole predators

In peak years of abundance, *A. terrestris* makes up 80% of the diet of the barn owl, *Tyto alba*, in the French Jura (P. Delattre, pers. comm., 1981). *Asio otus* and *Falco tinnunculus* are other examples of birds of prey that specialise on voles. Among the mustelids, *Mustela nivalis* and *M. erminea* mostly depend on voles as their principal prey, with *Arvicola* and *Microtus* species making up more than 50% of their diet (Debrot 1981; Erlinge 1981). From an applied point of view, it would be highly desirable to support predators in such a way as to increase their influence on vole populations. There are a few examples where predators have been used to solve vole control problems—the best known being the successful attempt to expel *A. terrestris* from the Dutch island of Terschelling (Van Wijngaarden 1961). However, specialised predators are restricted in their numbers by the minimum density of the prey species during the low phase of their cycle. Since predators are regarded as principal factors driving the cycles of small mammals (e.g. Henttonen 1999; Klemola et al. 1999; Sittler 1999), there is sufficient reason to believe that a diversely-structured landscape and provision of shelter—such as heaps of wood or stones to support mustelids, and nesting places and perches for birds of prey—could assist in keeping vole populations at a low level and to dampen outbreaks. However, experimental data for voles to support this idea are still missing. The scientific challenge would be to provide evidence for the ecological benefits of predator support.

Provision of alternative food

Provision of diversionary food is a method of habitat modification designed to temporarily satisfy part, or a majority, of the food requirements of a problem species in a localised area (Howard 1967; Sullivan 1979). A good example how such a system can work has been the diversionary feeding of mice that has been successfully applied for the prevention of damage by *Apodemus sylvaticus* to pelleted sugar beet seeds (Pelz 1989). From an energetic point of view, it is much more efficient for these mice to take the seeds provided instead of digging up hundreds of seeds that farmers have planted in the soil.

Although the requirements of a bark-consuming vole may not be directly comparable with those of a seed-consuming mouse, the key question to be answered is identical: What makes up the relative attractiveness of the target cultivated plant? Can the basic nutritional needs of the rodents be satisfied alternatively and in this way the cultivated plants be protected? Laboratory and field studies on nutritional requirements of voles revealed that the need of certain minerals like sodium, calcium or phosphorus may have an influence (Hansson 1991), but also the conversion of starch to glucose at low temperatures (Murneek 1942) may trigger the debarking behaviour of voles. Reduced availability of preferred food plants during autumn and winter is indicated by a higher proportion of less preferred grasses in the diet of voles at this time of year (Cengel et al. 1978). Servello et al. (1984) found that the digestibility of apple tree root bark for *Microtus pinetorum* was 15–30% lower compared to the proportion of digestible dry material and digestible energy usually found in the stomachs of this vole species caught in apple orchards. But sugar content of root bark was significantly higher in winter than in summer. These findings suggest that a bark diet helps voles to get through times of food shortage during winter, and that the palatability of tree bark derives from its sugar content.

Experiments with diversionary feeding to prevent voles from debarking trees have been conducted by Sullivan and Sullivan (1988) in Canadian apple orchards and in forest plantations (Sullivan et al. 2001). They distributed alfalfa-, wood- or bark-pellets formed to blocks with wax and sunflower oil. Although a significant reduction of damage could not be achieved in all of these trials, the results do show that diversionary feeding is a method deserving further exploration (Pelz 2002).

Physical detection of vole infestations

Due to their subterranean and crepuscular habits, it is sometimes difficult to be aware of the presence of voles in plantations. In woody plants, damage caused during winter often does not become obvious before the next spring when buds are not put forth. The ability to detect vole populations while they are at low density is important for the success of any vole management strategy. New techniques are now available that may make the early detection of voles possible. These include the use of infrared cameras and sound detectors.

Infrared cameras

These may be useful tools for thermal-imaging of plantations to detect vole burrow systems and to observe immigration of voles. Small, lightweight, digital infrared cameras are now available at an affordable price (Gago 2002).

Sound detectors

Gnawing by voles on roots or trunks of trees creates characteristic sound waves. With a newly developed detection system, these specific sound waves can be recognised at an early stage (Schönherr et al. 2000). For this purpose, the sound detectors are fixed to selected stems of trees and the oscillation is permanently monitored. The system steadily calculates an average reference signal, which is caused by structure-borne sound waves in the environment. This reference signal is transferred to an adjustable comparator step, where the reference signal is continuously compared with the presently measured signal. If roots are gnawed by water voles, the gnawing procedure produces strong, impulse-like sound waves that significantly change the signal. The gnawing sounds predominantly occur at a frequency range around 100 Hz and they are transferred to the stem of the tree to which the sensor is fixed. If the present sound signal, caused by a gnawing vole, exceeds the average reference signal for a certain time, the detector will identify and indicate vole gnawing activity by a flashing light-emitting diode (LED). The alarm message can also be radio-transmitted to a receiving station. If more than one detector is in use, each signal will be specific to enable the identification of the infested tree and immediate control measures can be undertaken (Pelz 2002). Such a system, with detectors distributed in a strategic way to receive an alarm call as soon as voles invade a plantation and start doing damage, could greatly improve and facilitate control. The system is now about to be tested under field conditions.

Conclusion

Vole damage to cultivated plants is a complex problem with much of the ecological background still unexplored and satisfactory damage prevention not yet available. The approaches suggested at the meeting in Braunschweig on *Prevention of vole damage in organic farming* require further investigation and testing under practical conditions. They are regarded as a basis for planning research and development of projects in order to improve the situation in organic farming. As conventional agriculture and forestry too are looking for measures other than the application of pesticides for vole control, there is no doubt that they will readily adapt measures that prove efficient in organic farming. However, due to the complex nature of the problem, a single control strategy will probably remain insufficient. A successful strategy for the prevention of vole damage will have to integrate several of the approaches suggested.

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Overcoming rat infestation in Australian sugarcane crops using an integrated approach that includes new rodenticide technology

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Abstract. Two Australian native grassland rodent species cause significant, but seasonally sporadic, damage at several stages of the crop cycle in Australian sugarcane areas. These rodent infestations represent one of the most important pest problems for sugarcane growers. A series of interrelated management practices has recently been introduced to minimise the occurrence of rodent infestations and to achieve better management of those infestations that arise in the sugar crops. Components of the integrated pest management (IPM) approach include improved short- and long-term management of harbourage areas, in-crop weed control, rodent population monitoring, and baiting of emerging populations using new technology. A new rodenticide, RATTOFF® (patent pending), presents small, localised quantities of grain coated with zinc phosphide that is protected from the wet tropical environment by a biodegradable and edible cellulose membrane. This baiting approach allows the minimum effective application of chemical to control rats. Application of RATTOFF® is based on objective monitoring of emerging rodent problems and is implemented as part of (and not a replacement for) a total IPM strategy. This combined approach reduces the potential for large-scale rat plagues and reduces crop damage throughout the production cycle. An industry-wide extension program was implemented at district and regional levels to mitigate overall damage potential.

Introduction

In the 1999–2000 harvest seasons, rats in Australian cane fields destroyed approximately 825,000 tonnes of sugarcane valued at US$50 million. Rodents can potentially damage sugarcane at all stages of cane growth. In ratoon cane, rats gnaw the stems and apical meristems of young plants. As the cane grows, the rats attack the mature stalks, resulting in reduced sugar content and harvestable tonnage (Wilson and Whisson 1993). Even minor gnawing damage can predispose cane stems to infestation by insects, bacteria and fungi, and desiccation (Robertson et al. 1995). Rodent damage can cause brittle cane that shatters when harvested, or deteriorated cane quality through the fermentation of the cane juice (Rao 2001).

Rodent pest species

The main species responsible for sporadic damage in Australian sugarcane crops are the cane field or ground rat (*Rattus sordidus*) and the grassland melomys or climbing rat (*Melomys burtoni*) (Wilson and Whisson 1993). Both species are native grassland species common through the coastal tropical areas of northern Queensland. Generally the species do not pose problems for commercial crops and do not require control in grassland habitat, however they are both well suited to the introduction of sugarcane crops which provide appropriate crop habitat. Thus, these rodents have expanded their ranges to include cane fields. *R. sordidus* requires friable soil for burrow construction, and "close and substantial ground cover" (McDougall 1946), thus the soil preparation used for establishment of raised beds provides an ideal opportunity for this species to establish nest sites early in the cane-growing season, and this rat remains within the crop at all stages. Both plant cane and ratoon cane blocks are affected. *M. burtoni* is usually associated with taller native grasses that provide suitable cover, protection and support for their nests in the canopy (Redhead 1973), so this species more commonly infests cane crops from canopy closure through to harvest.

Rodent outbreaks

Populations of *R. sordidus* follow a cyclic annual pattern that is modified according to seasonal, environmental and crop conditions that regulate breeding success and mortality (McDougall 1946). Significant rodent infestations arise from a combination of factors including:

- poor in-crop weed control, leading to seeding of summer grasses that trigger the onset of rat breeding;
- abundant and uncontrolled grass cover on adjacent harbourage areas that provides habitat and food, and

thus a potential source for recolonisation of cane crops by rats;
- high spring rainfalls that facilitate summer grass and weed growth, and that lead to an early commencement of breeding;
- failure to detect and control residual or rising populations of rodents in crops that provide a breeding base for future seasons; and
- the presence of stand-over cane (after excessive wet weather that prevents harvest), providing additional harbourage for rats.

Previous management strategies for rodent control in cane fields

Control of rodents in Australian cane fields has traditionally involved large-scale baiting campaigns. Historically, these have been conducted at the time of peak rodent numbers at the end of the breeding phase in autumn. One method was based on the distribution of paper sachets containing the sulfate salt of the heavy metal thallium, coated onto grain (Wilson and Whisson 1993). Re-infestation of crops with rats from adjacent habitats occurred rapidly (Redhead and Saunders 1980) and this bait was withdrawn due to environmental residue concerns (Robertson et al. 1995).

More recently, wax blocks containing the second-generation anticoagulant brodifacoum (available commercially without restriction) were used to reduce rodent populations in cane fields (Story 1993). The blocks were often applied in reaction to very large rodent infestations late in the growing season. Often the treatments were applied long after a significant amount of early crop damage had occurred and at a time of maximum rodent infestation that required the application of large quantities of bait. Multiple applications over an extended period were sometimes used to achieve the required level of control. However, second-generation coumarin anticoagulants, such as brodifacoum, have a long biological half-life and can accumulate in the food chain (Eason et al. 1999). Also, because the action of anticoagulants is delayed, rodents can accumulate super-lethal doses of active ingredient before succumbing to the initial dose ingested. These features of potent second-generation anticoagulants have led to concerns about the potential impact on non-target species, especially birds of prey or scavenging animals that feed on the poisoned carcasses. These chemicals posed an unacceptable risk of secondary poisoning if applied in high quantities over large areas of broad-acre crops (Howald et al. 2000) and second-generation anticoagulant wax block formulations were withdrawn from the sugar industry by suppliers in 1998.

Development of an integrated pest management (IPM) strategy

The approach now adopted by the Australian sugar industry has arisen after consideration of the early work of McDougall (1946) who researched the ecology, biology and control of rodents in sugarcane crops. This work was extended by the studies of Redhead (1973) on *M. burtoni* populations. These investigations, combined with further research conducted by the Queensland University of Technology (QUT), Bureau of Sugar Experiment Stations (BSES) and the Cane Protection and Productivity Boards (CPPBs), facilitated the development of an integrated plan to control rodent pests in sugarcane (Wilson and Whisson 1993).

Traditionally, growers were accustomed to lethal control treatments applied reactively at a time of high rodent numbers and after severe cane damage was observed. In such circumstances, bait uptake was high and large numbers of rodents were killed. However, though seen as successful control by landowners, most of the crop damage had already occurred before the reactive treatment of high rodent populations (Wilson and Whisson 1993). Thus, while rodents were killed, little damage was prevented, and presumably the small proportion of survivors provided the base for the next season's rodent problems. In contrast, the present procedures of habitat manipulation, weed control and other components of the IPM program, including application of bait when rodent populations are emerging, focuses on suppression of breeding rather than killing rats *per se*, but does greatly reduce losses of crop and sugar (Robertson et al. 1995).

Since the impact of a proactive, early approach is subtle, some growers initially doubted the effectiveness of these IPM techniques compared to their previous practices. To overcome this perception, an extension program coordinated by BSES and participating CPPBs was implemented to encourage growers to adopt whole-farm management of rodent populations.

In-crop weed control

Suppression of weed and grass growth in-crop is required to restrict the available food source and habitat area for rodent breeding and development. Grass seed provides protein that is essential for rodent breeding (Wilson and Whisson 1993).

Changes in farming practices, such as green-cane harvesting and trash-blanketing, have also impacted on rodent numbers within the crop. The retention of a trash-blanket in ratoon cane improves moisture retention and reduces weed competition, and though providing a rat refuge source immediately after harvesting, reduces eventual cane damage by suppressing weed growth that leads to rat breeding (Whisson 1996). Several pre-emergent and knockdown herbicides are available as tools to reduce weed infestation at specific stages of the crop cycle, and strong extension and advisory programs are well established within the industry to maximise the effectiveness of in-crop weed control. Since weed control reduces competition within the crop and improves cane yields directly, the industry has readily accepted the collateral benefit of improved rat management in clean, weed-free crops.

Harbourage management

Non-crop habitats such as headlands, drains, river and creek banks, tram-lines and steep slopes often support weeds and other grasses, and provide refuge for rats, especially after rodent dispersal during mechanised cane-harvesting activities. Large numbers of rats can remain within these undisturbed harbourage areas until the cane canopy develops sufficiently to provide enough protection within the crop, at which time rodents return to recolonise the crop. With the development of highly effective new technology for rodent control in-crop, there is no need to use lethal control methods in the harbourage. Instead, the focus is on modifying the harbourage immediately adjacent to the crop to reduce its suitability as a reservoir for reinvasion of crops by rodents.

Where chemical and physical weed control (slashing) are impractical due to waterlogging, steepness or lack of vehicle access, the harbourage can be reduced by grazing of stock and by revegetation of difficult terrain with trees that shade out grasses. Native, fast-growing species achieve a closed canopy after only a few years (BSES 2000). Revegetation along waterways also benefits the environment by reducing erosion, stabilising banks, improving water quality and providing wildlife corridors between habitats, thus, as for weed control, a focus on rats can have collateral benefits for other aspects of responsible land management and improved crop productivity. Some growers continue to manage harbourage by burning grass during dry periods. This is a short-term solution, since the establishment of larger trees is prevented, and regrowth of weeds in the cleared areas is rapid. The present extension message therefore encourages longer-term management of difficult harbourage areas by replanting rather than seasonal burning.

Rodent population monitoring

Monitoring can be undertaken by the individual grower or at the regional level by advisory bodies. Regional programs can describe the population dynamics of the target species over a period of time and in a variety of environmental conditions. These data can be incorporated into a population model that predicts the influence of environmental conditions on future breeding intensity, juvenile recruitment, recolonisation, natural attrition, and crop damage. Feedback of regional data to growers via discussion groups and a web site are promoted by industry agencies and increase awareness well ahead of the major population rises. Thus, weed control and strategic baiting can be conducted in areas expected to incur high levels of crop damage. This early feedback is also used to alert and stimulate growers to check their own fields. Regional monitoring includes assessment of reproductive condition of female rodents. The presence of healthy females in breeding condition increases the likelihood of a rapid population increase and, therefore, the need to apply a rodenticide pre-emptively to prevent further population build-up (Robertson et al. 1995).

Development of new rodenticide technologies

In 2000, the development of RATTOFF® zinc phosphide bait sachets introduced a new option for rodent management in Australian sugarcane. The active ingredient of RATTOFF® is the acute toxin zinc phosphide. Since the 1940s, zinc phosphide has been used widely throughout the world to control rats and other rodents in crops, including sugarcane in Hawaii and the Philippines (Sugihara et al. 1995; Hoque and Sanchez 2000). Because zinc phosphide degrades once exposed to moist acidic conditions, the absorption of moisture and subsequent physical degradation of pelleted baits may reduce their acceptability to rodents in wet conditions (Sugihara et al. 1995). To overcome this problem, a more weather-resistant zinc phosphide bait presentation suitable for humid and wet conditions was developed. RATTOFF® consists of inactivated whole wheat grains coated with zinc phosphide and packaged in 10 g degradable cellulose membrane sachets, providing a localised lethal quantity for consumption by the rat. The cellulose membrane protects the bait against moisture degradation but is readily opened by the rats. Sachets are placed at 10 m intervals within the crop, which is equivalent to 100 sachets/ha, or 1 kg/ha. Only a few grains are required to kill a rat, therefore the low application rate of 1 kg/ha is sufficient to significantly reduce rodent population numbers within the crop.

In cage studies, *R. sordidus* rats typically ingest a lethal dose on first exposure to the sachet, and under field conditions often take sachets back to nests. *M. burtoni* rats appear to exhibit a more cautious initial approach, but cage-testing confirmed that they return to the sachets even after an initial sub-lethal exposure. In most instances, rats readily locate the sachets placed within the crop area and are killed within a few hours of ingesting very small quantities of RATTOFF®. Due to the high potency of the bait and the neophobic propensity of rodents, only small quantities of poison are ingested before the rodent dies, and super-dosing does not occur. In addition, zinc phosphide residues degrade quickly within the carcass (measured half-life of less than 1.5 days), resulting in a very low risk of secondary poisoning (Johnson and Fagerstone 1994). Zinc phosphide also degrades in the environment within weeks, leaving no residues, and is not readily taken up by plants (EPA 1998). This type of bait thus overcomes many of the risks associated with the use of second-generation anticoagulant baits in crops.

Strategic baiting

Robertson et al. (1995) demonstrated that where both effective weed control and strategic baiting were employed, significant reductions in damage could be achieved. Wilson and Whisson (1993) suggested that rodent management is most effective if rodenticides are applied before populations are large. Therefore, it is recommended that baiting programs be conducted during the non-breeding period from November to January, well before the maximum rodent numbers occur in March to May. In the Australian cane industry, this optimum period for bait application is during the early ratoon stage of the crop cycle, before canopy closure during the summer, and just before the wet season. At this time, the access to planted areas for both weed management and rodent control is good. From an organisational perspective, the combination of both aspects of rodent management can be achieved in the same application of labour and machinery, and this is now accepted as a more strategic time to apply lethal control methods.

Apart from RATTOFF® zinc phosphide bait, a first-generation anticoagulant, coumatetralyl, is commercially available in a wax block form and is currently registered for use in crops within bait stations. As coumatetralyl has a shorter biological half-life than the second-generation anticoagulant compounds, it is considered to pose a much lower risk of accumulation in the food chain (Mount et al. 1986). However, the short half-life also means that prolonged exposure to the bait by the rodents is required for effective rodent control. This is achieved by multiple applications or by replacing bait taken from bait stations over a period of weeks.

It is imperative that the timing of any chemical control measures be correlated with rodent population dynamics. Components of IPM such as weed control and monitoring are implemented *before* there is a resort to baiting and may overcome the need for baiting at all, even though baiting forms part of the overall IPM.

The future of rodent management in the Australian cane industry

A significant effort has been made by industry advisory bodies, chemical suppliers, farm management. and extension groups to change the reactive approach to rodent management of the past to a more proactive approach using best practice approaches. The IPM objective is to prevent the rodent problems from occurring (proactive management) rather than attempting to control rodent numbers after the population has reached an excessive level during the breeding season (reactive management). The introduction of RATTOFF® to the Australian sugar industry has satisfied the growers' requirements of simple bait application, quick effect and high efficacy, while at the same time presenting few environmental problems.

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Review of recent advances in studies of the ecology of *Mastomys natalensis* (Smith 1834) (Rodentia: Muridae) in Tanzania, eastern Africa

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Abstract. The objective of this review is to highlight the recent advances in our knowledge of the ecology of *Mastomys natalensis.* In Tanzania in East Africa, the commonest and by far the most serious rodent pest is the multimammate or *shamba* (field) rat, *Mastomys natalensis* (Smith, 1834) (Rodentia: Muridae). Populations of *M. natalensis* sometimes erupt, reaching high densities which are favoured by ecological factors that were not well understood, but are now the subject of intensive studies in Tanzania. Recent studies have led to better understanding of the ecology of *M. natalensis.* Rainfall pattern (timing, duration and amount) is instrumental in the timing of breeding and plays an important role in regulating populations of *M. natalensis*. Spatial distribution of *M. natalensis* in both fallow and crop fields shows overlaps in home range between individuals of the same or different sexes and between habitats. Because of the variations in the suitability of habitats for colonisation, changes in them invariably affect the population dynamics of *M. natalensis*, an important consideration in developing management strategies for this pest species.

The potential for ecologically based management of *M. natalensis* lies in (i) the use of avian predators which have been shown to decrease its survival probability, and (ii) manipulation of cultivation methods and land management practices which invariably affect the population characteristics of *M. natalensis*, spatial distribution and levels of crop damage in fields. A limited and selective use of rodenticides is recommended, particularly in routine control of *M. natalensis*. A system for forecasting rodent outbreaks based on the link between unusual rainfall and population dynamics of *M. natalensis* has been developed for early preparedness of the community to control them. In plague outbreak areas, *M. natalensis* is widely distributed in peri-domestic areas, both in fallow and cultivated lands, and forms a continuum for the spread of plague between predominantly forest species and human beings in plague affected areas.

Introduction

In sub-Saharan Africa, the major rodent species causing severe damage to crops belong to the genus *Mastomys* (Muridae). In East Africa, the commonest and by far the most serious rodent pest is *Mastomys natalensis* (Smith 1834) (Fiedler 1988a,b, 1994). Certain characteristics of the species, such as high reproductive capacity and dispersal, are thought to contribute to the success of *M. natalensis* as a serious pest (Meester et al. 1979; Leirs et al. 1993). Outbreaks of populations of this species are favoured by certain ecological conditions that were previously not well understood, but are now the subject of intensive research in Tanzania.

Numerous outbreaks of *M. natalensis* have occurred in Tanzania in the past (Leirs et al. 1996b). The outbreaks are sometimes localised, but they often occur in a wide geographical area where enormous amounts of poisons would be required to control them. The idea of an ecological approach to management of *M. natalensis* has been advocated in Tanzania (Leirs et al. 1996b; Makundi et al. 1999). The major constraint in formulating ecologically-sound rodent management is lack of knowledge on the ecological processes involved in rodent outbreaks. However, in the past 10–15 years, a keen interest in the ecology of *M. natalensis* by a group of researchers in Tanzania has led to new findings which could enable the design of management strategies which are ecologically sound and appropriate. The purpose of this paper is to review the advances that have been made in understanding the ecology of rodents in Tanzania.

The ecology of *Mastomys natalensis* in Tanzania

The studies in Tanzania have been aimed at understanding: (i) the ecological processes that maintain rodent populations at low levels (and hence of no economic importance) in certain seasons or in some years, but which at times lead to eruptions of the population to proportionally high densities, and (ii) the involvement of rodents in zoonotic diseases.

Investigations carried out since 1986 addressed the following ecological aspects:

1. The environmental factors with major impact on demographic processes that affect the population dynamics of *M. natalensis.*
2. How rainfall, in particular, influences demographic parameters and rodent density.
3. The relationship between rainfall patterns and life history variations and whether such relationships could be used to forecast outbreaks.
4. Spatial patterns of distribution in the field.
5. The impact of habitat alteration on abundance and distribution.
6. Re-colonisation capacity of the species following control activity.
7. The demographic characteristics of different generations pertaining to reproduction, growth and maturation, survival and productivity.
8. The influence of people's activities (particularly agricultural practices) on population characteristics and population dynamics.
9. Management practices, including predation.
10. The relationship between rodent densities, spatial patterns and the risks of outbreaks of diseases (plague, leptospirosis etc.).

Role of rainfall

Studies of the population biology of *M. natalensis* in Tanzania have clearly indicated an association between rainfall and breeding (Telford 1989; Leirs 1992). Seasonal variations in breeding and growth have been reported (Leirs et al. 1989; Leirs 1992; Christensen 1993). These studies confirmed the previously established relationship between rainfall and reproduction of *M. natalensis* (Taylor 1968; Delany 1972; Taylor and Green 1976; Neal 1986). Further, population fluctuations, reproduction, growth and survival are strongly related to the rainfall patterns (Leirs 1992). There is evidence that the abundance of the rain early in the wet season could create conditions favourable for the occurrence of outbreaks later in the year (Mwanjabe and Leirs 1997).

Population dynamics

A range of population densities of *M. natalensis* has been reported in the field. Telford (1989), Leirs (1992) and Christensen (1996) reported densities of 1125, 900 and 384 animals/ha, respectively, in Morogoro, Tanzania. This further illustrates that wide-ranging population fluctuations between seasons and years occur. For a species whose breeding characteristics are strongly dependent on the rainfall patterns, such fluctuations are expected to be the rule rather than an exception. Further, the population dynamics of *M. natalensis* are influenced by both density-dependent and density-independent factors occurring simultaneously and these regulate population size (Leirs et al. 1997). Temporal fluctuations in the population size of *M. natalensis*, as illustrated in Figure 1, result in different levels of crop damage and losses. Makundi et al. (1991) reported losses of 15% in cereals, while Mwanjabe and Leirs (1997) estimated damage levels of 40–80% of maize seedlings, which could lead to serious losses of food at harvest.

Spatial patterns

An understanding of the spatial patterns of space use is important to develop ecological strategies for management of *M. natalensis* in Tanzania. A negative correlation between high rodent numbers and open space, and a positive correlation between high numbers and high dense grass have been reported (Leirs et al. 1996a). It has further been shown that there is a considerable overlap of home range between individuals and members of the same sex and between farms and fallow land (Leirs et al. 1996a). The home range, spatial distribution and abundance of *M. natalensis* in crop fields also appears to be influenced by activities such as methods of cultivation and cropping

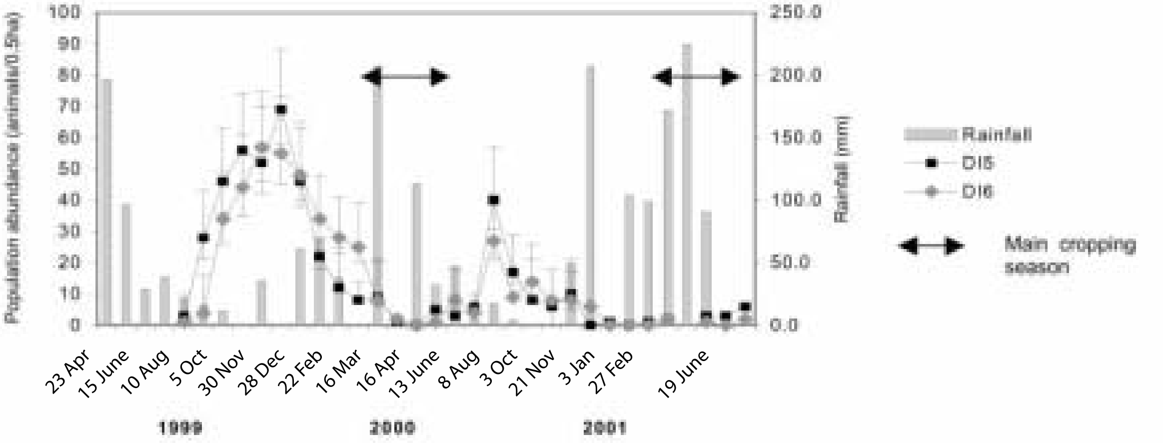

Figure 1. Rodent population fluctuations in relation to rainfall pattern in two crop fields (D15 and D16) at Morogoro, Tanzania.

systems (A.W. Massawe, unpublished data). Other studies on the home range of *M. natalensis* (Christensen 1996; Leirs et al. 1996a) have revealed that a large proportion of individuals in the population do not migrate far from their established home ranges.

Forecasting outbreaks

The idea that population eruptions of *M. natalensis* in East Africa could be predicted is not new. Harris (1937), Neal (1977) and Taylor (1968) suggested that outbreaks of *M. natalensis* were associated with wet years. The wet years, due to prolonged rainfall, appear to favour survival and breeding (Fiedler 1988a,b). Comparisons of several recorded outbreaks with the rainfall regime that preceded the outbreaks indicated that, before they occurred, there was abundant rainfall early in the season (Leirs et al. 1996b). It has been shown that, in Tanzania, abnormal (unseasonal) rainfall is correlated with population outbreaks (Leirs et al. 1996b). Outbreaks were not preceded by a long dry spell as previously thought (Fiedler 1988b) but occurred after high rainfall at the end of the previous year (Leirs et al. 1996b). The relationship between the timing of the rainfall and the population density of *M. natalensis* has been instrumental in developing a system for forecasting outbreaks of *M. natalensis* in Tanzania (Leirs et al. 1996b; Mwanjabe and Leirs 1997). A rodent forecasting model (Leirs et al. 1996b) based on the relationship between rainfall and breeding season has been developed and successfully tested to predict rodent outbreaks in Tanzania (Mwanjabe and Leirs 1997). The forecasting system will enable early preparedness of the community to carry out control activities.

Involvement of rodents in the plague cycle in north-eastern Tanzania

Among the major biological factors that have been identified to contribute to the persistence of plague in the western Usambara Mountains in north-eastern Tanzania is the existence of several species of reservoir hosts of the plague bacterium, *Yersinia pestis*. Human plague has afflicted the Lushoto District in the western Usambara Mountains for more than 20 years (Kilonzo et al. 1997). Several species of rodents are involved in the plague cycle (Figure 2) (Makundi and Kilonzo 1994; Makundi 1995). The distribution of different species of rodents in the western Usambara Mountains shows close proximity of suitable habitats and an overlapping of these habitats with human settlements. This facilitates the transfer of the disease from wild rodent reservoirs to the human population. Plague in the western Usambara Mountains occurs predominantly between October and March. To reduce the disease transmission to humans, it is recommended that case treatment, vector (fleas) control, and reservoir (rodent) management are intensified during this period (see also Makundi et al., this volume).

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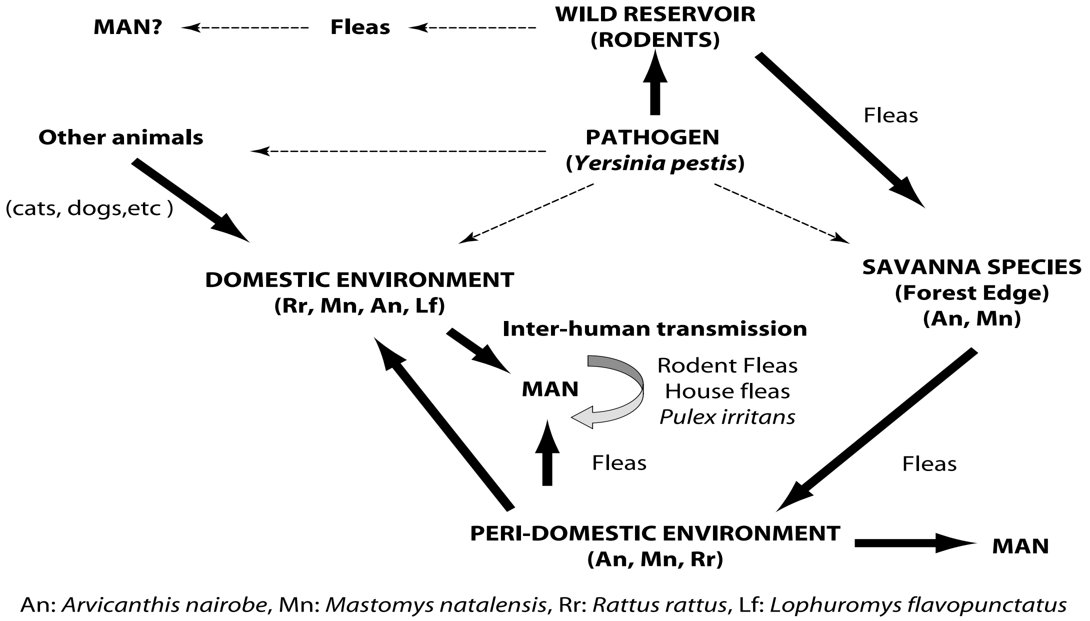

Figure 2. The plague cycle in Lushoto District, north-east Tanzania (An = *Arvicanthis nairobe,* Mn = *Mastomys natalensis*, Rr = *Rattus rattus*, Lf = *Lophuromys flavopunctatus*).

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Conservation of rodents in tropical forests of Vietnam

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Abstract. The establishment of protected areas in Vietnam has important implications for rodent conservation. However, knowledge of rodent species distribution is poor, especially in many protected areas. We examined the rodent species diversity in five protected forest areas, including sites in the poorly known Truong Son mountain range of northern Vietnam. Thirty rodent species were found in Sapa (Lao Cai province), 22 in Pu Mat (Nghe An), 18 in Huong Son (Ha Tinh), 12 in Biodup (Lam Dong) and 4 in U Minh Thuong (Kien Giang). Most squirrels (e.g. *Ratufa bicolor*, *Petaurista* spp. and *Callosciurus* spp.) were observed or captured on trees both of the understorey and the overstorey. Some squirrels (e.g. *Dremomys* spp. and *Tamiops* spp.) and some rats (e.g. *Niviventer langbianis*) and mice (e.g. *Chiropodomys gliroides* and *Typhlomys chapensis*) were captured on shrubs. Most rat species were captured on the ground. Human activities have greatly affected the distribution and species composition of rodents, especially squirrels living on trees and rats and mice of forest habitats. Our data also identify particular rodent species as characteristic of each protected area: e.g. *Petaurista elegans*, *Typhlomys chapensis*, *Eothenomys melanogaster* and *Dremomys gularis* in Sapa; *Rattus osgoodi*, *Maxomys moi*, *Menetes berdmorei*, *Vandeleuria oleracea* and *Callosciurus flavimanus* in Biodup; and *Callosciurus finlaysoni* in U Minh Thuong. The high rodent species diversity in the tropical forests of Vietnam is attributed to the combination of complex habitat structure and a biogeographical mosaic.

Introduction

In recent years, clearing of forests for cultivation and human settlements has had a major impact on forest conservation. Forests have been reduced in area and increasingly fragmented, and the habitats of many rodent species have disappeared or become insufficient for their survival. In Vietnam, forests occupy 8,630,965 ha and cover 28.1% of the land area. Deforestation is occurring at a rate of 150,000 ha annually (MSTE 1991). To protect biodiversity, the Vietnamese government established a system of protected areas; these total 2,119,500 ha and cover 5.7% of the total forest area of the country (Huynh 1997). An important step towards conserving the biodiversity of these protected areas is a systematic survey of their fauna and flora. Species composition and abundance of rodents are considered important indicators of biodiversity, but their taxonomy and distribution have not been thoroughly investigated in Vietnam. In this paper, we report on the diversity of rodent species in five protected forest areas in Vietnam: Sapa, Pu Mat, Huong Son, Biodup and U Minh Thuong (Figure 1).

Methods and study areas

The Sapa forests are located between 22°09'–22°30'N and 103°30'–104°50'E, and contain mountain peaks of 1500–3000 m in altitude. Bioclimatically, the area is unique in Vietnam. Annual temperatures range from –3.2°C to 29.7°C with a mean of 15.2°C (Moi et al. 1985). The coldest months are from November to February, and the warmest months from June to September. Mean annual precipitation is 2701 mm. Snow covers the Fasipan ridge every year. Vegetation in the area is highly varied and includes tropical montane forest, submontane forest and subalpine forest, with high species richness and diverse structure and composition (Thin 1998).

The Pu Mat forests occur between 18°46'–19°12'N and 104°24'–104°56'E, and cover an area of 91,213 ha. The area features an altitudinal range of 200 m to over 1800 m, with limestone mountains, small rivers and streams, and slopes of 25–35°. The climate of Pu Mat is characterised by a mean annual temperature of 23.5°C, with temperatures >18°C in the coolest months, and mean annual precipitation of about 1500 mm. The vegetation is classified as evergreen tropical forests (Tam and Sung 2000a,b).

The Huong Son forests are located at 18°20'N and 105°14'E and include mountains of 200–1250 m in altitude (Tam 2001).

The Biodup forests occur at 12°05'N and 108°20'E and include mountains rising to 200–1800 m in altitude.

The U Minh Thuong forests are located between 9°29'–9°42'N and 105°01'–105°09'E. This low-lying area within the Mekong River Basin supports a mosaic of *Melaleuca* forest and agricultural habitats (N.M. Tam, unpublished report).

Figure 1. Map of Southeast Asia showing location of the five study areas in Vietnam.

In each area, transects of 19–36 traps were set for six consecutive nights. Traps were set every 10 m for traps on the ground and every 20 m for traps on the trees (Adler 1996). In all, 5644 trap-nights in 22 transects were set at Sapa; 6342 trap-nights in 25 transects at Pu Mat; 3215 trap-nights in 16 transects at Huong Son; and 2050 trap-nights in 12 transects in Biodup. Trapping at U Minh Thuong was more opportunistic and the total trapping effort cannot be estimated. Three types of trap were used to sample rodents: a live-capture cage-trap, a snap-trap and a Sherman aluminum live-capture trap. These were used in the ratio of 100 live-traps for 100 snap-traps and 20–30 Sherman live-traps. All traps were baited with manioc (cassava) smeared with vegetable oil. Maize seeds, cut apple or banana were sometimes added to the bait.

Captured rodents were identified using external criteria and some individuals for each species were vouchered; these are stored at the Institute of Ecology and Biological Resources. For each captured male rodent, the testes were scored as abdominal or scrotal; for each captured female specimen, we scored vaginal perforation, lactation activity and obvious pregnancy. Maturity was also assessed on the basis of pelage characteristics.

Results and discussion

The rodent species recorded from each of the five study areas are listed in Table 1. Species recorded only from observations are distinguished from those based on actual captures.

Rodent diversity

The high diversity of rodent species in tropical rainforests of Vietnam is probably due to a combination of complex habitat structure and the interactions between two biogeographical zones (Tien 1985). Habitat diversity is promoted by the complex relief and the climatic differences across a broad latitudinal range.

In the Sapa forests, 179 individuals were captured belonging to 12 rodent species. Thirty species of rodents have been recorded in the vicinity of Sapa (N.M. Tam, unpublished report). *Niviventer fulvescens* was common and widely distributed, while *N. confucianus* was the most abundant species below 2000 m in altitude. The following rodent species are typical for the area: *Typhlomys chapensis*, *Eothenomys melanogaster*, *Dremomys gularis* and *Petaurista elegans*; all are endemic to the north-western region of Vietnam.

Of the 22 rodents known from the vicinity of Pu Mat, 17 species were caught in 1998, including representatives of seven genera of Muridae (*Rattus*, *Maxomys*, *Chiromyscus*, *Chiropodomys*, *Niviventer*, *Leopoldamys* and *Berylmys*) and four genera of Sciuridae (*Callosciurus*, *Dremomys*, *Ratufa* and *Tamiops*) (Tam and Sung 2000a,b). *Niviventer langbianis* was widely captured on trees and sometimes on the ground. *Chiropodomys gliroides* was captured only in forests mixed with bamboo. Many squirrels, including *Callosciurus erythraeus*, *C. inornatus* and *Ratufa bicolor*, were captured and observed on trees, both of the understorey and the overstorey.

At Huong Son, 18 rodent species were captured or observed. *Niviventer fulvescens* was common on the ground between 240–1240 m in altitude, while *N. langbianis* was caught predominantly on shrubs. *Chiropodomys gliroides* was captured most often on bamboo at 1–2 m above the ground. *Leopoldamys sabanus* was caught on the ground at 1250 m in altitude. There are no endemic rodent species in the North Truong Son mountain range.

At Biodup, we collected and observed 11 rodent species. One additional species, the endemic *Rattus osgoodi* (Musser and Newcomb 1985) is recorded from this area. Other rodent species typical of this forest are *Callosciurus flavimanus*, *Maxomys moi* and *Vandeleuria oleracea*.

The U Minh Thuong forests and associated agricultural habitats supported the lowest diversity of rodents (N.M. Tam, unpublished report). The only characteristic rodent species is *Callosciurus finlaysoni*; this species is otherwise widespread through Cambodia, southern Laos and Thailand.

Threats to rodents

In recent years, increased human pressure on forest areas has resulted in a great reduction in forest area and an increased level of fragmentation of surviving forests. These trends have a detrimental influence on rodent habitats. Clearing of forests for cultivation and human settlements has had a large impact on forest ecology, and has rendered many areas unsuitable for rodent survival and led to changes in species composition and abundance. These changes have threatened the survival of many species. Some rodent species have already disappeared locally, while others that are better adapted to disturbed conditions have replaced them.

In some areas, *Callosciurus* spp., *Dremomys* spp. and *Tamiops* spp. survive by utilising areas of cultivation and adjacent regrowth forest. However, in other areas, commensal rodents such as *Rattus* spp., *Mus* spp. and *Bandicota* spp. have entirely replaced the native rodents. *Rattus rattus* and *Mus* spp. are the dominant species in cultivated areas and villages in Sapa, Pu Mat and Ben En, and these rodents are regarded as serious pests in crops and grassland.

Population pressure in some areas has resulted in the exploitation of even quite remote forests. In the Sapa area, even forest on very steep slopes is cleared. After removal of some large canopy trees, all understorey trees and ground vegetation are removed. Ginger was planted alongside streams up to 2400 m in altitude on the way to Fasipan peak. This widespread disturbance of vegetation undoubtedly has deleterious impacts on the species composition and population density of rodents, especially squirrels (e.g. *Petaurista* spp., *Callosciurus* spp.) and arboreal rats (e.g. *Chiropodomys gliroides* and *Niviventer confucianus*).

Forest mammals are valued by local people as food, medicine and a source of revenue. Interviews conducted in all villages indicated that hunting and trapping contributed significantly to their consumption and cash income. Hunting pressure is most intense during the dry season when mammal activity is highest and there is less work to do in the gardens. The most common method of hunting involves the use of guns and dogs. A typical hunting group consists of two or three local people who enter the forest for several days. They generally use home-made flintlock rifles and snap-traps to capture rats and squirrels. During our survey in the Sapa forests in 2000, we encountered one party who had about 50 snap-traps in a basket, as well as eight guns and four dogs; the party had one captured bamboo rat (*Rhizomys sumatrensis*). Hunting activity was also observed in recent years in forest areas in Pu Mat (Nghe An), Huong Son (Ha Tinh), Ben En (Thanh Hoa) and Biodup (Lam Dong). Live-captured squirrels (*Callosciurus erythraeus*, *C. inornatus*, *Dremomys rufigenis* and *Tamiops* spp.), skins of flying squirrels (*Petaurista petaurista*) and quills of porcupines were often observed in villages around the margin of the forests.

Some threatened rodents

Early work on rodent taxonomy and ecology in Vietnam was conducted by Osgood (1932) and van Peenen et al. (1969, 1970). More recently, this work has been continued in Vietnam by Khoi et al. (1979), Sung (1983, 1990), Sung et al. (1980), Tien (1985), Sung and Tam (2000, unpublished report), Tam (2001), and Tam and Sung (2000a,b, 2002). Other taxonomic research involving Vietnamese material was published by Musser (e.g. Musser et al. 1979; Musser and Newcomb 1985). Research on rodent control in Vietnam was carried out by Sung et al. (1997, 1999).

Despite this prior research, knowledge of the taxonomy of Vietnamese rodents is incomplete, especially for those rodents living in forests of the Truong Son mountain range. Information on the abundance of rodent species, whether common, threatened or rare, is also essential for management and conservation. Therefore, additional research on the taxonomy, distribution and abundance of rodent species is needed urgently in order to assess their status and to develop more effective measures for their protection.

We consider the following rodent species to be under significant threat, mainly as a consequence of the continued clearance and fragmentation of their habitat:

- Giant squirrel *(Ratufa bicolor condorensis*) is a frugivore that inhabits large trees in the Con Dao forests. Deforestation is a major factor in the decline of its population.
- Giant flying squirrel (*Petaurista elegans*) is a nocturnal species that occurs in primary forests of Sapa (Lao Cai) and Xuan Nha (Son La). Its status is endangered, due to deforestation and hunting pressure.
- Porcupine (*Hystrix brachyura*) occurs in secondary and primary forests of Na Hang and Dinh Ca (Tien 1985). It lives in natural cavities in limestone hills and feeds mainly on plant roots and bulbs.
- Tree squirrel (*Callosciurus finlaysoni*) is a diurnal species that inhabits the canopy of *Melaleuca* forests in Kien Giang (N.M. Tam, unpublished reports). It is now rare in Vietnam due to the destruction of forests by burning in preparation for cultivation.
- *Dremomys gularis* is a ground-dwelling species that feeds on vegetation and insects; it is found only at elevations above 2000 m in the Sapa forests (Tam 2001). Deforestation is the major factor behind the reduction in population size of this species.
- *Typhlomys chapensis* is only found at elevations greater than 1800 m in the mixed bamboo forests of Sapa (Tam and Sung 2002). It is classified as endangered, due mainly to destruction of forest habitat.

Conclusion

The establishment of additional protected areas is clearly of the highest priority for rodent conservation in Vietnam, especially for those areas of the greatest rodent diversity and endemism. For example, the recently established Hoang Lien Son Nature Reserve of north-western Vietnam is a unique area for biodiversity conservation.

Table 1. List of rodent species recorded in five study areas (+ = present; +* = observed only).

Taxon	Sapa	Pu Mat	Huong Son	Biodup	U Minh Thuong
Hystricidae					
Atherurus macrourus	+	–	+	–	–
Hystrix brachyura	+	–	–	–	–
Rhizomyidae					
Rhizomys pruinosus	+	–	–	–	–
R. sumatrensis	+	–	–	–	–
Pteromyidae					
Petaurista elegans	+	–	–	–	–
P. petaurista	+	–	–	–	–
Sciuridae					
Callosciurus erythraeus	+	+	+	–	–
C. inornatus	+	+	–	–	–
C. finlaysoni	–	–	–	–	+
C. flavimanus	–	–	–	+	–
Dremomys gularis	+	–	–	–	–
D. rufigenis	+	+	+	+	–
Ratufa bicolor	+	+*	+*	–	–
Tamiops maritimus	+	–	–	–	–
T. rodolphei	–	+*	+*	–	–
T. swinhoei	+	–	–	–	–
Arvicolinae					
Eothenomys melanogaster	+	–	–	–	–
Platacanthomyinae					
Typhlomys chapensis	+	–	–	–	–
Murinae					
Bandicota indica	–	–	–	–	+
Berylmys bowersi	+	+	–	+	–
B. mackenziei	–	+	–	–	–
Chiromyscus chiropus	+	+	–	–	–
Chiropodomys gliroides	+	+	+	+	–
Leopoldamys edwardsi	+	+	+	+	–
L. sabanus	–	+	+	–	–
L. neilli	–	+	–	–	–
Micromys minutus	+	–	–	–	–
Maxomys moi	–	–	–	+	–
M. rajah	–	+	–	–	–
M. surifer	–	+	+	–	–
Mus caroli	–	–	–	+	–
M. musculus	+	–	+	–	–
M. pahari	+	–	+	–	–
Niviventer bukit	+	–	–	–	–
N. confucianus	+	+	–	–	–
N. fulvescens	+	+	+	+	–
N. langbianis	+	+	+	+	–
N. tenaster	+	+	+	–	–
Rattus argentiventer	–	–	–	–	+
R. nitidus	+	+	+	–	–
Rattus sp.	–	+	+	–	–
R. osgoodi	–	–	–	+	–
R. rattus	+	+	+	–	+
R. sikkimensis	+	+	+	+	–
Vandeleuria oleracea	–	–	–	+	–

The following characteristic rodents occur in this reserve: *Typhlomys chapensis*, *Petaurista petaurista*, *P. elegans*, *Eothenomys melanogaster* and *Ratufa bicolor*. The Biodup Nature Reserve supports important populations of *Rattus osgoodi*, *Vandeleuria oleracea* and *Maxomys moi*; and *Callosciurus finlaysoni* is found in the U Minh Thuong Nature Reserve within Vietnam. However, effective long-term protection of each of these significant rodent species will also depend on an improved understanding of their habitat requirements in each reserve; and on the critical and ongoing assessment of the population density for each species.

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Testing a biological control program for rodent management in a maize cropping system in Kenya

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Abstracts. Birds of prey could potentially act as control agents for rodents in some agricultural systems. However, little has been done to encourage the breeding of avian predators and subsequently to evaluate their potential as biological control agents in maize crops, an important staple food crop in eastern Africa. We set out 400 perch poles and 20 nest boxes in each of two 100 ha experimental grids in maize fields in the Kenyan Rift Valley. A capture–mark–recapture (CMR) study was set in 1 ha grids of 10 × 10 box traps in each experimental and two control sites to evaluate rodent demography. Owl abundance and diet was monitored by regular assessment of regurgitated pellets at nest boxes.

Preliminary results showed an increase in barn owl numbers and barn owl reproduction on the experimental grids. In the two experimental grids, there was over 60% occupation of the nest boxes with successful breeding taking place in 40% of the 40 boxes within a period of 12 months. During the same period, rodent catch rates dropped from a peak of 45% to 0.3% trap success in the first experimental grid, 40% to 1% in the second, and 22% to 6% in the controls. The study is in its second maize cropping season, and from these preliminary findings, avian predators appear to have promising results in control of rats. However, this will become clearer once all the demographic parameters are fully analysed.

Introduction

Rodents are recognised pests in many agricultural systems and there is a need for their control. There is a dearth of quantitative information on economic losses due to rodents in Kenya. Earlier reports (Taylor 1968) indicated 20–30% damage to maize crops, and a 34–100% loss during rodent outbreaks. Current control is symptomatic and based on the use of chemicals, some of which are proving to be ineffective due to development of resistance (Lam et al. 1982; Lee et al. 1983). Continuous use of these chemicals also has undesirable effects to the environment with risks to non-target species or domestic animals (Godfrey 1985). There is an increasing need to develop ecologically benign rodent management techniques in order to reduce the costs and risks associated with rodenticides. However, little attention has been directed to biological control as an integrated approach, partly because little information exists on predator–prey relationships. A recent, non-replicated pilot study suggested increased survival of some rodent species in predator-exclusion areas (Van Gulck et al. 1998). The barn owl and other raptors have been suggested as potent predators (Duckett 1986b; Smal 1989; Vibe-Petersen 1999). These findings have given rise to an increasing interest in understanding how predation affects rodent populations and its potential in biological control. Our ongoing study began in December 2000 to evaluate the potential of avian predators to control rodents in maize fields in eastern Africa, and here we report some preliminary results.

Study area

The study was carried out in the Kenyan Rift Valley at latitudes 35°28'–35°36'E, longitudes 0°13'–1°10'S, and altitudes of between 1822 and 1950 m above sea level. The climate in this area falls between semi-arid (annual rainfall less than 760 mm) in the lower areas and dry sub-humid (annual rainfall of 1270 mm) regions at the higher altitudes. Rainfall is bimodal with peak precipitation (70–80%) in March to May and late August to October, though great variations may occur from year to year. The maximum temperature is about 30°C, with December to March being hottest, and July being coolest at an average of 23.9°C (Nakuru District Development Plan 1997). The area is largely under maize, with a few large-scale farms growing wheat. Rodents are acknowledged as major pests in both cropping systems. There are resident and migratory raptors, as well as a resident population of barn owls in this area, making it suitable for this particular study.

Materials and methods

The study was carried out in two experimental areas (Goga and Elia) and two control areas (Beth and Kurgat), each measuring 100 ha under maize crop. In each of the two experimental areas, 400 artificial bird perches were erected at 50 m intervals to attract avian predators. Each pole had two perching points at heights of 2 m and 4 m, suitable for owls and raptors, respectively. Nest boxes were placed strategically to enhance breeding of owls. Twenty boxes were placed at 5 ha intervals in each experimental grid. The experimental grids were 15 km apart and each 5 km from controls.

In each experimental and control site, a 1 ha grid was set up for capture–mark–recapture (CMR) studies. Rodents were live-trapped using Sherman's LFA traps measuring 23 × 8 × 9 cm, from June 2001 to June 2002 in all the four grids. One trap was placed at each station during trapping. Primary trapping sessions were organised every 28 days with secondary sessions for three consecutive days and nights during each primary trapping. Traps were baited with fried coconut cubes mixed with peanut butter. Barn owl use of nest boxes was monitored monthly. Regurgitated pellets were collected from areas around the perch poles, nest boxes, and under trees.

Rodent population densities were estimated using Schnabel–Schumacher method. The monthly rate of change in *Mastomys* density was estimated by determining density differences for consecutive months for each study site. The means for the treatments and their replicates were lumped together and compared using student *t*-test.

Results and discussion

Owl activity index and diet

Twelve nest boxes were occupied between March 2001 and June 2002 at the Goga experimental site and successful breeding of barn owls took place in eight boxes. Nesting took place between June and October 2001 (Figure 1a). Thus, breeding here was noted for 5 consecutive months only in 2001. At Elia farm, 11 nest boxes were occupied with successful breeding of barn owls in seven boxes between June 2001 and March 2002 (Figure 1b). At Elia, two short breeding seasons were recorded, June–August 2001 and February–March 2002. The mean (± sem) number of eggs laid was 6.3 (± 0.4) and 6.6 (± 0.4) for Goga and Elia grids, respectively. While mean number of fledglings were 5.3 (± 0.4) and 6.1 (± 0.7), respectively. Six hundred pellets were collected from experimental grids, and preliminary analyses of 120 intact skulls recovered indicate that *Mastomys* cf. *erythroleucus* formed 80% of the predator diet. Skulls of *Crocidura* and *Tachyoryctes* species were also positively identified from the pellets. No nesting activities were recorded or pellet recovered in control areas to date.

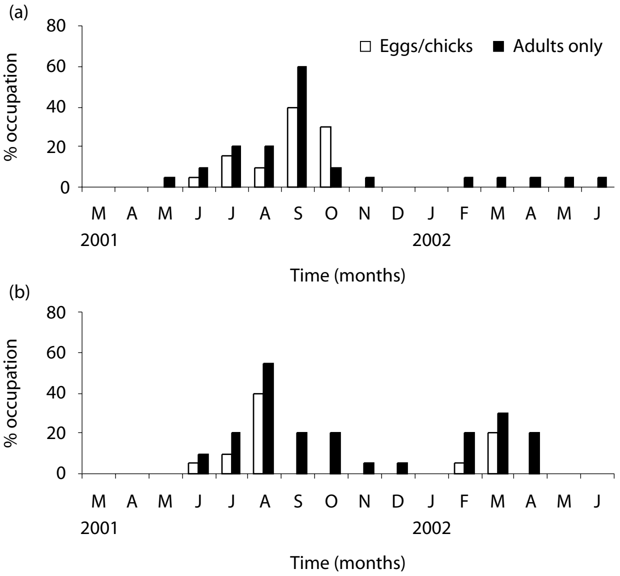

Figure 1. Occupancy rate (%) of nest boxes and breeding index by barn owls in two experimental sites in the Kenyan Rift Valley, (a) Goga and (b) Elia.

Rodent abundance

A total of 1490 rats representing six species were trapped in the four grids (Table 1). *Mastomys* cf. *erythro-*

Table 1. Species composition and number of individual rodents captured in experimental and control grids in 3600 trap nights from June 2001 to June 2002.

Species	Goga (520)	Elia (490)	Kurgat (250)	Beth (230)	Total (Proportional abundance)
Mastomys cf. *erythroleucus*	425	441	212	198	1276 (90.2%)
Arvicanthis cf. *newmanii*	10	25	21	23	79 (5.6%)
Lemniscomys striatus	5	15	2	2	24 (1.7%)
Thallomys sp.	5	0	2	4	11 (0.8%)
Mus minutoides	5	5	6	4	20 (1.4%)
Dendromus sp.	0	5	0	0	5 (0.4%)

leucus was the most common species, accounting for 90% of all captures. *Mastomys* populations declined at significantly different rates (*t* = 2.281, *P* = 0.022, *n* = 12), being higher in experimental 9.4 (± 2.0) and lower in control grids (5.1 ± 0.9). The mean monthly rate of change is shown in Figure 2.

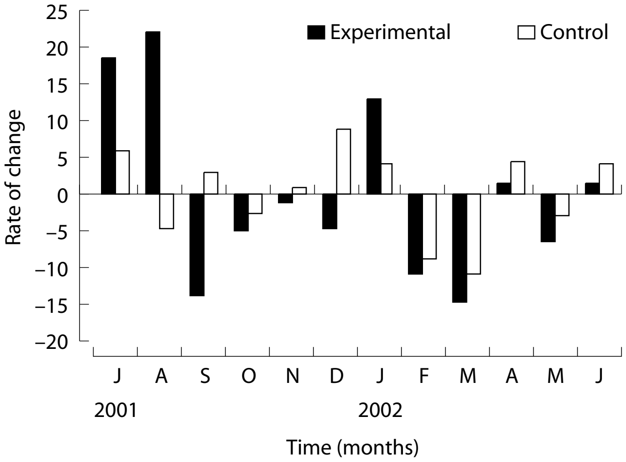

Figure 2. Rate of monthly change in *Mastomys* abundance in experimental (Goga and Elia) and control (Kurgat and Beth) grids in maize fields between June 2001 and June 2002 (data from the two replicates pooled and analysed together).

Conclusions

Our study has shown that barn owls used and successfully bred in nest boxes erected in maize fields (Figure 1). They also consumed *Mastomys,* the most common species (Table 1), in higher proportions than other species. Although *Mastomys* were more abundant on experimental grids at the beginning of the study, their rate of change in monthly numbers was higher in these grids compared to control areas (Figure 2). The higher rate of decline of *Mastomys* numbers in experimental compared with control grids may be indicative of a predation effect. However, further analysis is required before we can infer the direct effects of barn owl predation on *Mastomys* populations. This work is ongoing and will involve another season of data collection and demographic analyses of the rodent populations to provide a clearer picture of predation effects. We conclude for now that provision of nest boxes has the potential of increasing the barn owl populations in maize fields in Kenya, and this provides a potential avenue for biological control in this agricultural system.

Acknowledgments

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The effects of *Tephrosia vogelii* and land preparation methods on mole rat activity in cassava fields

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Abstract. Mole rats cause considerable damage to tuber crops in eastern Africa. In experimental cassava fields in Zambia, we tested whether different land management techniques and the presence of a deep-rooted poisonous shrub, *Tephrosia vogelii*, affected mole rat activity in those fields. The bush was planted as a barrier around the field or dispersed throughout the field; cassava was planted on ridges or in mounds. Since the start of the experiment until two years later, there were significantly fewer molehills in fields with *T. vogelii* bushes and cassava planted in mounds. Future comparison of yield in the experimental fields will indicate whether this strategy offers good opportunities for the management of damage by mole rats.

Introduction

In eastern Africa, mole rats are notorious rodent pests of cassava tubers, and methods for their sustainable control are badly needed. Mole rats live and feed underground and are capable of making numerous burrows leading to granaries, latrines and feeding places. Sichilima and Zulu (1998) demonstrated that activity of mole rats in creating molehills can be associated directly with the search for food. The same study reported that some Zambian farmers claim that land preparation methods may have an effect on mole rat activity in cassava fields. In some other areas in eastern Africa, 'fish bean', a poisonous, deep-rooted shrub, *Tephrosia vogelii*, is reported to repel mole rats effectively from cassava fields (unpublished information from farmers). Here we report on an ongoing study to evaluate the effects of land preparation and *T. vogelii* on mole rat activity in cassava fields in Zambia.

Materials and methods

Twenty-four plots, each 50 m × 50 m, were selected in Solwezi district in Zambia. All plots had been used as crop fields (but not cassava) 1 or 2 years before and all plots had previously experienced heavy mole rat problems. The area is located at the average altitude of 1300 m above sea level with annual rainfall >1100 mm per year. The main rain season starts in mid-November and extends to mid-March and this is followed by the cold dry season from May to mid-August. The hot dry season starts from September and extends to mid-November. Main crops in the region are sweet potato and cassava.

The experiment was set up following a randomised controlled block design with two treatment levels (planting *T. vogelii*, land management) and four replications for each treatment combination. *T. vogelii* bushes were planted as three barrier rows spaced 1 m around the field edges, scattered at 3 m spacing throughout the field, or not present in controls. Cassava was planted in ridges or in mounds. The fields were set up in January 2000 and monthly data on the presence of fresh molehills were collected through until August 2002.

The data were analysed using a two-way analysis of variance with repeated measurements (STATISTICA).

Results and discussion

We found highly significant effects of both the presence of *T. vogelii* ($F = 31.45$, df = 2,18, $p < 0.001$) and land management ($F = 12.38$, df = 1,18, $p = 0.002$). Significantly more fresh molehills were counted in fields without *T. vogelii* (Newman-Keuls *a posteriori* comparison of means, $p < 0.001$) but the difference between the two types of *T. vogelii* planting was not significant ($p = 0.117$). The differences changed over time, but remained clear (see Figure 1). There was no interaction between the presence of *T. vogelii* and land management ($p = 0.608$).

Our results show that mole rat activity can be reduced when cassava is planted on mounds with the deep-rooted *T.vogelii* shrub in barriers around or scattered in fields.

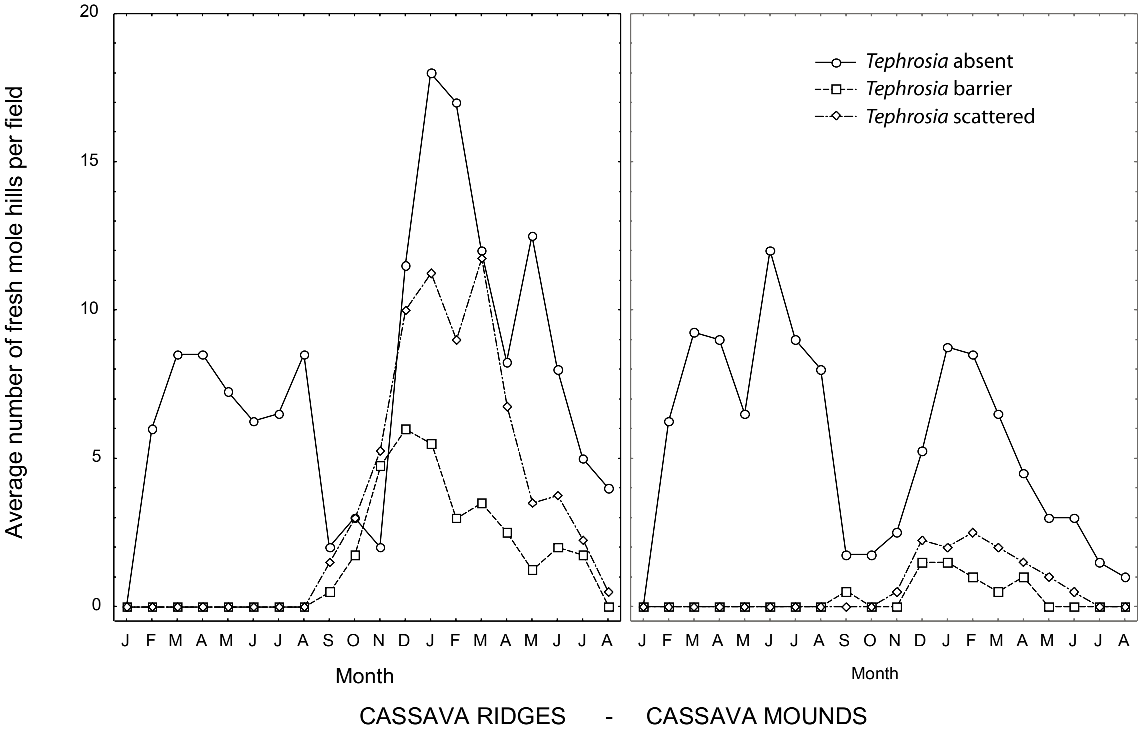

Figure 1. The mean number of fresh molehills dug by mole rats in Zambia in cassava fields with different densities of the deep-rooted shrub *Tephrosia vogelii*: molehills recorded where cassava was planted (a) along ridges; and (b) in mounds. The study was conducted from January 2000 to August 2002.

These results suggest that a simple biological method can be implemented to reduce the impact of mole rats in cassava fields in eastern Africa. This in turn will lead to reduced use of rodenticides and savings to farmers through reduced costs of rodent management. In late 2002, cassava tubers will be harvested to see how these treatments affect final yield.

T. vogelii is also used as a green manure crop and as a shade tree in young plantations (Simute 1992). Its leaves contain insecticidal products that can be prepared as an extract or powder (Karlsson 1994; McDavid and Lesseps 1994). The repellent effect on mole rats further increases its value as an agroforestry plant.

Acknowledgments

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Changes in community composition and population dynamics of commensal rodents in farmhouses in the Dongting Lake region of China

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Abstract. From the 1970s to 2001, there have been marked changes in the commensal rodent communities and population densities in dwellings of the countryside in the Dongting Lake plain area. The buff-breasted rat (*Rattus flavipectus*) was the dominant species in farmhouses in the 1970s and rodent population densities were low. With the excellent harvest in the early 1980s and changes in the way grains were stored in rural China, the Norway rat (*Rattus norvegicus*) became the dominant species and its population density increased quickly. In the late 1980s, the structure of farmhouses and grain storages was further improved, and a rodenticide, natrium diphacin, was used to control the pest rodents in some areas. This led to declines in the populations of *R. norvegicus* while *Mus musculus* became more dominant in the rodent community. The Norway rat and buff-breasted rat increased in numbers in the early and mid-1990s coincident with increases in livestock breeding. Following the improvement in the living standards of farmers and the farmhouse structures, people have paid greater attention to rodent pests and the methods to manage them. Subsequently, the densities of the pest rodents have declined gradually, especially the population of *R. norvegicus*, and *M. musculus* has become the dominant species in the dwellings.

Introduction

The Norway rat, *Rattus norvegicus*, house mouse, *Mus musculus*, and buff-breasted rat, *Rattus flavipectus*, are the main rodent species inhabiting farmhouses throughout China (Li et al. 1988). They consume and contaminate large quantities of human food and animal feed, as well as damaging building structures by their gnawing and burrowing. Rodents also are potential threats to both human and animal health through transmission of diseases (Wang 1996). The population structure and density of the commensal rodents are affected markedly by human activities in the environment because they live in close proximity with humans in residential premises (Langton et al. 2001). This paper describes the numbers of commensal rodents in the Dongting Lake region from the 1970s to 2001 and suggests some reasons for the observed changes.

Study site and methods

Study site

The Dongting Lake region is located in the northern part of Hunan province, China (28°13'–29°55'N and 111°11'–113°43'E). It is in a subtropical region, and shows four defined seasons. The weather is warm and humid, with a mean annual temperature of 16–17°C and a mean annual rainfall varying from 1200 to 1470 mm. It is one of the most important regions for agricultural production (grain, cotton, rapeseed, soybean, sesame, and some aquatic and husbandry products) in the Yangtze Valley of China. Each farming family owns one house, usually with five rooms, and it is one of many dwellings in local villages. In the 1970s, houses were made of clay or wooden walls and had clay floors. From the mid-1980s, houses were constructed with brick walls and concrete floors. By the end of the 1990s, more than half of the houses were made with these materials and many farmers had also built storage rooms in their homes.

Methods

A census of rodents was conducted from the early 1980s in the farmhouses in the countryside in the Dongting Lake region. Snap-traps were used throughout the census (no less than 100 traps per site). The traps were situated in each room close to a wall, behind an object or in a dark corner, with one trap in a small room (≤ 15 m^2) and two traps in larger rooms. Traps were baited with fresh sunflower seeds and placed on the ground in the afternoon. Captured animals were collected the next morning and the animals were brought back to the laboratory to be identified. Every month there was a survey in two sites in Taoyuan county. The survey in Hanshou county alternated between two villages and was carried out once every two months before 1997 and three times per year (March, July and December) from 1998 to 2001.

The survey sites in Taoyuan and Hanshou counties had similar surroundings. The rodent density was defined as the percentage of trap success per 100 traps. The data of Taoyuan county in 1970s, which were collected using snap-traps in 1975–1978, were obtained from the Health and Anti-epidemic Station of that county.

Results and discussion

The rodent community comprised *R. norvegicus*, *M. musculus* and *R. flavipectus* in farmhouses, although the most numerous species varied at different times during the period of census trapping (Table 1). Several other rodent species, *Apodemus agrarius*, *Rattus confucianus*, *Rattus losea*, and an insectivore (shrew), *Suncus murinus*, were also trapped, but in insignificant numbers. The population densities in farm buildings were low from the 1970s. Thereafter, there were two outbreaks of rodent populations—the first peak appeared in the 1980s and the second in the 1990s. According to Guo et al. (1992), no damage due to rodents was noticed until 1980 in Taoyuan, and there was only occasional harm in paddy fields in summer and houses in winter in 1981. However, there was a widespread outbreak across the county in 1983. The highest population occurred in 1986 (Table 1). The density in Taoyuan was lower than in Hanshou, due to a campaign to kill rodents using natrium diphacin across the entire county of Taoyuan in 1984. From the limited data (1992–1995) in Taoyuan and Hanshou, it was not clear in which

Table 1. Rodent density and community composition in dwellings in the Dongting Lake region.

Site	Years	No. of traps	Percentage trap success[a]				
			Rattus norvegicus	*Mus musculus*	*Rattus flavipectus*	Other	Total
Taoyuan	1975–1978	6000	1.25	1.45	1.88	0.02	4.60
			(27.17)	(31.52)	(40.87)	(0.44)	
	1982–1984	6300	6.67	1.60	0.35	0.17	8.79
			(75.81)	(18.23)	(3.97)	(1.99)	
	1986	591	8.29	9.48	0.68	0.17	18.62
			(44.55)	(50.91)	(3.64)	(0.91)	
	1987	4625	6.83	4.52	1.06	0.24	12.65
			(54.02)	(35.73)	(8.38)	(1.88)	
	1988	3657	4.87	2.93	1.45	0.03	9.27
			(52.51)	(31.56)	(15.63)	(0.29)	
	1989	3090	5.02	6.96	1.26	0.06	13.30
			(37.71)	(52.31)	(9.49)	(0.49)	
	1990	2814	3.84	7.11	0.64	0.43	12.01
			(31.95)	(59.17)	(5.33)	(3.55)	
	1991	512	3.13	10.94	1.37	0.58	16.02
			(19.51)	(68.29)	(8.54)	(3.66)	
Hanshou	1986	310	34.84	20.32	2.58	0.00	57.74
			(60.34)	(35.20)	(4.47)	(0.00)	
	1987	882	23.02	9.18	3.63	0.57	36.39
			(63.24)	(25.23)	(9.97)	(1.56)	
	1988	772	15.54	10.62	2.33	0.13	28.63
			(54.30)	(37.10)	(8.14)	(0.45)	
	1989	464	12.28	12.72	0.22	0.65	25.86
			(47.50)	(49.17)	(0.83)	(2.50)	
	1990	198	2.02	2.02	5.05	0.00	9.09
			(22.22)	(22.22)	(55.56)	(0.00)	
	1996	455	29.23	15.52	6.47	0.00	51.21
			(57.07)	(30.30)	(12.63)	(0.00)	
	1997	1091	11.55	12.07	1.75	0.10	25.48
			(45.34)	(47.37)	(6.88)	(0.40)	
	1998	853	7.32	7.71	1.57	0.39	17.00
			(43.08)	(45.38)	(9.23)	(2.31)	
	1999	968	5.14	4.46	1.35	0.00	10.95
			(46.91)	(40.74)	(12.35)	(0.00)	
	2000	489	2.30	5.75	0.86	0.29	9.20
			(25.00)	(62.50)	(9.38)	(3.13)	
	2001	317	1.26	2.84	0.95	0.00	5.05
			(25.00)	(56.25)	(18.75)	(0.00)	

[a] The numbers in parentheses are percentages of each species of the total trap success for that year, giving an indication of species composition.

year in the early 1990s the second increase in numbers of rodents began, but the highest density occurred in 1996. Thereafter, the rodent densities began to decline.

The buff-breasted rat, *R. flavipectus*, was the dominant species in farmers' houses in the 1970s (40.9%), followed by the house mouse, *M. musculus* (31.5%), then the Norway rat, *R. norvegicus* (27.2%). Each species had a low population density in 1970s relative to later years. The capture rate increased and the species composition changed in the early 1980s, with the population of Norway rats increasing and buff-breasted rats declining. The Norway rat became the dominant species, comprising more than half of the captured animals. The possible reasons for this included changes in the agricultural practices in the countryside of China in the late 1970s and early 1980s, the bumper harvest, and a change in the methods of grain storage (from collective stores to individual storage in a farmers' houses), which meant that there was abundant food that rodents, especially Norway rats, could readily obtain (Guo et al. 1992; Zhang et al. 2002a). Some investigations have shown that the building structure and materials of the farmhouse were the main factors influencing the activity of pest rodents in farmhouses (Zhang et al. 2002a). In the early 1980s, farmhouses were built of wood or clay brick, and there were no effective ways to prevent entry by pest rodents and no barns to store grains. Thus, pest rodents could obtain food grain easily when farmers put their harvest in the house.

In the 1970s and before, there was an attic in every farmhouse, and wood was the main material for walls. This benefited the buff-breasted rat until brick replaced the wood walls and attics were no longer built in the farmhouse. We conclude that this was the main factor that has limited the buff-breasted rat in recent years.

In the late 1980s, the proportion of Norway rats was decreasing, while house mice were increasing and became the dominant species. The possible reason was that most farmers had built a proper granary within the farmhouse and this could store all of their grain, making less food readily available to the Norway rat (Guo et al. 1992). Along with the improved brick housing, natrium diphacin was used regularly to kill rodents from the mid-1980s. The populations of Norway rat continued to decrease, as it is more susceptible to the anticoagulant than *M. musculus* and *R. flavipectus*. The proportions of residual individuals of *M. musculus* and *R. flavipectus* in residential premises were higher than those of *R. norvegicus* after each campaign of rodent control (Zhang et al. 2002b).

Due to the increase in livestock breeding in the early to mid-1990s, rodents again increased in this area. The Norway rat became the dominant rodent species and the population density of the rodents increased to another peak. Since the mid-1990s, the population densities of rodents in this area have been decreasing, especially populations of *R. norvegicus*. *M. musculus* has become the dominant rodent species in dwellings. Some of the reasons include an improved standard of living for the people, especially in the countryside, more fired-brick houses with concrete floors have been built, the residential premises are neat and clean, and farmers are less tolerant of rodents. By the end of 1990s, more than half the farmhouses had been changed to fired-brick structures with concrete floors. The census data show that rodent densities were very low in tidy, clean houses, and the dominant species was the house mouse rather than the Norway rat (Zhang et al. 2002a). Another reason for decreasing rodent densities is that the people have a better understanding of integrated methods of controlling rodent pests and have accepted the use of anticoagulants rather than rapid rodenticides. The dominant species in 2001 was the house mouse.

Conclusion

Commensal rodents in farm buildings experience a more stable environment and climate than field rodents. This study has shown population changes in pest rodents in dwellings of the Dongting Lake region were affected by the impact of man on the environment. The bumper harvest in the countryside in the 1980s and the growth of stockbreeding in the 1990s contributed to rodent outbreaks. The changes in house structures and the improvement in living standards have caused a decline in the rodent population and altered rodent community composition. The activity of humans was one main factor leading to the changes in the populations of commensal rodents. Thus, it is necessary to evaluate the possible effects of human economic activities on the environment and on the population dynamics of pest rodents. We forecast that the population of rodent pests in the countryside of the Dongting Lake region will continue to decease with continued improvements in living standards.

Acknowledgments

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Evaluation of thiram and cinnamamide as potential repellents against maize-seed depredation by the multimammate rat, *Mastomys natalensis*, in Tanzania

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Abstract. In maize fields in Tanzania, rodents are responsible for high levels of seed depredation at sowing and cutting of the seedlings at emergence. We evaluated the potential of two seed-dressing compounds, thiram and cinnamamide, as rodent repellents to protect maize against damage by multimammate rats, *Mastomys natalensis*. The two compounds were evaluated in the laboratory using choice and no-choice tests. In the choice experiment (single cages), <10% and <2% of cinnamamide- and thiram-treated seeds, respectively, were damaged compared to 20–50% damage in untreated seeds. In the no-choice experiment (room), only a few seeds were damaged (0–6 seeds for cinnamamide and 1–5 seeds for thiram in 4 days, out of about 70 seeds provided), although the animals had no alternative food. These experiments clearly indicate the potential for thiram and cinnamamide to protect seeds from depredation by rodents. Further evaluation of these compounds will be carried out to establish efficacy in the field.

Introduction

Maize is most susceptible to rodent damage at planting and during the seedling stage (see Mulungu, Makundi, Leirs et al., this volume, for review). This period spans 2 weeks and is the most critical period for damage throughout the growth stages of the maize crop. Farmers will likely avoid crop losses (seed loss, replanting, extra labour etc.) if an appropriate seed dressing, capable of repelling depredation of seed at the susceptible planting stage, could be used. This paper reports on two seed-dressing compounds, cinnamamide and thiram, for repellence against the multimammate rat, *Mastomys natalensis*, a major pest species in Tanzania. Germination tests indicated no phytotoxic effects of these compounds on the seeds.

Materials and methods

Tests were carried out in the laboratory with wild-captured animals, after an acclimatisation period of 4 days. The seeds were dressed with the candidate repellent 24 hours before supplying them to the experimental animals. In a choice experiment with 10 singly caged animals, treated (20 g) and untreated (20 g) seeds were supplied in two crucibles in each cage. The number of seeds in each 20 g lot was counted before placement in the cage. The positions of the crucibles were changed daily to prevent location preferences. The number of seeds consumed or damaged was counted every morning and the crucibles were replenished with fresh treated and untreated seeds. The evaluation was carried out over 4 days with the same animals in each cage.

In a no-choice test in a room (222 × 278 × 122 cm), a group of 10 animals was supplied with 20 g of treated seeds in crucibles. The seeds were inspected for rodent damage/consumption for 4 days as in the choice experiment and were replenished every day for a period of 4 days. Drinking water was provided *ad libitum* to animals. Nesting boxes were provided in the experimental room.

Results and discussion

The choice tests clearly showed that cinnamamide- and thiram-treated seeds were less preferred by *M. natalensis* compared to untreated seeds (Figure 1). Consumption of seeds generally was lower in the test with thiram-treated seeds in the cage, perhaps due to the repellent effect of the strong smell of thiram. In the no-choice tests, there was also a strong repellence to *M. natalensis* by the two products (Table 1). Only a few seeds were damaged or consumed, and the repellent effect persisted for at least 4 days, although the animals had no alternative food available. This suggests that the seeds were also unpalatable due to treatment. Most mammals, including rodents, have developed a behavioural mechanism to cope with toxic substances in their food, including avoidance (Bull 1972). In the current investigation, we did not expect 100% protection of the seeds. This is clearly shown by the low levels of damage that occurred in the treated seeds.

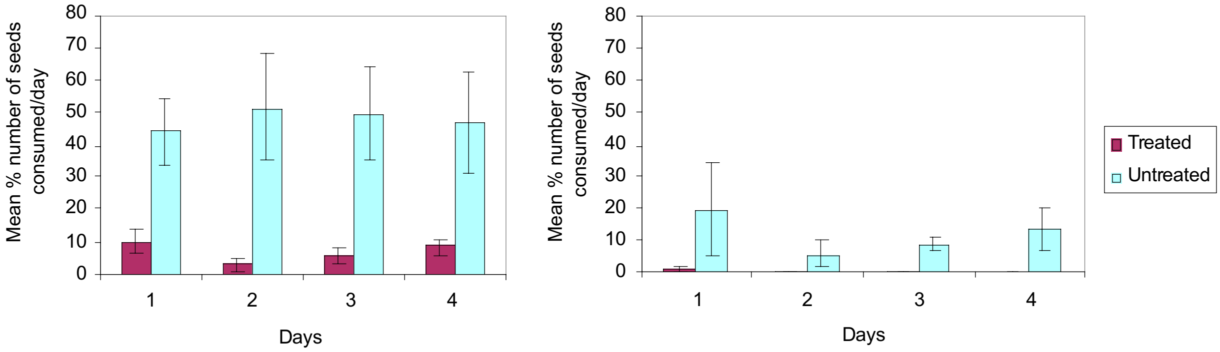

Figure 1. Mean daily percentage (± se) consumption of untreated and repellent-treated maize seeds by singly caged animals. Left: treatment with cinnamamide; right: treatment with thiram.

Table 1. Consumption of seeds treated with either cinnamamide or thiram in the no-choice room experiment.

Days	Cinnamamide		Thiram	
	Mean no. (± se) of seeds supplied	Mean no. (± se) of seeds consumed or damaged	Mean no. (± se) of seeds supplied	Mean no. (± se) of seeds consumed or damaged
1	70.5 ± 1.19	6.0 ± 1.3	68.3 ± 0.63	5.0 ± 2.9
2	70.3 ± 1.60	0.3 ± 0.3	68.3 ± 0.85	1.0 ± 0.7
3	70.3 ± 1.60	0.3 ± 0.3	68.3 ± 1.11	1.5 ± 0.9
4	70.0 ± 1.47	0.5 ± 0.5	68.3 ± 1.22	3.8 ± 3.4

Thiram has been found to repel not only rodents but also a number of birds (Young and Zevallos 1960; Sandhu et al. 1987). Other studies showed that thiram repelled ground squirrels causing damage to corn seeds (Zucher et al. 1983). Cinnamamide, a non-lethal bird repellent, has been evaluated against house mice and wood mice, and was found to have greater potential for control of house mice (Gurney et al. 1996). Repellency of cinnamamide against *Rattus norvegicus* also indicated its potential for prevention of damage in crops (Crocker et al. 1993).

The preliminary laboratory results in the current study suggest that dressing maize seeds with thiram and cinnamamide can reduce damage to seeds by *M. natalensis*. Further testing will be conducted to establish the efficacy of the two compounds to repel *M. natalensis* in fields planted with maize seeds.

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Composition of rodents and damage estimates on maize farms at Ziway, Ethiopia

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Abstract. Rodent composition and estimates of rodent damage were investigated in maize fields of central Ethiopia. The most common species caught were *Arvicanthis dembeensis*, *Mastomys erythroleucus*, *Mus mohamet*, *Tatera robusta* and *Graphiurus murinus*. Both live-trapping and snap-trapping of rodents were conducted at different stages of maize development. The snap-trapping yielded 277 small mammals from 2400 trap-nights. The live-trapping yielded 591 small mammals from 3000 trap-nights. The population abundance of each species varied with season and with vegetation cover and type. Maize seeds sown in both fenced and unfenced plots differed as a result of variation in the distances between planting holes. Percentages of seedlings missing in the fenced and unfenced plots were 9.6 and 12.6, respectively. Yield loss at the harvesting stage of maize where rodents were admitted was 26.4%.

Introduction

The diverse topographical features of Ethiopia, coupled with variations in temperature, have resulted in diversification of the mammalian fauna (Yalden and Largen 1992; Yalden et al. 1996). Out of a total of 277 mammalian species that are recognised in the country, 84 are rodent species. About a dozen of these rodent species are significant agricultural pests. *Arvicanthis* sp. and *Mastomys* sp. are the major pests in maize, bean and tomato plantations. Both species have a wide distribution in many parts of Ethiopia (Afework Bekele et al. 1993; Lavrenchenko et al. 1998). In Ethiopia, comprehensive studies on the effect of rodent damage to agricultural crops are lacking. Afework Bekele and Leirs (1997) described the population ecology of two common species of rodents in grasslands, but there are no quantified estimates of the crop yield that is lost to rodents. In this paper, we present preliminary data about the rodent species composition, and the damage rodents cause in maize plantations in central Ethiopia.

Materials and methods

The study was conducted at Ziway agricultural station, 160 km south of Addis Ababa, from March to November 2001. Removal and live-trapping grids of 50 traps each were located within the maize fields, with 5 additional lines of 20 traps each set at different distances from the edge of the target crop. Trapping sessions (three trapping nights) were conducted before and after planting, during the different growth stages of maize, and after harvesting of the crop. All rodents were identified to species.

In order to estimate the damage and yield loss caused by rodents in maize fields, five control and five rodent-proof, fenced experimental plots, each 10 × 10 m, were used to estimate damage at the seedling stage and at harvest. In both fenced and unfenced plots, seeds sown varied from grid to grid since the distance between holes was not proportional. The distance between holes ranged from 15 to 30 cm. Only one seed per hole was used.

Results and discussion

Species composition and abundance

Removal-trapping yielded 277 small mammals in 2400 trap-nights with a trap success of 11.5%. The species composition was: *Mastomys erythroleucus*, 128 (46.2%); *Arvicanthis dembeensis*, 98 (35.4%); *Tatera robusta*, 25 (9.0%); *Graphiurus murinus*, 12 (4.3); and *Mus mohamet*, 11 (4.0%). *Mastomys* and *Arvicanthis* are recognised as the major pest species, while *Tatera* and *Mus* are minor pests. Density estimation of rodent populations using Sherman live-traps was conducted also before sowing, and at the seedling, vegetative, harvesting and post-harvesting stages of maize. A total of 591 small mammals in 3000 trap-nights were live-trapped. *M. mohamet* comprised 210 (35.5%), *M. erythroleucus* 184 (31.1%), *T. robusta* 135 (22.8%) and *A. dembeensis* 61 (10.3%) of those captured. *A.*

dembeensis and *M. erythroleucus* made up 81.6% of those rodents caught in snap-traps, however this decreased to just 41.4% of rodents caught in live-traps. The decline in the capture of *A. dembeensis* was highly pronounced. There were differences in ground cover on the snap-trap and live-trap grids. Therefore the differences in trap success may be due to effects of habitat preference and selection, especially where ground cover at the maize farm was devoid of vegetation. Delany and Roberts (1978) have observed similar changes in densities of rodent populations between scrub and grassland vegetation, the scrub serving as a refuge habitat during adverse periods. The higher density of *M. mohamet* in the live-trapping grid (35.5%) compared to the snap-trapping grid (4.0%) may suggest better habitat for rodents that are good climbers. The population abundance of the respective species fluctuated across the seasons; further studies are required to ascertain the key factors influencing these fluctuations.

Table 1. Number of maize seeds sown and missing seedlings in fenced (to reduce access by rodents) and unfenced grids.

Grid	Seeds sown		Missing seedlings	
	Fenced	Unfenced	Fenced	Unfenced
1	1221	1554	120	180
2	1200	1440	85	170
3	1332	1443	95	190
4	1116	1680	105	135
5	1332	1170	190	240
Total	6201	7287	595	915

Table 2. Actual (kg maize) and proportionate yield (kg maize per planted seed) on different grids.

Grids	Actual weight		Proportionate weight	
	Fenced	Unfenced	Fenced	Unfenced
1	87.91	54.74	0.072	0.035
2	61.95	48.67	0.052	0.034
3	77.82	67.52	0.058	0.047
4	40.00	55.06	0.036	0.033
5	63.66	51.05	0.048	0.044
	Total: 331.34	Total: 277.04	Mean ± sd: 0.053 ± 0.012	Mean ± sd: 0.039 ± 0.006

Rodent damage to maize

A total of 6201 and 7287 maize seeds were sown in both experimental and control plots, respectively (Table 1). There were 595 seeds missing in the experimental and 915 in the control plot. Damage by rodents at the seedling stage in the unfenced plot was 12.6%, whilst in the fenced plot it was 9.6%. By comparing the obtained yield per planted seed (proportionate weight), the final yield loss was estimated to be 26.4% in the unfenced fields (Table 2). This suggests that an important part of the damage occurred after the seedling stage. These are preliminary results, with further work planned for another 12 months.

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MOUSER (Version 1.0): an interactive CD-ROM for managing the impact of house mice in Australia

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Abstract. *MOUSER* is an interactive training and resource package that provides decision support for the management of house mouse plagues. This knowledge management software has been developed to run from a CD-ROM on personal computers. The number of farmers who have computers is increasing: in 1999, nearly half of Australia's rural properties had computers. *MOUSER* is designed for use by growers, grower groups and State Government departments. This new version of *MOUSER* has been written using web-based software so that users can link directly to web pages for updates and for further information. It contains the most recent information available for managing house mice and includes an expanded decision key, more information and new videos. Another feature is an economics model (*EcoNoMice*), which can be used to compare the relative costs and benefits of different control techniques. The model is based on a gross margin for wheat for the mallee region of north-western Victoria. This technology can be applied to a wide range of rodent problems and can include identification keys, simple economic and population models, videos and training modules.

Introduction

MOUSER VERSION 1.0 is a CD-ROM for the management of house mouse plagues in south-eastern Australia. The concept of developing *MOUSER* came from Geoff Norton's keynote address at the 10th Australian Vertebrate Pest Conference in Hobart (Norton 1995). From this, a prototype version of *MOUSER* was developed in collaboration between the Cooperative Research Centre (CRC) for Tropical Pest Management and the Commonwealth Scientific and Industrial Research Organisation (CSIRO). This was completed in 1998 and was presented at the 11th Australian Vertebrate Pest Conference in Bunbury (Brown et al. 1998b). Funding was obtained from the Natural Heritage Trust (through the Bureau of Rural Sciences) to further develop the prototype software, to build an economics module, and to update the software. *MOUSER VERSION 1.0* was released in 2001. This type of software could be useful for managers of rodents and other pests in many countries around the world.

Features of *MOUSER*

MOUSER VERSION 1.0 contains a number of sections that provide a wide range of information to assist with the management of mouse plagues. The topics listed on the main screen of *MOUSER VERSION 1.0* are:

- *Contents*—allows users to access information directly on any topic.
- *Biology of mice*—information about the biology and ecology of the house mouse (*Mus domesticus*) in Australia such as breeding, food and nesting requirements, home range size, movements, behaviour, and population dynamics.
- *Mouse control*—information about types of control methods for house mice such as where, when, and what type of control methods should be used and includes information about chemical or non-chemical control techniques.
- *Mouse plagues*—information on the impact of mouse plagues, why they occur and the type of damage caused.
- *Monitoring*—information about various methods for monitoring the abundance of mice, both directly (e.g. trapping, census cards) and indirectly (e.g. faecal pellets, number of active burrows found per unit of area).
- *Damage assessment*—contains information about the type of damage and how to assess damage caused by mice to various crops and in buildings (e.g. damage to electrical wires, gnawing).
- *Decision key*—steps the user through a series of questions to provide possible management options. Information is provided for the central mallee region of Victoria and for the Murrumbidgee Irrigation Area of

southern New South Wales, two areas significantly affected by mouse plagues.

- *Common questions/myths*—answers some of the frequently asked questions about mouse plagues and exposes some of the myths.
- *Economic model (mouse control simulator)*—see below for more information.
- *Further information*—provides additional resources and information such as a list of references, a direct link to related web site addresses (using the browser contained on the CD-ROM), some brochures, acknowledgments, and a link to email support (<Mouser-Support@cse.csiro.au>).

Other features of *MOUSER VERSION 1.0* are:

- *Video*—showing some of the control practices, monitoring methods and behaviour of mice.
- *Graphs and pictures*—to help explain information.
- *Hotlinks to other sections*—to give more detail on a topic or see information about a related topic.
- *Audio*—listen to experts explaining good practice and hear the sound of a mouse squeak!
- *Active glossary*—click on technical words to find their meaning.
- *Print pages*—print off information.
- *Keyword search*—perform a search of the CD-ROM to find related information.

Economics module (mouse control simulator)

A review of current literature and existing knowledge was conducted to provide the best available information for inclusion into building the economics module (see Brown and Singleton 2002 for details). The main sources of information came from two projects conducted to assess the effects of farm management practices on mouse populations in different farming systems (Brown et al. 1997; Brown, Davies, Croft and Singleton, this volume). Additional information came from Brown et al. (1998a, 2002).

Options for managing mouse populations were split into two categories: routine actions; and preventative actions implemented only when mouse numbers were increasing. A list of mouse control actions was compiled and information was sought on the cost per hectare or kilometre for each mouse control action, the effectiveness (percentage reduction) of each action and the effect on the available food supply (e.g. grain remaining on the ground after harvest).

The basic population model underlying the economics module was modified from the mouse population model developed by CSIRO (used to predict mouse outbreaks in the Victorian mallee region). The population model was derived using the numerical response of mice over a 15-year period in the Victorian mallee region (Pech et al. 1999). Abundance of mice was related to estimates of food availability from cereal crops and grazed pasture and a density-dependent factor representing the effects of predation, disease and intrinsic regulatory processes. The Centre for Agricultural and Regional Economics (CARE) built the economics model using Excel with input from CSIRO. The model was converted into a stand-alone executable file in Delphi.

Results of the simulations provide a comparison of ‘control’ with ‘no control’ over a 12-month period. Graphs are used to show the effect on the response of the mouse population, gross margins, cost of control, and wheat yields. Much of the data used to generate the economics model have come from the Victorian mallee, and so caution must be made when using the model in other agro-ecosystems.

MOUSER software

The Centre for Pest Information Technology and Transfer (CPITT) at the University of Queensland reprogrammed the prototype version of *MOUSER* using an in-house web-based software package (WebGIST). WebGIST utilises Internet Explorer 5, which can be installed as part of the package if the user does not already have it installed. WebGIST provides a number of advantages over the prototype software, including supporting HTML, providing easier navigation around the CD (especially the decision key), providing ‘seamless’ links to remote web sites, and comes with a built-in search facility. WebGIST also supports executables, such as the economics package developed by CARE. Another advantage is that the HTML content of the CD version of *MOUSER* could easily be transferred to a server for web delivery.

The information contained in *MOUSER* was updated. New images and text were added directly to *MOUSER* and the Decision Key was updated and modified to incorporate the recommendations from the recently-completed Bureau of Rural Sciences-funded project on farm management practices for mouse control in southern New South Wales (Brown, Davies, Croft and Singleton, this volume). Also, new video footage showing farm management practices and footage of wild mice was digitised.

How to obtain a copy

If you would like to obtain a copy of *MOUSER VERSION 1.0*, see the demonstration at the Conference and add your name to the list provided, or contact Peter Brown (contact details given above). *MOUSER VERSION 1.0* costs A$19.95 plus $10.00 postage and handling (GST included).

Applicability of software for management of other rodent species

The software described here could be modified to assist with the management of other rodent species, providing there is a good understanding of the ecology and biology of the pest species. A valuable addition would be to include an interactive identification key, such as Lucid (Centre for Pest Information Technology and Transfer 2001). Lucid has been developed as an interactive key for a wide range of insects, fungi and plants. A key for the rodent species of Southeast Asia is currently being developed using Lucid, and would include diagnostic characteristics, detailed photos to aid identification, and a description of the species biology and ecology.

Another example of a CD-ROM for the management of pests is RiceIPM (Centre for Pest Information Technology and Transfer 2002). RiceIPM is an interactive training and resource package on CD-ROM for those who want to learn more about integrated pest management (IPM) for tropical rice crops. It contains a wealth of information that can be accessed in a variety of ways, including the use of Lucid keys, and should be of interest to rice-growers, advisors, researchers, students and anyone interested in learning more about IPM in tropical rice. It contains some basic information about the management of rice rats in tropical rice crops.

If developing software for pest management, it is important to build the software from readily available programs, such as Internet Explorer, and to allow the program to be upgraded easily. Now that the Internet is becoming more accessible in many countries, it would be useful to include Internet links with any software for updates, provide links to web pages, and for new information. Finally, it is desirable to collaborate with people who know how to design, build and test software to ensure a high-quality product.

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Observations of bamboo flowering and associated increases in rodent populations in the north-eastern region of India

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Abstract. The phenomenon of an outbreak of a rodent population synchronous with flowering of bamboo was investigated in the north-eastern region of India. In order to study the activities of rats and their association with different types of vegetation, the rodent-infested and bamboo-flowering areas were extensively surveyed. Various species of bamboo flowered during the study. During the period of flowering of *Bambusa tulda* (1976–79), five major species of wild rats and mice occurred in the study area. *Rattus rattus brunneusculus* was the most common rat in Mizoram and *Rattus nitidus* in Manipur and Nagaland. The populations of these rats were high in crop fields and caused extensive damage to paddy crops. The population density of *R. r. brunneusculus* and *R. nitidus* in abandoned crop fields was highest in January, whereas in freshly cultivated areas, the populations peaked in November and December. The flowering of the bamboo had no measurable effect on rodent population dynamics.

Introduction

A peculiar phenomenon observed in the north-eastern, hilly areas of India, namely, Mizoram, parts of Meghalaya, Arunachal Pradesh, Nagaland and Manipur, is the periodic mass-flowering and seeding of certain bamboo species which is accompanied by a tremendous increase in populations of certain rodent species. Enormous increases in the populations of species of *Nesokia*, *Mus*, *Rattus*, *Golunda* and *Rhizomys*, coinciding with bamboo flowering, have been reported in various parts of India (Win 1951; Kermode 1952; Chatterjee 1960; Santapau 1962; Nath 1968; Rao et al. 1995). The occurrence of similar phenomena has been reported from many other parts of the world, such as Madagascar, Burma, Japan, Brazil, southern Chile and Argentina (Janzen 1976; Jaksic and Lima 2002).

This biological phenomenon results in severe famine conditions due to rodent damage to agricultural crops. A study was conducted in the north-eastern region during 1976–79, the period of flowering of the bamboo *Bambusa tulda*. In this region, following the flowering of bamboo, there is a sudden increase in the number of rats, which causes damage to such an extent that it results in almost famine-like conditions. This was first reported by Elles (1881) in his military report on the Chin-Lushai Hill county. As a great famine is expected sometime during 2003–2005, there is an urgent need for a detailed study on bamboo flowering and ecology and behaviour of rodent species in this region. This paper reports on a population study of the rodent community conducted in the north-eastern region from 1977 to 1979.

Materials and methods

Study area

The north-eastern region of India comprises of Mizoram, Nagaland, Manipur and Meghalaya union territories and is situated on the eastern border of India. The land is between Chin Hills (Burma) in the east and south, and Chittagong hill tracts (Bangladesh and Tripura) in the west.

The climate and soil of the north-eastern region is suitable for growing many kinds of tropical crops. The principal crop is paddy rice (*Oryza sativa*), with other crops including maize (*Zea mays*), ginger (*Zingiber officinalis*), sweet potato (*Ipomoea batatas*), turmeric (*Curcuma longa*), chilli (*Capsicum* sp.), tobacco (*Nicotiana tabacum*), orange (*Citrus* sp.) and certain vegetables. One-fifth of the area is covered with tropical forest. Thick bamboo forests are in abundance on the low-lying hills and valleys. Shifting cultivation (*jhum*) is widely practised and results in the serious destruction of forests. Terrace and wetland farming has recently begun.

In Mizoram, the famines associated with the flowering of *Melocanna bambusoides* (local name, 'Mautak') and *Bambusa tulda* (local name, 'Rawthing') are locally known as 'Mautam' and 'Thingtam', respectively. These famines occurred in 1880–81, 1927–29, 1976–78 (associated with

'Thingtam') and 1910–12, 1956–59 (associated with 'Mautam'). 'Mautam' flowering is expected in 2005. Other minor bamboo species found to be associated with 'Mautam' are *Dendrocalamus longispathus* (Rawnal), *Melocalamus campactiflorus* (Sairil) and *Dendrocalamus sikkimensis* (Rawmi) (Parry 1928) and with 'Thingtam' are *Melocalamus campactiflorus* (Sairil), *Dendrocalamus sikkimensis* (Rawnal), *Dendrocalamus longispathus* (Rawmi), *Bambusa spinosa* (Phar) and *Pseudostachyum polymorphum* (Chal) (Mohan Ram and Hari Gopal 1981). 'Thingtam' is associated with a famine of lesser magnitude than 'Mautam' and occurs at an interval of approximately 48 years; 18 years after the occurrence of 'Mautam'.

The bamboo-flowering areas and rodent species were studied by undertaking extensive field surveys of crop fields (*jhum* and wetland cultivation areas), bamboo forest, other adjoining forests and tribal settlements in Mizoram, Meghalaya, part of Manipur and Nagaland. Rats and mice were regularly collected from crop fields, bamboo forest and tribal settlements of Mizoram by extensive digging of burrows or trapping. Collection sites were periodically changed to provide adequate sampling of an entire area.

The rodent-infested and bamboo-flowering areas, village sites and forests were extensively surveyed in order to study the activities of rats and their association with different types of vegetation. Simultaneously, bamboo seeds and fruits were collected for the purpose of using them in 'feeding experiments'.

The relative density of rat populations was estimated by counting live burrows and capturing rats through excavation of their burrows. Population estimates were conducted 2–8 times a month in fallow and freshly cultivated crop fields from January to December 1978 and May 1978 to March 1979, respectively.

Results and discussion

In the total collection of about 2500 rats and mice, 8 species were identified. In Mizoram, *Rattus rattus brunneusculus* constituted the major part of the collection (92.5%). In Manipur and Nagaland, the Himalayan rat, *Rattus nitidus*, was the predominant species. Other species collected in low numbers were *Rattus bowersi mackenziei*, *Bandicota* sp., *Cannomys badius*, *Rattus rattus* and *Mus musculus*. The first three species occurred in the cultivated areas whereas the latter species occurred mainly in tribal settlements and granaries.

R. r. brunneusculus and *R. nitidus* were both collected from paddy fields. They make simple to complex burrows, which contained stored paddy grains and vegetable matter. After harvest, the grain stores of burrows were slowly depleted, but paddy husk, chilli, ginger, brinjal, tomato etc. could still be seen. These observations suggest that although the main food of these rodent species is rice, when it is not available they feed on other vegetable matter and tender shoots. *R. b. mackenziei* rats make complex, deep burrow systems mainly in the paddy fields. They feed on the tender shoots of various crop plants and underground vegetables. Rats of *Bandicota* sp. are fossorial in nature. They are normally found in low-lying areas cultivated for wetland rice and near marshy stretches. They have complex but shallow burrow systems. Although the population of these rats was not as high as it was during 'Mautam' flowering time (as reported by local people), the damage caused by them to paddy crops often was quite extensive. Bamboo rats, *C. badius*, usually occurred in sugarcane, arabi (*Colocasia* sp.), ginger and sweet potato fields. They were found also in grassy areas near bamboo thickets, bushes and trees. They make complex burrow systems which usually contained ginger and sugarcane pieces. At times, nearly 5–6 kg of these food materials were collected from a single burrow. They also feed on other plants, grasses, seeds and fruits. *Vandeleuria oleracea dumeticola* occurs in bushes, trees and bamboo thickets and feeds on fruits, buds, rice grains etc. Their nests were usually found in tree cavities or between the branches.

During the flowering period of *Bambusa tulda*, large numbers of *R. r. brunneusculus* and *R. nitidus* were found in paddy fields. They caused extensive damage to the paddy crop. Due to deforestation in preparation for cultivation or after harvesting of crops, perhaps these rats disperse to bamboo forests and later recolonise freshly cultivated land. The presence of live burrows, paddy husks, damaged panicles, cut leaves and faecal matter on their runways were signs of their increasing population and activities.

In abandoned crop fields, the numbers of live burrows and rats captured per hectare during 1978–1979 were significantly correlated ($Y = 2 + 0.4x$, $r = 0.935$) (Table 1). In January, a peak population level was observed (live burrows/ha: 36 ± 1.71, rats captured/ha: 15 ± 1.27), which later declined and remained low from April to December. The lowest number of live burrows was in July (3 ± 1.53) and lowest rat captures were in June (2 ± 0.50). In the freshly cultivated land, the population estimates based on the number of live burrows per hectare and the number of rats captured were not correlated ($Y = 10 \pm 0.46x$, $r = 0.447$, $P > 0.1$). The number of live burrows revealed peak population levels in May (30 ± 1.4). The number of rats caught from burrows was also relatively high in May (21 ± 0.70), then decreased in the following few months, but started increasing after July and attained a peak in November (36 ± 1.40). Thereafter, the population again showed a gradual decrease and reached a low level in March (12 ± 0.70).

In this study, counting of live burrows and rats captured from them were found to be the most practical methods for estimating the relative density of *R. r. brunneuculus* and *R. nitidus* inhabiting the north-eastern hilly areas. These population indices showed marked monthly changes for both species, both in abandoned and freshly cultivated fields during 1978–79. The factors governing these fluctuations may be both biotic and abiotic. Monthly fluctuations in the relative density of the rats have been discussed mainly in relation to biotic factors such as seasonal periodicity in breeding activity and food availability. These biotic factors have been found to be of considerable importance in the regulation of population density of many rodent species (e.g. Bindra and Sagar 1968; Prakash 1981; Taitt and Krebs 1981).

In the abandoned crop fields, the maximum population is observed in January (post-harvest period) following high breeding activity from July to October during the crop of the preceding year. Marked decline in the population thereafter (January to April) may be mainly due to the cessation of breeding activity and a progressive decrease in the amounts of available food, which probably enables a majority of animals to move out to areas where they can obtain sufficient food and shelter. Declines in other rodent populations have been also reported to be due to food shortage and/or termination of breeding activity (e.g. Pearson 1963; Desy and Thompson 1983). If there is no migration of the rats from the abandoned crop fields, then the reduction in the population may also be due to starvation. Increased intra- and interspecific competition, through greater incidence of cannibalism and fighting behaviour, possibly due to scarcity of food, may also be responsible for the decline in population. No direct evidence for their emigration and mortality was obtained, so further studies are required to test the importance of these factors on population decline.

The population density remained low from April to December even though this period coincided with the breeding season of these rats. Therefore, the scarcity of food might have led to increase pre-natal and infant mortality and decreased fecundity, which ultimately reduced the population to low levels. The food available at that time included only a few vegetables and wild plants, which might be just sufficient to maintain a small population of the rats.

In freshly cultivated areas, the significant rise in populations of rats in July, before the onset of breeding, is likely to be due to the immigration of large numbers of rats from surrounding areas in search of sown paddy grains. Later, with the exhaustion of paddy grains, either due to consumption by the rats or their germination into seedlings, the population temporarily disperses to surrounding areas in search of alternative food. In the ensuing months, the population shows an increasing trend coinciding with the growth of the paddy crop, especially the development of rice panicles, which are their favourite food, and many vegetables. The onset of rainfall could possibly be an indirect factor regulating the population by causing vegetation growth, and thus an increase in food supply. Growth and maturation of paddy panicles also probably attract rats from surrounding areas, which—along with intense breeding—results in further population increases. The population was highest during November–December, the period when paddy was harvested.

The common bamboo rat, *C. badius*, that is believed to be the only species that causes sufficiently extensive damage to paddy crops to result in famine, was not found to be of much significance. These rats were uncommon in the paddy fields, inhabiting mainly the sugarcane, arabi, ginger, sweet potato fields and grassy areas near the bamboo forest.

Table 1. Monthly variation in the relative density of *Rattus rattus brunneusculus* based on the number of live burrows and rats captured in abandoned and fresh crop fields during 1978–79.

Year	Month	Abandoned crop fields		Freshly cultivated fields	
		Number of live burrows/ha (mean ± se)	Number of rats captured from burrows/ha (mean ± se)	Number of live burrows/ha (mean ± se)	Number of rats captured from burrows/ha (mean ± se)
1978	January	36 ± 1.71	15 ± 1.27	–	–
	February	22 ± 1.27	13 ± 1.10	–	–
	March	14 ± 1.22	8 ± 0.50	–	–
	April	9 ± 0.55	7 ± 0.58	–	–
	May	8 ± 0.58	4 ± 0.28	30 ± 1.40	21 ± 0.70
	June	6 ± 0.33	2 ± 0.50	25 ± 1.00	16 ± 0.58
	July	3 ± 1.53	3 ± 0.70	13 ± 2.20	12 ± 2.20
	August	6 ± 0.36	4 ± 0.58	18 ± 3.00	15 ± 1.00
	September	6 ± 0.42	6 ± 0.33	19 ± 1.40	16 ± 1.15
	October	8 ± 0.58	4 ± 1.22	20 ± 0.52	19 ± 3.00
	November	8 ± 0.58	6 ± 0.70	25 ± 0.70	36 ± 1.40
	December	9 ± 0.71	6 ± 0.55	18 ± 0.96	24 ± 0.82
1979	January	–	–	9 ± 1.40	19 ± 2.20
	February	–	–	11 ± 3.40	18 ± 1.00
	March	–	–	13 ± 1.92	12 ± 0.70

The flowering of bamboo results in abundant food supply in the form of bamboo seeds and fruits. These bamboo seeds and fruits are not only palatable but are preferred by some rodent species, attracting them to flowering areas (Janzen 1976). Despite a constant vigil, no sign of rat migration from *jhum* to bamboo forest or vice versa was observed in Mizoram during flowering of *B. tulda*. The rats mainly inhabited paddy fields, and showed variation in their numbers in relation to the crop cycle during the flowering of *B. tulda*. Only a few rats were noticed in the forests during this period. This suggests that the extent of bamboo flowering and seed production during these years may not be sufficient enough to attract the rat population. Only in a very few places in the north-eastern region did the bamboo flowering result in seed formation. Most of the flowers were destroyed by heavy rain and high-velocity winds. Therefore, ultimately the food available in the form of bamboo seeds and fruits in these areas was negligible and insufficient to generate an explosion of rodent populations. The effect of bamboo seeds and fruits on the reproduction of rats and the rate of growth of their populations need to be investigated further.

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Rodent removal with trap–barrier systems in a direct-seeded rice community in the Philippines

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Abstract. The rat population in a rice-based agro-ecosystem was monitored with four trap–barrier system plus trap crop (TBS+TC) set-ups, each measuring approximately 7 m × 20 m, during the 2002 dry-season rice crop in Maragol, Muñoz Science City, Philippines. The highest number of rats caught coincided with the period of field operations (preparation and planting of the surrounding rice crops). This period of disturbance may have forced the rats to disperse, resulting in high numbers of trapped rats. During the growing period of the rice plants, more rats were trapped at the seeding to maximum tillering stages than from the panicle initiation–booting stage through until the milking stage of the rice plants. No rat was trapped during the dough stage through until harvest. More females than males were trapped during the field operations' period and until the maximum tillering stage of the rice. Thereafter, more males than females were trapped. More females were trapped during the entire study period, suggesting that use of TBS+TCs may decrease the reproductive performance of rat populations. Although the initial cost of each TBS+TC is US$54.50, about 10% is recovered with the sale of paddy rice harvested from the trap crop. The capture of 368 rats indicated that this system has potential, if used together with a rat campaign of 1–2 weeks immediately after the crop has been sown. This study continues to obtain more data on the population dynamics and demography of rats that will provide baseline information for the implementation of rat control strategies in the area.

Introduction

Rats have been causing immeasurable damage to crops for thousands of years. Although some progress in rodent management has been reported in the past decades (Singleton et al. 1999a), rodents still cause serious economic damage and pose health risks worldwide. In the Philippines, rats cause substantial yield loss to rice crops (Ahmed et al. 1987). In a 1998/99 survey, farmers considered rats as one of the major pests of rice, causing serious damage to the crop in irrigated and rainfed rice fields in all regions of the Philippines (R.B. Malasa, pers. comm.). The use of rodenticides, in the form of poison bait, is the most common means of rat control in the Philippines (Sumangil 1990). However, anticoagulant resistance and bait shyness (Buckle 1999), potential hazards of rodenticides to non-target organisms, and the pollution of the environment are risks posed by constant and indiscriminate use of rodenticides. Knowledge of the population dynamics of pest rodents is important in the proper application of control strategies. In this study, we tested the performance of the trap–barrier system plus trap crop (TBS+TC) (see Singleton et al. 1999b) in a rice agro-ecosystem to gain knowledge about population dynamics of pest rodents and to determine the best time to implement rat control strategies.

Materials and methods

Study site

We selected a 40 ha contiguous rice-growing area in Maragol, Muñoz Science City, Nueva Ecija, Philippines as a study site. A high level of rat infestation was reported in the previous crop (wet season 2001) where about 45% of the fields were planted with the popular, high-yielding rice variety IR64. PSB Rc28 and PSB Rc82 were the other major varieties planted. The location of the paddy-field parcels was mapped with a global positioning system to determine their distance from the TBS. The size and ownership of the farms was also checked with the local cadastral maps and records. Data on farm inputs of fertiliser and pesticide usage and other farm information, such as variety planted and time of planting, was collected in interviews with the farmers. During the 2002 dry season, 73% of the fields in the study site were directly wet-seeded and the rest was transplanted. Most of the fields were planted with IR64 (52%) and PSB Rc82 (33%).

TBS+TC establishment

Four TBS+TCs were established in the study site near the irrigation embankments. Generally, each TBS+TC measured 7 m × 20 m. Dimensions did vary slightly, depending on the dimension of the paddy field. The TBS+TCs were erected about a month before the general planting time in the area. A polyethylene sheet about 0.5 m from ground level was fastened with staple wires on the outer side of bamboo sticks to serve as protection for the rice plants growing inside the barrier system. To attract the field rats, an aromatic rice variety, MS8, was used as trap crop. The small size of the TBS allowed for manual land preparation and broadcasting of pre-germinated rice seeds inside the TBS.

Traps

The multiple-capture rat traps used in this study were made of metal wire mesh and measured 50 × 20 × 20 cm. The entrance tunnel was cone-shaped, narrowing to the end with bent metal wires to prevent the captured rat from escaping. One trap was installed in the centre of each side of the TBS+TC, with its entrance facing an opening at the base of the polyethylene sheet.

Data gathering

Daily counts of rats began a day after TBS+TC establishment. The rats trapped were removed and killed, and their sex and the growth stage of the rice crop were recorded.

Results and discussion

Rats were trapped as soon as the TBS+TC was established but at a low rate. An abrupt increase in the level of rat catches occurred a week after the start of field operations in the study site. This may be due to the flooding and destruction of the rats' burrows in the levees of the rice field. This indicates there is a time window to conduct community-wide physical rat control to reduce the initial population in the field present at the beginning of the cropping season. However, there was a gradual decline in the number of trapped rats at the time when most fields were established. This was possibly caused by the presence of abundant food in the fields decreasing the rats' motivation to enter traps. The catches during the early growing stage of the rice were lower than at field operations' period and gradually declined up to the maximum tillering stage of the rice plants. Most rats were trapped during the seeding to maximum tillering stages (Figure 1). A similar trend in rat captures in a TBS+TC was recorded in Indonesia and Vietnam (Singleton et al. 1999b). A reduced level of rat catches occurred at mid-rice growth stage but this slightly increased at the booting to milking stages of the rice plants in the surrounding area (Figure 1). No formal identification of rat species was conducted during the study period. However, all rats trapped have longer tail length than head–body length.

Before the trap crop emerged, only four male rats were trapped. However, during the field operations period, 70% of the trapped rats were females. This indicates the potential for a high rate of increase in population size after the establishment of food sources and commencement of breeding. The first pregnant rat trapped was recorded within a month after crop establishment. Of the 32 female rats caught from 13 February to 30 March 2002 (tillering stage), nine were pregnant. They were dissected and yielded a total of 74 foetuses. Although the proportion of female rats declined during seeding to the maximum tillering stage, there were still more females (58%) than males (42%). Thereafter, more males than females were trapped (Figure 1).

In this study, the cost of establishing one TBS+TC with an area of 140 m^2 was about US$54.50. This is slightly higher than the cost of a TBS+TC in Indonesia but

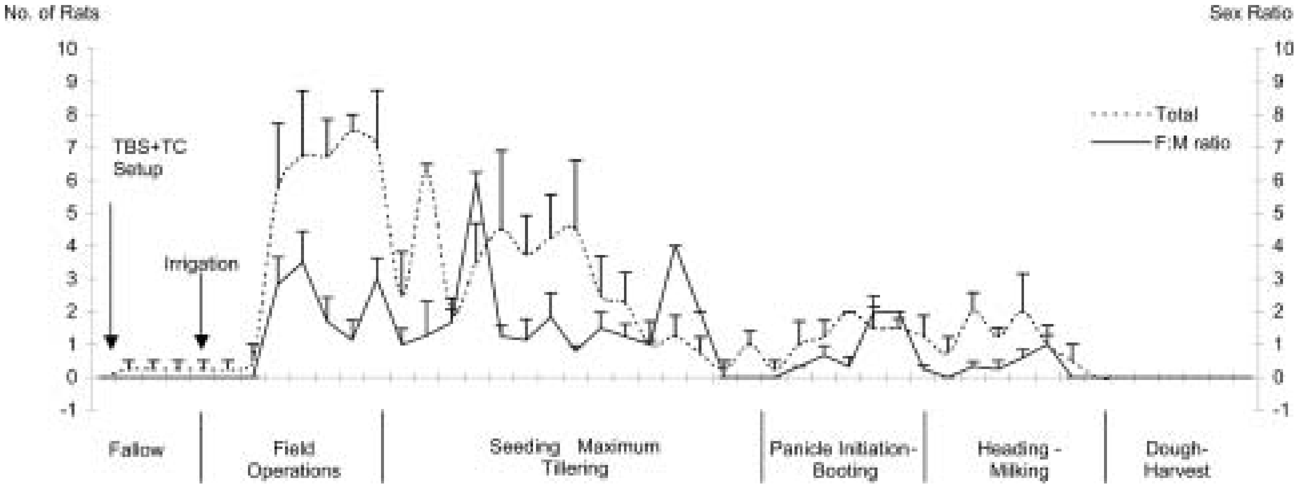

Figure 1. Average number of field rats and sex ratio (female/male rats) trapped at 3-day intervals in four strategically installed trap–barrier system plus trap crop (TBS+TC) set-ups before and during the rice-growing period (+1 se), Nueva Ecija, Philippines, dry season 2002.

lower than in Malaysia and Vietnam (Singleton et al. 1999b). The polyethylene sheet accounts for about 37% of the total cost; followed by the labour cost in land preparation and installing the system (35%). The other expenses were minimal, but the cost of four traps was about 18% of the total cost. However, the farmers harvested about 75 kg of paddy rice from each trap crop, resulting in a US$15.00 return. In effect, the cost of each TBS+TC was about US$39.50. The cost would be reduced further because the polyethylene sheet and traps are re-used in the following cropping season. In addition, the farmers can consume the trapped rats because poison baits are absent during the fallow period and the time that the TBS+TC is in operation.

Conclusion

The population dynamics of the field rat caught in the TBS between the start of irrigation-water delivery to the farm and subsequent field operations suggested that this was a strategic time for rat management. The capture of 368 rats, most before the onset of breeding that occurs at maximum tillering, indicates that TBS+TC holds potential for rodent management in the Philippines. Detailed knowledge about population dynamics and the activity of pest rodents is useful for the development of a strategic rat management system for rice-based agro-ecosystems in the Philippines. The study continues and alternative materials for the TBS that are cheaper and locally available to the farmers are being tested. The crop damage will also be assessed in relation to the distance from the TBS+TC.

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The use of the barn owl, *Tylo alba*, to suppress rat damage in rice fields in Malaysia

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Abstract. We investigated the damage caused by rice-field rats to rice crops in Malaysia in areas where barn owls were provided with nest boxes. We measured damage from February to May 2002 (first planting season), and assessment was made for three rice growth stages: tillering, booting and harvesting. Three plots with five nest boxes were set up to provide a nest box density of 1 box per 5 ha (plot A), 1 box per 10 ha (plot B) and 1 box per 20 ha (plot C). Rice damage assessment involved sampling of damaged tillers and hills using 0.5 × 0.5 m quadrats every 5 m along ten parallel, linear rows of paddy. Damage on all plots for all three paddy growth stages was less than 2%. In areas where there were no nest boxes, damage by rat activities was as high as 12%. The average damage levels for plots A, B and C were 0.63%, 0.68% and 1.58%, respectively. The difference in damage levels between A and B was not significant ($p > 0.05$) but differences between A and C ($p = 0.003$) and between B and C ($p = 0.029$) were both significant. At the tillering stage, damage levels were lower by a factor of 3 in plot A and 7 in plot B; at the booting stage, by a factor of 2 in A and B; and at the harvesting stage, by a factor of 2 in A and B compared with the low owl density plot C. While the results suggest that an owl nest box in every 10 ha may be sufficient for the effective control of rats in rice fields in Malaysia, a properly replicated experiment is required with more levels of treatment before an effective threshold density of nest boxes can be defined.

Introduction

Rats are important pests in Malaysian rice fields. They attack all stages of paddy, from seedling until harvest, as well as the stored grain (Lam 1982; Shamsiah and Goh 1991) The rice-field rat, *Rattus argentiventer,* is the most common rat species attacking paddy, although other species have been occasionally recorded—*Rattus tiomanicus, R. exulans, R. rattus diardii, R. norvegicus* and *Bandicota indica* (Lam 1982).

The average rice crop loss due to rat activities in Peninsular Malaysia varies from 5% (Lam and Abdullah 1975) to 18% or even higher in some years and some areas (Department of Agriculture, cited in Hafidzi et al. 1999). Chemical control using various formulations and classes of rodenticides has been the normal practice in dealing with rat infestations. Rodenticides have a number of undesirable side effects, including secondary toxicity to non-target animals and the prospect of rats developing resistance to rodenticides. The natural propagation of barn owls, *Tyto alba,* in the oil palm sector (Duckett 1976; Lenton 1980; Smal 1988) has opened the way for similar efforts in rice fields, starting in 1988. The barn owl program in rice fields has successfully reduced crop loss from as much as 12% to less than 2% within a year of its implementation (Hafidzi et al. 1999).

There have been several suggestions as to the optimal nest box density for barn owls to produce stable and effective rat control in oil palm. Smal (1988) placed boxes at approximately one box per 2 ha in new areas to encourage *T. alba* breeding. Ali et al. (1995) suggested one box per 10–15 ha in newly established oil palm areas and to increase nest box density to one box every 10 ha once the owl population is established. Lim et al. (1993) estimated the occupancy rate was 72% from a census in an oil palm plantation in Johore, Malaysia, where the nest box density was one box per 10.9 ha. Smal et al. (1990) constructed a model to predict the behaviour of rat populations subject to barn owl predation and suggested that theoretically *T. alba* can control rats effectively (without poison baiting) at a density of one box every 6–8 ha. However, Chia et al. (1995) argued that, at high rat infestations, a nest box density of one box every 3–4 ha is more effective and can give rise to sustainable control, i.e. sustain a viable population of *T. alba.*

In rice-field areas of Malaysia, the Department of Agriculture recommends a nest box density of one box for every 20 to 40 ha (Anon. 1997). In practice, however, this is rarely conformed to because farmers normally put up nest boxes on their own initiative, leading to a higher nest box density than recommended. The objective of this study was to determine the effect of intraspecific competition between barn owls as a consequence of varying nest box density and how this affects rat control indirectly through damage assessment.

Materials and methods

The area selected for the study was at Sawah Sempadan in Tj Karang, Selangor, where rice is planted using direct seeding. There are two planting seasons per year: the dry season (first planting season) and the wet season (second planting season). Rice varieties planted are the MR 102, MR 129 and MR 185, which can be harvested after 110 days.

Fifteen nest boxes were set up in December 2001 in a designated area where there were no boxes previously. The nearest nest box to the study site was more than 1 km away to reduce any residual effect from neighbouring nest boxes. This distance was thought to be sufficient, as the foraging area of female owls as determined from radio telemetry, is relatively small, ranging from 0.6–2.8 ha (Hafidzi et al. 2000). The boxes were arranged in three clusters of five boxes (plots A, B and C), each according to the plan shown in Figure 1. Four nest boxes constitute the corners of a square plot with a central box. In this study, *T. alba* is assumed to hunt over a circular area and maintain an exclusive home range with respect to the outlying boxes, giving a coverage of 4.9 ha (r_a = 126 m) (r = radius from the nest box to the perimeter of the circle), 9.95 ha (r_b = 178 m) and 19.95 ha (r_c = 252 m) for plots A, B and C, respectively. The linear distances between plots A and B of 356 m ($2 \times r_b$) and between B and C of 504 m ($2 \times r_c$), were judged to be sufficient to eliminate any impact of one plot on the adjacent plot, since breeding females seem to maintain an exclusive home range (Hafidzi et al. 2000).

Rat damage assessment was divided into three paddy growth stages: tillering (4 weeks after seeding) in the third week of February 2002; booting (9 weeks after seeding) in the fourth week of April; and harvesting (2 weeks before harvesting) in the second week of May. The method involved sampling along ten parallel, linear rows of paddy chosen at random within each plot. Ten quadrats of 0.5 × 0.5 m, 5 m apart, were sampled along each row for a total of 100 quadrats. Damage was calculated as follows:

$$\% \text{ damage} = (a \times c)/(b + c) \qquad (1)$$

where a is number of damaged hills out of 100 sampled; b is the number of undamaged tillers in the hills with damage; and c is the number of damaged tillers in the hills with damage (Buckle 1994, p. 223).

Damage estimates were combined for all stages of plant growth by taking the average for the percentage damage during tillering, booting and before harvesting for each plot.

Results and discussion

All boxes put out in December 2001 were occupied by January 2002. We made no attempt to inspect the breeding status of barn owls using the boxes to avoid disturbance of the newly arrived birds. There was an inverse relationship between damage and nest box density, i.e. there was lower damage in plots with higher nest box density (Figure 2). Damage on all plots for all three stages was less than 2%, which is the level of damage recorded in most areas in Tanjung Karang where the barn owl program has been implemented (Hafidzi et al. 1999). More importantly, the damage levels in the one box per 5 ha plot (A) and the 10 ha plot (B) were lower than damage levels in the one box per 20 ha plot (C) which represents the normal nest box density at Tanjung Karang. The average damage was 0.63%, 0.68% and 1.58% for plots A, B and C, respectively. The difference in damage levels between plots A and B was not significant ($p > 0.05$) but differences between plots A and C ($p = 0.003$) and between plots B and C ($p = 0.029$) were significant.

At the tillering stage, the number of rats is low and *T. alba* may have to forage over a larger area to fulfill its daily food requirements. When the rice crop reaches the booting stage, rats start to produce their first litters (Leung et al. 1999) and the number of rats increases rapidly in the field, producing higher crop damage. The second litter of rats is usually born during the ripening stage, which leads to still higher damage as is apparent in this study, and third litter arrives shortly after harvest (Leung and Sudarmaji, cited in Leung et al. 1999).

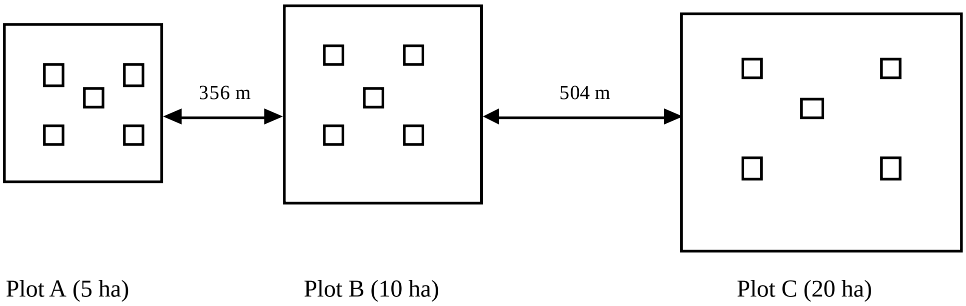

Figure 1. Arrangement of nest boxes.

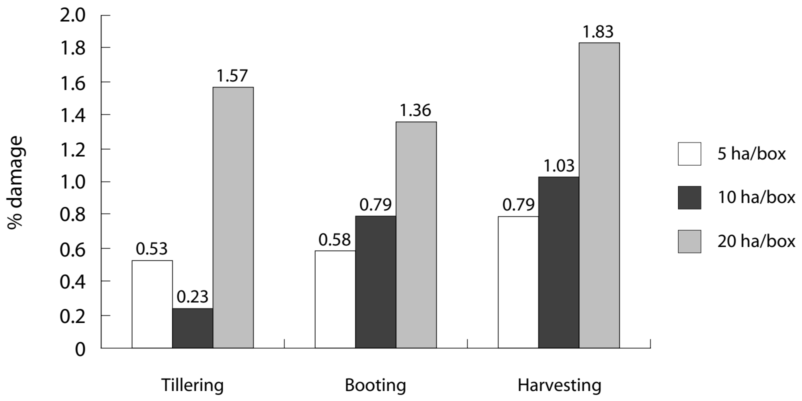

Figure 2. Rat damage in rice fields with different barn owl nest box densities. Data from the first planting season of 2002.

The current study suggests that at five nest boxes per ha and 10 nest boxes per ha, barn owls may be able to control rat numbers and thereby reduce crop damage at all stages of paddy growth. If we compare the 5 and 10 nest box treatments relative to the 20 nest box treatment, at the tillering stage, damage levels were lower by a factor of 3 and 7; at the booting stage, by a factor of 2.3 and 1.7; and at the harvesting stage by a factor of 2.3 and 1.8, respectively.

Conclusion

This study suggests that a density of one nest box per 10 ha may be sufficient to permit barn owls to reduce crop damage in rice fields in Malaysia. However, the results of this study are only suggestive because we need more replicates and simultaneous controls with no nest boxes provided. This study needs to be carried out over a larger area with more nest boxes to provide at least three replicates for each nest box density before definitive conclusions can be reached. The second planting season starts in late July 2002 and forthcoming data at the time of print would substantiate these findings.

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Pre- and post-harvest movements of female rice-field rats in West Javanese rice fields

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Abstract. This study examined changes in the spatial behaviour of rice-field rats (*Rattus argentiventer*) associated with the harvest of lowland irrigated rice. Radio-collared female rice-field rats were tracked before and after harvest in rice fields in West Java, Indonesia. The rice-field rats clearly reacted to the changes in habitat structure caused by the harvest by relocating their home ranges on average 300–400 m to piles of rice straw left on the fields and to unharvested areas. Post-harvest, there was a decrease in home-range size of 67% (0.6 ha pre-harvest; 0.2 ha post-harvest) and a decrease in range span of 35% (139 m pre-harvest; 90 m post-harvest), which may indicate an immediate response to predation risk. Most rats remained in the rice fields for 2–3 weeks post-harvest. This contrasts to their pre-harvest preference for refuge habitats near the margins of crops.

Introduction

Small mammals are a common feature of agricultural landscapes but for many rodent species very little is known about the impact of farming practices on spatial behaviour. Exceptions include wood mice, *Apodemus sylvaticus*, which relocate to adjacent refuges from areas disturbed by harvest (Tew and Macdonald 1993) and common voles, *Microtus arvalis*, which considerably reduce spatial activity after the harvest of grain (Jacob and Hempel 2002).

Home-range size of small mammals can vary due to intrinsic factors including breeding activity (McShea 1989; Krebs et al. 1995) and population density (Erlinge et al. 1990), as well as extrinsic factors including food availability (Ostfeld 1986) and vegetation height (Tew and McDonald 1993; Jacob and Hempel 2002). The removal of vegetation by mowing of verges and grazing stubble is often used as a management tool to minimise food and shelter. This can also expose pest rodents to predators thereby reducing pest rodent density (White et al. 1998). However, exposed prey may adapt behaviourally and decrease spatial activity as a counter-strategy to minimise predation risk.

Rice-field rats (*Rattus argentiventer* Robinson and Kloss 1916) are the most important pre-harvest pests in lowland flood-irrigated rice systems of Java, Indonesia (Singleton and Petch 1994). They and other species including black rats (*R. rattus*) and Norway rats (*R. norvegicus*) also invade facilities for processing and storing rice.

We used radio-telemetry to estimate the home-range size of female rice-field rats from about 3 weeks before harvest until about 3 weeks after harvest in lowland rice fields of West Java, Indonesia. We hypothesised that there would be (1) a decrease in spatial activity post-harvest leading to smaller home-range size and smaller range span and (2) a change in habitat use due to preference by the rats for refuge areas post-harvest.

Material and methods

The study was conducted between Sengon and Sukamandi (06°20'14"S, 07°39'24"E) Subang district, West Java, Indonesia. The climate in the region is tropical with small variations in annual average temperature (28°C). About 75% of the annual rainfall (1450 mm) occurs during the wet season (November–April) but rain is also frequent during the dry season (May–October).

The West Javanese agro-ecosystem is characterised by lowland irrigated rice fields, which are partitioned by many dikes, dams and irrigation channels. Individual farmers typically manage 1–2 ha of rice. Usually, one rice crop is grown in each of the seasons. Rice is sown in nurseries and after 2–3 weeks transplanted by hand into the fields. The main crop stages are tillering (55 days after sowing), booting (75 days) and ripening (95 days). Rice is harvested by hand about 120 days after sowing. Rice-field rats usually breed from about 2 weeks before maximum tillering until a few weeks after harvest (Leung et al. 1999).

We used a contiguous rice-growing area of about 400 ha for the study. Harvesting (rice variety 'Ciherang') was conducted from 25 July to 31 July 2001. Rice-field rats (*n* = 14) were trapped with multiple-capture wire-cage live-traps set along a drift fence in early June and fitted with 4.8 g single-stage radio transmitters (Sirtrack, New Zealand). For this study, we tracked the rats from 10 July (generative stage of rice crop) until harvest. Four of these rats were also followed for about three weeks post-harvest. Seven additional rats trapped and radio-collared in mid-July were tracked until the end of August. Radio locations (fixes) were obtained once a day and twice a night. Incremental area analysis (Kenward and Hodder 1996) revealed that 20 locations were sufficient to determine 80% of the 95% minimum convex polygon (MCP) home ranges of the rats. Therefore, only rats with ≥20 radio locations pre- or post-harvest were included in the analyses of home-range size and range span (pre-harvest, only *n* = 10; post-harvest, only *n* = 3; pre- and post-harvest *n* = 4). For seven individuals radio-tracked before and after harvest we calculated centres of activity using the recalculated arithmetic mean (Kenward and Hodder 1996) to detect shifts in the position of home ranges during harvest.

Rats were radio-tracked in five plots of about 2–23 ha within the study area. The distance between plots was at least 400 m. For each of the plots, habitat was classified as rice field, refuge (channel banks, gardens, roadsides) and village. Vegetation height of the ripe rice plants was about 0.9 m and the height of the stubble after harvesting was about 0.25 m.

We compared ln-transformed data of 95% MCP home ranges and range spans of rats pre- and post-harvest using general linear regression. We calculated the Jacobs' index (Jacobs 1974) as a measure of habitat use relative to habitat availability for all rats that were located in >1 habitat. The index results in values between 1 (complete preference) and –1 (complete aversion). The proportion of the rat population that did not move outside rice fields was compared pre- and post-harvest with generalised linear regression for binomially-distributed data (radio locations in rice field only yes/no) using a regression model including time (pre- and post-harvest) and plot. Range measurements were calculated in Ranges V (Kenward and Hodder 1996).

Results and discussion

Home range and range span

A total of 672 radio-locations were used for analyses. Home ranges pre-harvest of 0.59 ha (se = 0.12 ha) were about 67% larger than home ranges post-harvest (F = 20.99, df = 1,18, $p < 0.001$) (Figure 1a). Similarly, range spans pre-harvest of 139 m (se = 13 m) were about 35% larger than post-harvest range spans (F = 9.75, df = 1,18, p = 0.006) (Figure 1b). This was in agreement with hypothesis 1. Pre-harvest home ranges were similar to the home ranges of rice-field rats during the vegetative stage of the rice crop (Brown et al. 2001). However, post-harvest home ranges were much smaller, indicating a considerable decrease in spatial activity shortly after harvesting.

Vegetation height was considerably shorter after harvest and consequently the shelter available to rice-field rats decreased. The reduction of shelter exposes small mammals to increased predation risk (Sheffield et al. 2001) and can lead to changes in spatial behaviour (Jacob and Hempel 2002). We believe the changes in home-range size found post-harvest were due to decreased vegetation height and not a result of a potential decrease in food availability. A decrease in food availability should have caused an increase in home-range size but home range size decreased. An effect of breeding on home range size seems also unlikely because breeding in rice-field rats continued for 2–3 weeks post-harvest when the study was completed. Given high activity by farmers in conducting rat control measures, 'predation by humans' could have

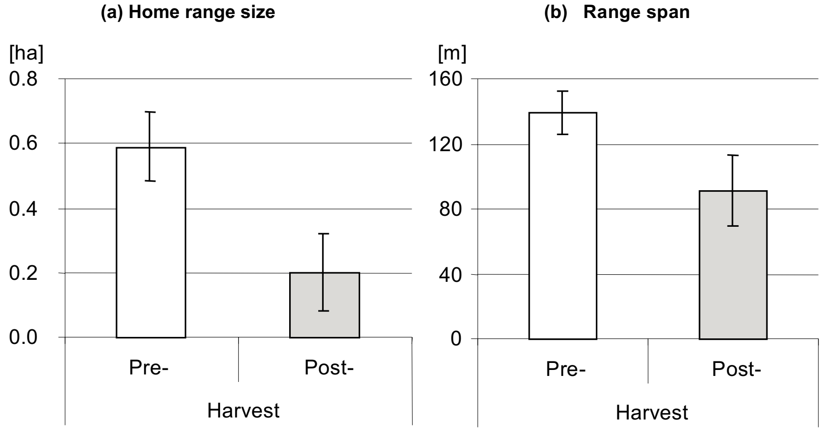

Figure 1. 95% minimum convex polygon home ranges (a) and range span (b) for female rice-field rats pre- and post-harvest. Rats were radio-tracked on three plots (13 rats pre-harvest, 7 rats post-harvest). Error bars are standard errors.

been a major factor in determining the rice-field rats' home-range size.

Centres of activity

For the seven rice-field rats we were able to track pre- and post-harvest, we found a relocation of the centres of activity by an average of 367 m (se = 130 m) during harvesting. This is a distance more than three times longer than the average range span before and after harvest (115 m). Other species of small mammals, such as common voles, do not shift home ranges when grain fields are harvested (Jacob and Hempel 2002). Harvesting of the rice continued for about one week and unharvested patches as well as piles of rice straw left on the fields provided shelter during that time. Two of the radio-tracked rice-field rats moved >700 m to reach unharvested patches of rice field. The rats left their pre-harvest home range, which resulted in a shift of their centres of activity. The pre- and post-harvest home ranges overlapped for only one rat. The concentration of the activity of the rice-field rats in unharvested patches may have led to high rat densities there. This may have resulted in smaller home ranges post-harvest because high density is correlated to small home ranges in small mammals (e.g. Erlinge et al. 1990). The aggregation of rats in unharvested areas could have led to pronounced damage in areas harvested late.

Habitat use

The mean availability of the different habitat types in the five plots were: 94% (±3%) rice field, 8% (±4%) refuge and 1% (±0.2%) village. Pre-harvest, rats tended to not prefer rice fields (Jacobs' index = –0.50, n = 7) and to prefer refuge habitats (Jacobs' index = 0.38, n = 7). There was a difference in habitat use pre- and post-harvest. Pre-harvest, 74% (±14%) of the rats did not leave the rice fields, while post-harvest, all of the rats stayed in rice fields only (F = 5.69, df = 1,23, p = 0.017). The avoidance of refuge habitats post-harvest was unexpected (hypothesis 2). The rats may have stayed in the rice fields because this habitat became suitable for nesting after the water was drained from the rice fields shortly before harvest. The piles of rice straw left on the fields post-harvest may also have provided shelter. In addition, nesting in the fields may have provided the rats with the opportunity to avoid rat control by farmers who focus fumigation and digging on refuge habitats (channel banks, dikes). The pre-harvest strategy to travel between refuge habitats and rice fields may have become more risky post-harvest because it would have resulted in moving through unharvested sections of the crop. It is possible that the rats tried to avoid exposure to predators in unharvested sections by remaining in the rice fields.

Conclusions

The behavioural response of rice-field rats to harvesting of rice may have general relevance for population trends and management of rice-field rats in rice-based agro-ecosystems. The relocation of rice-field rats from harvested to unharvested patches may lead to higher rat damage in the fields harvested last. Targeting these areas for rat management may help the owner of these fields to minimise damage there. A carry-over effect of such management to the next growing season would only occur if there were a short fallow period. This is normally not the case after a dry season crop, when the fallow period lasts for 2–3 months before the wet season crop is planted.

Our findings emphasise the importance of synchronous harvesting because removal of shelter and food within a short period of time will maximise the length of the fallow period and minimise the risk of sustaining populations of rice-field rats during the fallow period. Grazing stubble as well as the removal or burning of rice straw will minimise shelter for rice-field rats after harvest. Prey perceive tall vegetation as good protection (Tchabovsky et al. 2001) and removal of shelter leads to higher direct and indirect risk of predation. However, low vegetation post-harvest restricted spatial activity that may in turn lessen the direct impact of predation. Therefore, the success of pest rodent management relying only on the decrease of vegetation height may be compromised.

Our study showed that rats persist in rice fields until 2–3 weeks post-harvest. From a management perspective, it would be beneficial to know when the rats leave harvested rice fields and to where they move.

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Comparison of different baits to attract rats to traps in rice fields in Bangladesh

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Abstract. Rats are a chronic problem for Bangladeshi agriculture. The use of rodenticides and traps are the common tactics adopted for rat control by Bangladesh farmers. They use different kinds of bait materials for trapping rats. We tested the response of rats to four types of common baits—paddy grains, dry fish, coconut meat, and snail flesh—in both the *boro* (dry season) and *aman* (monsoon) rice-growing seasons. Tests were conducted during the reproductive phase of the rice crops on an experimental farm at Gazipur in 2001 and 2002. About 94% of the trapped rats were *Rattus rattus* and only 6% *Bandicota bengalensis*. Some predators such as gray mongoose and snakes were caught as well. In both seasons, paddy grains were the bait most preferred by rats, while snail flesh was the least preferred. Preference for dry fish and coconut meat was similar and moderate compared to paddy grains. Considering preference, cost and availability, it is recommended that paddy grains be used as bait for trapping *R. rattus*.

Introduction

Rats are serious pests of rice in Bangladesh. They damage the standing crops and also grains in stores. Rodent droppings and urine spoil stored grains and make them unfit for human consumption. Some rodents damage irrigation systems through their burrowing activity, thus causing loss of irrigation water and plant nutrients. In a recent integrated pest management (IPM) needs assessment survey, it was emphasised that rodents are important pests during pre- and post-harvest periods in areas of both low and high crop diversity. It was stressed in a national IPM workshop in November 2000 that more effort is required to develop IPM strategies for rodent pests. This is consistent with recent research elsewhere in Asia, Australia and Africa that focuses upon ecologically based rodent management strategies (Singleton et al. 1999).

In Bangladesh, control strategies for rodents have been traditionally based upon the use of poison baits (rodenticides) and traps. Zinc phosphide baits, and snap- and live-traps are most commonly used in rat control. A bait is necessary to attract rats to the trap and the preference of the rat for particular baits will influence trapping success. The preference for baits may vary between rodent species. So far, information on bait preference of different rat species is scanty. Islam and Karim (1995) reported that in a deepwater rice environment, bandicoot rats preferred snail flesh, paddy grains and dry fish rather than coconut meat and banana. Environmental conditions influence rat species composition and abundance. In the annually flooded environment, bandicoot rats are the most abundant, while in the non-flooded situations, *Rattus* sp. is more abundant. Therefore, the bait preference of rats in the non-flooded environment could be different from that of bandicoot rats in the flooded environment. In this study, we evaluated bait preference of field rats in a non-flooded rice environment of Bangladesh.

Materials and methods

Preference of four bait materials—dried coconut meat, snail flesh, dry fish, and paddy grains—were evaluated at the experimental farm of the Bangladesh Rice Research Institute in Gazipur. Tests were conducted at the reproductive phase of rice crops in the *boro* (dry) and *aman* (monsoon) seasons. Single-capture live-traps were used. Trapping was done on 68 consecutive nights in the 2001 *aman* season (19 September to 26 November) and 46 nights in the 2002 *boro* season (25 March to 10 May). Three traps were used with each type of bait. Average weight of each type of bait was 3.98, 4.64, 2.36, and 3.37 g for dried coconut meat, snail flesh, dry fish, and paddy grains, respectively. Paddy grains were wrapped in a piece of white nylon net. Traps were placed at random near active rat burrows in paddy fields. Traps were set in the field in the evening and checked the next morning. Each trapped animal was examined and identified to species.

Results and discussion

Rodent species composition

During the *aman* season, 50 (89.3%) of the 56 trapped animals were rats, four were shrews (7.1%) and two were gray mongoose (3.6%) (Table 1). Of the rats, 48 (96.0%) were *Rattus rattus* and only two (4.0%) *Bandicota bengalensis*. In the *boro* season, 18 animals were trapped of which 17 (94.4%) were rats and one (5.6%) was a snake. Similar to the *aman* season, 15 (88.2%) out of 17 rats trapped in the *boro* season were *R. rattus* and only two (11.8%) were *B. bengalensis.* In these non-flooded rice environments, *R. rattus* was the dominant rat species and *B. bengalensis* was present at low population densities. The latter is the dominant species in the annually flooded rice environments (Islam and Karim 1995; Catling and Islam 1999). Predators such as the gray mongoose and snakes were active in the non-flooded prone rice environment. There was higher rat activity (populations) in the *aman* than the *boro* season, which is consistent with farmers' perception of higher rat damage to the *aman* than to the *boro* rice crops.

Bait preference

In the *boro* season 47, 29, 18, and 6% of trapped rats were caught in traps that had paddy grains, dry fish, coconut meat, and snail flesh as bait, respectively. In the *aman* season, 44, 26, 24, and 6% of rats were caught with paddy grains, dry fish, coconut flesh, and snail flesh, respectively. Over the two seasons, 44.8%, 26.9, 22.4, and 6.0% of rats were caught in traps with paddy grains, dry fish, coconut flesh, and snail flesh, respectively. In the *aman* season, the number of rats caught in the trap with paddy grains was significantly higher ($P < 0.05$) than the number caught in traps with snail flesh (Table 2).

These findings for *R. rattus* contrast with a study of five tested baits which concluded that snail flesh was the most preferred and coconut flesh least preferred by bandicoot rats in a flood-prone environment (Islam and Karim 1995). The bandicoot rats had a moderate to high preference for paddy grains and dry fish. Considering the preference, availability and cost, this study recommended snail flesh and paddy grains for trapping bandicoot rats in flood-prone areas of Bangladesh.

Conclusion

In Bangladesh, bait preference varies among rodent species. Considering preference, cost and availability, paddy grains appear the best choice for use as bait for trapping of *R. rattus*. This bait is likely also to be effective where bandicoot rats are dominant or co-exist in high numbers with *R. rattus*.

Table 1. Rats and other animals trapped in the rice fields during the reproductive phase of the 2001 *aman* and 2002 *boro* seasons, Gazipur, Bangladesh.

Attributes	*Boro* season	*Aman* season	Total	Percentage
Trapping duration (nights)	46	68	114	
Animals trapped (total number)				
Rats – *Rattus rattus*	15	48	63	85.13
– *Bandicota bengalensis*	2	2	4	5.41
Shrews		4	4	5.41
Gray mongoose		2	2	2.70
Snakes	1		1	1.35
Total	18	56	74	100

Table 2. Bait preference of *Rattus rattus* during the reproductive phase of the *aman* 2001 and *boro* 2002 seasons, Gazipur, Bangladesh. Means followed by same letter(s) are not significantly different at the 5% level.

Type of bait	Rats trapped per trap per day (mean ± sd)	
	Aman season	*Boro* season
Coconut meat	0.05880 ± 0.04 ab	0.0217 ± 0.02
Snail flesh	0.01470 ± 0.01 b	0.0720 ± 0.01
Paddy grains	0.10780 ± 0.02 a	0.0580 ± 0.03
Dry fish	0.06370 ± 0.02 ab	0.0362 ± 0.03
Level of significance	0.05	Not significant
CV(%)	41.00	79.01

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Pest and non-pest rodents in the upland agricultural landscape of Laos: a progress report

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Abstract. Rodent communities have been monitored on a monthly basis since January 2000 in four provinces of Lao PDR using a regular trapping pattern across five habitats associated with upland agriculture. Rats have been collected sporadically from lowland habitats in two other provinces. The upland environment of Laos supports a rich array of rodent species, the great majority of which probably do little or no damage to crops. We recorded 21 different species of which 6 appear to be important pest species in crop production areas. Two forms of rats from the *Rattus rattus* complex (type A in the north and type B in the south) are the dominant rat species, and crop pest, in all six provinces. Population densities of both regional forms of *R. rattus* clearly fluctuate through the year in response to the availability of food resources, with a decline to very low resident populations and little or no breeding activity through the dry season. However, the same species also occupy the village habitat and these populations appear to be more stable and exhibit continuous breeding, presumably by feeding on high-quality stored grain as well as general refuse and household garden produce. Upland villages thus may represent a critical ‘source’ habitat for *R. rattus*, with migration into the fields once the cropping cycle is under way. Less certainly, the forest may also act as a refuge habitat through the dry season and a source of emigrants to the fields. Alternatively, the forest may be a ‘sink’ that absorbs individuals at the end of the cropping cycle but witnesses little, if any, subsequent breeding. These baseline studies provide a solid foundation for identifying key issues for developing ecologically based management of rodent pests and for conserving some non-pest rodent species that are classified by International Union for Nature and Natural Resources (IUCN) as ‘vulnerable’.

Introduction

Schiller et al. (1999) made a strong case for more research activity on rodent pests and potential management strategies in the Lao PDR (Laos), especially for the rainfed upland ecosystem which still plays a predominant role in meeting the food requirements of many ethnic groups. In the 2000 production year, this ecosystem accounted for 21% of the total area under rice cultivation in Laos; and it returned approximately 12% of the total rice harvest (Lao PDR Ministry of Agriculture and Forestry records). Most upland rice cultivation in Laos is still based on traditional ‘slash and burn’ methods of shifting cultivation. However, the productivity of this ecosystem is generally in decline due to myriad problems associated with weeds, insects and rodent pests, and soil erosion and degradation (Schiller et al. 1999; Roder 2001).

Rodent damage is cited by farmers as being second only to weeds as a cause of poor rice yields in the uplands (Schiller et al. 1999). Rodents are a chronic problem in most areas, although the severity of the damage varies from year to year and between localities. In addition, episodic but irregular rodent irruptions are sometimes responsible for extreme crop losses, occasionally leading to widespread famine (Singleton and Petch 1994; Schiller et al. 1999). These events are attributed locally to *nuu khii* (literally, rat of bamboo flower) and they are distinguished from the problem of chronic crop damage.

The research activities reported here commenced in 1998 and followed on from an earlier process of problem definition (Singleton and Petch 1994). Here, we provide a brief overview of progress made in respect to three main issues: (i) identification of the rodent species present in the various production environments and assessment of their pest or non-pest status; (ii) patterns of habitat use by the various rodent species in the upland system; and (iii) the breeding biology of the main rodent pest species. A companion paper by Douangboupha et al. (this volume) examines the historical pattern of *nuu khii* outbreaks across four provinces and speculates on possible causes.

Materials and methods

Research activities have concentrated on upland habitats in four provinces: Luang Prabang, Oudomxay and Houaphanh in the northern agricultural region and Sekong in the southern agricultural region. Some preliminary fieldwork was conducted also in lowland rice production areas in Sayabouly province, in the west of the country, and in Vientiane Municipality. Annual rainfall is highest in Sekong (>2000 mm) and lowest in parts of Luang Prabang and Sayabouly (<1440 mm; Sisophanthong and Taillard 2000). Houaphanh is generally at higher elevation than the other provinces and is significantly cooler in the winter months. Summer temperatures in Sekong are several degrees higher than in the more northerly provinces. The intensity of upland shifting cultivation is highest in Luang Prabang and Oudomxay (Sisophanthong and Taillard 2000).

In each of the four main study areas, rats were trapped on a regular basis starting in January 2000. Each month, traps were set for four consecutive nights in each of five habitats: upland rice field, upland maize or mixed cropping field, lowland rice field, forest, and village (around rice stores). Essentially, three kinds of traps were used: (i) a trap–barrier system (TBS) using multiple-capture traps, set with a linear barrier system in the upland crop/maize habitat and as an enclosed square around a village rice store; (ii) single-capture live cage-traps, set in the lowland rice crop and forest; and (iii) kill-traps of various kinds (large and small snap-traps, and traditional snares) set in all habitats except the village. Additional sampling was carried out in each province at variable intervals to investigate the breeding activity in the common pest species—for this purpose, rats were trapped, dug from burrows and hunted within the same general habitat types.

Rats were identified to species with reference to a taxonomic key developed by K. Aplin for Lao rodents (translated into Lao by B. Douangboupha), measured, weighed and dissected to assess reproductive status. Representative specimens, including whole bodies, skins or heads, were preserved in 70% ethanol. These are lodged in the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Australian National Wildlife Collection (ANWC), Canberra.

Results and discussion

Identity of the major agricultural pest species of Laos

Francis (1999) lists a total of 28 murid species and 3 rhizomyids (bamboo rats) for Laos as a whole, with a further 6 murid species expected on broader distributional grounds. We recorded a total of 20 species from our combined field areas, either from direct trapping or through purchase from villagers or markets (Table 1).

Ten species are classified in Table 1 as definite or probable agricultural pests in Laos. These include five species of *Rattus*, three of *Mus* and two of *Bandicota*.

Rattus rattus is by far the most abundant pest species in the upland ecosystem of Laos. There are two genetically distinct forms of *R. rattus* in Laos (see Aplin, Chesser and ten Have, this volume). Both forms were captured within their respective geographical areas in all habitat types, including villages, upland and valley floor cropping areas, and the forest margin. No other species of *Rattus* were caught other than in Houaphanh. Most importantly, we did not find any evidence either of the rice-field rat, *R. argentiventer*, or the lesser rice-field rat, *R. losea*. Both of these species are recorded from lowland areas of Laos—the former in Khammouane province in Central Laos (Francis 1999) and the latter from several localities in central and southern Laos (Musser and Newcomb 1985; Francis 1999). Neither species was found in suitable habitat in a broad lowland valley in Sayabouly province. Here, and on the Vientiane Plain, lowland rice fields harbour populations of *R. rattus*. Further geographical sampling is needed to map the current range of *R. argentiventer* and *R. losea* in Laos. This will provide a valuable baseline against which to chart any future range expansion by these potentially significant pest species.

Table 1. List of the murid and rhizomyid rodents of Laos, divided into four categories according to probable pest and conservation status. Species in **bold type** have been confirmed from our trapping and other collections. Species marked with an asterisk (*) are only provisionally recorded from Laos. The two taxa listed as ‘sp.’ in the right-hand column were mentioned as possible new species by Francis (1999).

Definite or probable pests	Possible pests	Non-pests but common	Non-pests and rare?
Murinae	Murinae	Murinae	Murinae
Bandicota indica	***Rattus nitidus***	***Berylmys bowersi***	***Berylmys berdmorei***
*B. savilei**	***Leopoldamys edwardsi***	*Chiropodomys gliroides*	*Be. mackenziei**
Mus caroli	***L. sabanus***	***Maxomys surifer***	***Chiromyscus chiropus***
M. cervicolor	*Mus cookii*	***Mus pahari***	*Dacnomys millardi*
M. musculus	*M. shortridgei*	*Niviventer confuscianus**	*Hapalomys delacouri**
*Rattus argentiventer**		***N. fulvescens***	*Maxomys moi*
R. exulans		***N. langbianis***	*Maxomys* sp.
R. losea		*Vandeleuria oleracea*	*Niviventer* sp. cf. *N. tenaster*
R. rattus **type A**		Rhizomyidae	***Rattus sikkimensis***
R. rattus **type B**		***Cannomys badius***	Arvicolinae
		Rhizomys pruinosus	*Eothenomys melanogaster**
		Rh. sumatrensis	*E. miletus**
			Placanthomyinae
			*Typhlomys cinereus**

The Pacific rat, *R. exulans*, has been collected in several localities on the Vientiane Plain, but not so far in any of the upland sites. This is somewhat perplexing, as *R. exulans* elsewhere extends to high elevations and is perfectly at home in village and garden habitats. In parts of the Pacific region where *R. exulans* and *R. rattus* coexist, it is generally the latter that occupies the houses (Marshall 1977)—it is possible that *R. exulans* is excluded from upland villages in Laos by the presence of the larger *R. rattus*.

Two *Bandicota* species are listed as potential pest species in Table 1. *Bandicota indica* has been trapped on a regular basis only in Luang Prabang and Sekong but it is nowhere abundant in the uplands. The smaller *B. savilei* is recorded only from specimens photographed by one of us (BD) in Savannaket province in central Laos. Musser and Brothers (1994) record this species from near the Mekong River in Ubon Ratchathani province of Thailand, immediately west of Champassak in southern Laos. Although *Bandicota* species are generally regarded as agricultural pests, it is not proven that they cause much damage to crops in Southeast Asia (Aplin, Chesser and ten Have, this volume).

Mus species were generally collected in small numbers and mainly by the TBS method. In Sayabouly province, *Mus caroli* was taken from burrows dug into narrow bunds in lowland rice fields—farmers claimed that their main activity in the fields is to clean up any cut tillers and panicles left behind by *R. rattus*.

All of the pest species mentioned so far probably contribute to the chronic annual damage that occurs throughout the uplands to varying intensity. Major outbreak events, attributed by many Laotian farmers to *nuu khii*, may in some cases involve extreme population increases or unusual movements of this same suite of species (Douangboupha et al., this volume). However, there are indications that some of these events might involve dramatic increases of different forest-dwelling species, possibly driven by the mass flowering and seeding of bamboos across large areas with subsequent outpouring into the agricultural landscape. To date, this process has not been well documented, despite reports of similar phenomena across large parts of South and Southeast Asia (see Chauhan, this volume).

Five other species are classified as possible agricultural pests in Laos, either because they were caught on a regular basis within cropping areas (*Leopoldamys* spp. in Sekong) or because they are known to damage crops in surrounding countries (*Rattus nitidus*, *Mus* spp.). *R. nitidus* was caught together with *R. rattus* type A and *R. sikkimensis* in forest margin habitat in Houaphanh. This species is an important agricultural pest in parts of southern China, but in Southeast Asia it is more often associated with upland village habitats (Aplin, Chesser and ten Have, this volume). In Houaphanh, *R. rattus* type B is the common village rat.

Bamboo rats are most often found in proximity to bamboo groves where they probably feed mainly on the rhizomes and young shoots. However, Marshall (1977, p. 392) reported some damage caused by these animals to cultivated tapioca and sugarcane. In the uplands of Laos, bamboo rat burrows, both active and abandoned, are frequently found in and around active fields. However, according to farmers in Luang Prabang province, the burrows are originally constructed under cover of forest or regrowth, but come to be located in garden areas when wooded areas are subsequently cleared for cultivation.

Some non-pest species were occasionally caught in traps set in upland fields (e.g. *Maxomys surifer* in Oudomxay, *Niviventer* spp. in Houaphanh). These captures may reflect low-level crop damage by these species, however they might equally reflect foraging in the fields for insects or other prey items. Twelve of the non-pest species are themselves considered to be rare in Laos and three of these are rated ‘vulnerable’ in the International Union for Nature and Natural Resources (IUCN) Red List. However, there does not seem to be any particular reason to believe that these taxa are under any special threat in Laos.

Habitat use and activity cycles

The trapping data from each of the four provinces present a similar picture—in all cases, trends in rat abundance are clearly linked to major events and phases of the cropping calendar. The pattern for Houay Khieu, Lamam district, in Sekong is shown in Figure 1. The period September–November 2000 saw the relatively late ripening and harvest for both upland and lowland crops, perhaps reflecting the late onset of the wet season in 2000. Rat numbers in all cropping areas fell in December, as harvest was completed, but increased around the village store as this was replenished. Rat numbers in the forest/bamboo habitat also declined through this period.

January and February 2001 saw a break in trapping effort at Houay Khieu and also represents the peak of the dry season. Maize and other upland crops were planted in March in response to early rains—rat numbers in this habitat and in the forest/bamboo were high at that time and remained so through to the harvest of upland crops and maize in August. A temporary surge in forest/bamboo rat numbers in June appears to be mirrored by a similar increase in rat captures in other habitats. Rat numbers were high in upland and lowland rice crops through June to September but showed a marked decline after harvest (September for upland rice; October–November for lowland rice). Capture rate around the village grain store increased sharply after harvest of all crops was complete, suggesting a process of immigration of rats from field to village.

The role of the forest ecosystem in these population cycles is unclear at present. At Lamam during 2000–2001 most of the forest captures were of *R. rattus*, with smaller numbers of *Leopoldamys* spp. and other species. Fluctuations in rat numbers in the forest appear to be linked to capture rates in the cropping areas, yet there is no obvious lag and thus no clear indication as to whether the forest is acting as a 'source' or a 'sink' habitat. One point favouring identification of forest as a source habitat is the decline in forest captures after harvest—a sink habitat would presumably be receiving immigrants at this time, as indeed the village appears to be doing.

Rat numbers in the forest habitat may start to increase immediately upon the arrival of the wet season. As food resources and ground cover start to develop in the upland fields over the followed weeks and months, rats may undergo some migration into the fields, perhaps coming both from the forest and from the village where their numbers have been maintained over the dry season by stored food and general refuse.

Breeding biology of *Rattus 'rattus'*

Although breeding data for *R. rattus* are available from five different months and from all four provinces, the coverage remains incomplete (Table 2). Nevertheless, there are enough data to suggest year-round breeding,

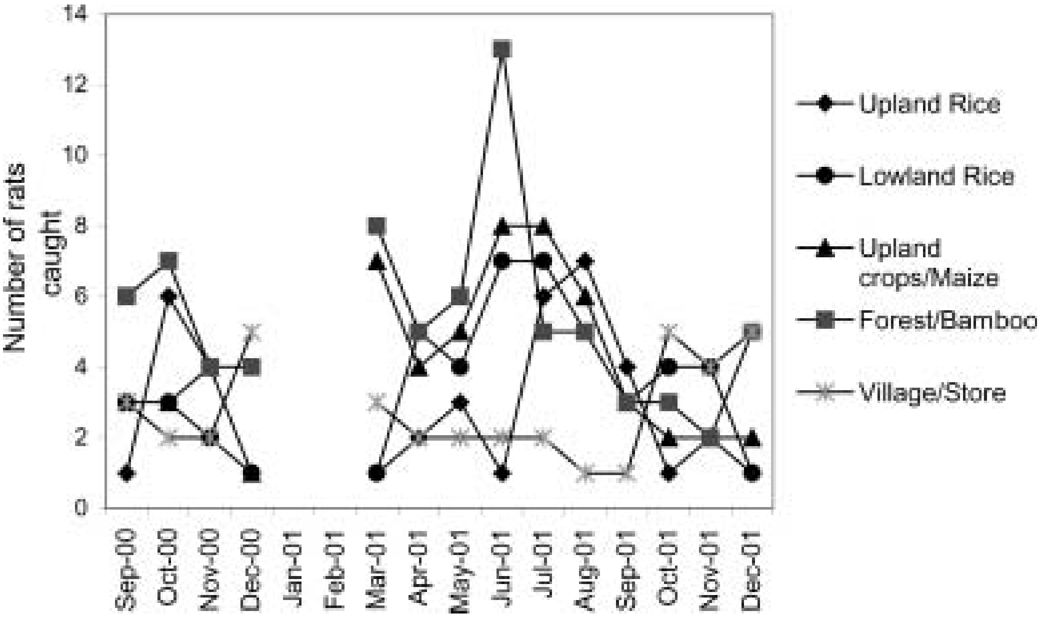

Figure 1. Monthly rat captures in five habitats at Houay Khieu in Lamam district, Sekong. Each trapping period represents 312 trap-nights, with 48 trap-nights in upland rice, 88 in lowland rice, 68 in upland crop/maize, 88 in forest/bamboo, and 20 around the village store. The village stores traps and 20 of those in the upland crop/maize were multiple-capture traps in linear trap–barrier systems; the remaining traps include a standard mixture of single-capture cage-traps, snap-traps and traditional snares. Upland crops and maize were harvested in August 2001; upland rice in September 2001; and lowland rice in October/November 2001.

Table 2. Monthly breeding data for *Rattus rattus* types A and B from intensive sampling across four provinces (*R. rattus* A from HP = Houaphanh, LP = Luang Prabang, OD = Oudomxay; *R. rattus* B from SK = Sekong). Samples were obtained by trapping, hunting and digging of burrows across a variety of cropping habitats. Total % breeding includes females that have embryos and/or placental scars. No sampling in October 2001 and in January and February 2002.

Month	Province	Number of adults	% pregnant	% with placental scars only	Total % breeding
Aug 2001	LP	6	66.7	16.7	66.7
Aug 2001	OD	39	59.0	30.8	89.7
Aug 2001	HP	13	46.2	38.5	84.6
Sep 2001	SK	98	39.8	54.1	93.9
Sep 2001	HP	4	75.0	25.0	100.0
Nov 2001	HP	12	0.0	83.3	83.3
Dec 2001	HP	13	0.0	84.6	84.6
Mar 2002	LP	27	55.6	25.9	81.5
Mar 2002	OD	27	48.1	51.9	100.0
Mar 2002	HP	42	54.8	23.8	78.6

except perhaps for a lull during the dry season (November to January?). This requires confirmation. Breeding in *R. rattus* was well and truly under way in at least three provinces by March 2002, with a high proportion of females already showing uterine placental scars from recent litters. The number of embryos ranged up to a maximum of 10 in the three populations of *R. rattus* type A, and to 14 in the Sekong population (*R. rattus* type B).

Year-round breeding of *R. rattus* has been reported elsewhere in Asia including Jodphur in the Indian arid zone (Advani and Rana 1982) and in a monsoonal environment in Mizoram, eastern India (Chauhan and Saxena 1992). However, previous studies of reproduction in members of this group have reported much lower pregnancy rates, typically no more than 20–30% of adult females. It is possible that the removal of animals from breeding burrows during this study has resulted in an over-representation of pregnant females. However, breeding data from the regular trapping (unpublished data) also point to very high reproductive rates in Lao *R. rattus*. Moreover, comparably high pregnancy rates are reported for other *Rattus* species in tropical agricultural contexts (Brown et al. 1999). The regular trapping data also show that breeding of *R. rattus* continues through the dry season within the village habitat, presumably reflecting the continued availability of high-quality food.

Conclusion

Much has been learned over the last few years regarding the rodent communities and general rodent ecology in the upland agricultural environment of Laos. We now know that the dominant pest species across most of Laos are two distinct, but closely related, members of the *R. rattus* complex, one found in the northern provinces and the other found in the south. Rather surprisingly, these species are dominant also in some lowland cropping systems, such as Sayabouly, where lowland rice is grown across a broad valley floor, and on the Vientiane Plain.

The emerging models of upland rodent ecology have important implications for rodent management in Laos. If the upland villages represent the major source habitat for the *R. rattus* population that attacks the crops, then a vigorous rodent control campaign in the villages just before the onset of the wet season might serve to reduce subsequent crop damage in the fields. This could be conducted without fear of non-target impact on native rodents, none of which seem to use the village habitat or its immediate surrounds. These targeted campaigns could replace the general bounties, which provide money for any rat species collected, that have been implemented in recent years (Singleton and Petch 1994).

On the other hand, if the field population of *R. rattus* is derived in part or whole from the forest habitat, proactive rodent control might be very difficult without harming native species. One solution may be to apply a trap–barrier system plus trap crop (TBS+TC) method of the kind that has been successful in controlling rodent damage in lowland irrigated rice systems (Singleton et al. 1999). However, there are significant technical challenges to be overcome before this system can be applied in the upland cropping environment, including:

- selection of an appropriate lure crop or range of crops;
- redesign of the barrier to operate without a moat and with a pest species that is a proficient climber; and
- consideration of optimal placement relative to the diverse habitat types in the upland cropping environment.

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Rodent communities and historical trends in rodent damage in the Mekong Delta of Vietnam: establishing an ecological basis for effective pest management

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Abstract. The Mekong Delta region of Vietnam features a variety of natural and agricultural landscapes that differ in flooding and cropping regimes, and in the nature of the associated pest rodent communities. Areas with regular, extensive floodwater inundation tend to show a predominance of *Rattus argentiventer* over other species. In contrast, areas that experience localised flooding support a broader range of species with less obvious dominance within the community. However, cropping regime is also important, and areas where two or three rice crops are grown each year also tend to show a dominance of *R. argentiventer* over other species. Historical records spanning the last decade show a general increase in rodent damage to crops, especially in those provinces that have seen a recent increase in cropping area or frequency. However, flood-prone provinces in the centre of the delta proper share a more complex history of rat damage that appears to correlate with inter-annual variations in river outflow associated with the El Niño cycle. Our improved understanding of the ecology and history of rodent problems in the Mekong Delta region allows us to frame a number of specific hypotheses that can be tested through studies of spatial and temporal patterning, and through manipulative experiments. Insights gained in this way will provide the necessary ecological foundation for sustainable, non-chemical rodent control under the variable conditions offered by the Mekong Delta.

Introduction

Several recent and ongoing projects in Southeast Asia are assessing the applicability of the community trap–barrier system (CTBS) as a potential method for chemical-free rodent control in the lowland rice cropping environment (Brown, Tuan et al., this volume; Russell et al., this volume; Sudarmaji, Rochman et al., this volume). The TBS approach, first developed by Lam in Malaysia for the control of the rice-field rat, *Rattus argentiventer*, was subsequently trialled and found to be effective in controlling the same species in irrigated rice crops in Indonesia (Singleton et al. 1999). However, extension to other countries within Southeast Asia requires a process of continuous assessment and adaptation of the technology. To be effective on a broad scale, it must be applicable across a range of subtly different ecosystems that differ, not only with respect to cropping systems, natural hydrology and water management systems, but which also host contrasting suites of rodent species. In addition, there is a growing awareness of the importance of social and cultural factors in determining the likely success of the CTBS approach (King et al., this volume; Morin et al., this volume; Sang et al., this volume).

Here we report on aspects of rodent community structure and community ecology in the Mekong Delta region of southern Vietnam. We also present new data on historical trends in rodent damage across the 21 provinces that make up the Delta region. These data were collected during a project funded under the Australian Agency for International Aid (AusAID) Capacity-building for Agriculture and Rural Development (CARD) scheme. Other elements of this multidisciplinary project are reported by Morin et al. (this volume), Palis et al. (this volume), and Le Quoc Cuong et al. (this volume), while Nguyen Tri Khiem et al. (this volume) describe the results of an associated study of the live-rat trade in the southern Mekong Delta. The results presented here provide a biological foundation for these other studies, and also, a platform for the formulation of a new set of hypotheses regarding the likely applicability of the CTBS approach in differing areas of the Mekong Delta.

Study area and methods

The Mekong Delta

The Mekong Delta region of southern Vietnam covers 39,500 km^2 or 12% of the total country area and is home for just over 15 million people (22% of total population). Much of the delta area was cleared of forest cover only quite recently, with a major increase in rice cropping area occurring between 1994 and 1996. This process continues with removal of mangroves and *Melaleuca* forest, especially due to the increasing human population and the expansion of shrimp aquaculture in the southern provinces.

Annual rainfall across the delta region is 2000–2500 mm, with most rainfall in the wet season (April to November). Regular flooding occurs during October and November, driven by monsoonal rains in more northerly parts of the Mekong River Basin. The likelihood and depth of inundation varies markedly across the Delta (Figure 1) and this has important implications for rodent ecology. Provinces located to the east of Ho Chi Minh City technically lie outside of the Mekong River Basin and are under the influence of local rainfall patterns; these include Ho Chi Minh City province itself and Tay Ninh, Binh Duong, Binh Phuoc, Dong Nai, Ba Ria Vung Tau and Binh Thuan. The main project activities have been conducted in Tien Giang and Soc Trang provinces, however associated projects have allowed information to be gathered in Ho Chi Minh City province, and in Bac Lieu and Binh Thuan provinces.

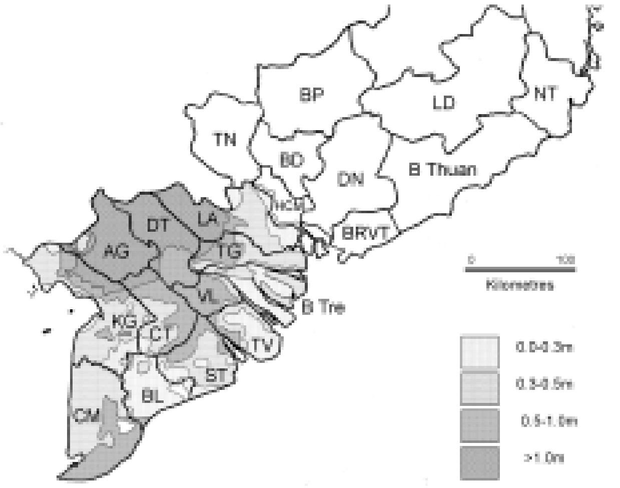

Figure 1. The Mekong Delta region of Vietnam showing the provinces and the approximate depth of seasonal inundation (based on Figure 4 in Hirsch and Cheong 1996). The provinces are abbreviated as: AG, An Giang; BD, Binh Duong; BL, Bac Lieu; BP, Binh Phuoc; BRVT, Ba Ria Vung Tau; B Thuan, Binh Thuan; B Tre, Ben Tre; CM, Ca Mau; CT, Can Tho; DN, Dong Nai; DT, Dong Thap; HCM, Ho Chi Minh City; KG, Kien Giang; LA, Long An; LD, Lam Dong; NT, Ninh Thuan; ST, Soc Trang; TG, Tien Giang; TV, Tra Vinh; VL, Vinh Long.

Cropping systems

In many parts of the Mekong Delta, rice production is supported by a dense network of irrigation canals. Where irrigation water can be accessed year-round, many farmers produce three crops each year. However, planting and harvesting times may be asynchronous, with adjacent fields differing in growth stage by several weeks or more. Two crops are usually grown in areas that lack access to irrigation water. Depending on the flooding regime, these are grown either as a floodwater recession crop in the dry season (December to March) followed by a rainfed early wet season crop (late March to early July) and then an extended period of inundation; or as two successive wet season crops (April to July; August to October), with an extended fallow period through the dry season. In most areas, short-maturing (90 day) rice varieties are now predominant, although traditional varieties (usually 120+ days) are sometimes also grown.

The rice cropping system in many regions is interspersed with villages and numerous small 'upland' areas where farmers grow fruit trees, vegetables and sugarcane. This heterogeneity is most prominent in areas that experience limited or no flooding, and in areas that are strictly rainfed.

Historical information

Information on rodent damage was obtained from records compiled over the last decade by staff of the Southern Regional Plant Protection Centre (SRPPC) in Tien Giang. During the cropping season, rodent damage is reported every 14 days by provincial officers of the sub-Plant Protection Department (sub-PPD). These data represent a summary of information provided by individual villages within each province. The sub-PPD officers estimate the total number of hectares that have experienced 'significant' rodent damage during the reporting period. These data show a clear geographical pattern suggesting limited observer bias. Data on the total number of hectares under rice cultivation also were compiled. A rat damage index (RDI) was developed as follows: for each province the mean number of hectares showing damage was calculated, and values for each year were scored as a ratio to that mean value. RDI values range from below 0.1 to slightly more than 3 (a score of 1 would indicate average damage for that province). Two provinces were subdivided during the 1990s: Minh Hai was divided to form Bac Lieu and Ca Mau; and Song Be to form Binh Phuoc and Binh Duong. We pooled the data from the subdivided provinces for consistency across the time period.

Information on rodent species and communities

The previous studies by Sang (1998) and Brown et al. (1999) relied principally on field identifications and the taxonomy of van Peenen et al. (1969) and Cao Van Sung (1984). Because there are known taxonomic problems in several groups of Southeast Asian rodents, we collected large series of voucher specimens with associated tissue samples appropriate for DNA analysis (to be reported elsewhere).

Rodent specimens were obtained from three provinces within the Mekong Delta proper (Tien Giang, Soc Trang and Bac Lieu) and from Ho Chi Minh City and Bin Thuan provinces to the east. They were captured by a variety of methods, including individual cage-traps, multiple-capture traps set within CTBS units, and by digging burrows. Some specimens were purchased from people involved in the live rat-meat trade. The voucher specimens are lodged in the Australian National Wildlife Collection (ANWC), the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Canberra, and at the Institute of Agricultural Science, Ho Chi Minh City. In Tien Giang province, systematic sampling using cage-traps was carried out over several periods during March–July 2002 at three sites (two at Cay Lay village; one at Cay Be).

Results and discussion

Historical and geographical patterns of rodent damage

The total area under rice cultivation within the study area has increased by more than a million hectares since 1990 and now stands at just over 4×10^6 ha (Figure 2). Across the entire region, the area of crops damaged by rats was very low during the early 1990s, with a dramatic increase since 1993 (Figure 2). In part, this reflects a lack of data from some provinces from the early period. However, the same trend is observed in individual provinces, with a ten-fold or higher increase in reported damage across four of the six provinces with data from 1991–93. An interesting trend is the apparent decrease in rodent damage in 1995 compared with the preceding and following years. This is consistent with data presented by Brown et al. (1999) for the Mekong Delta and for the whole of Vietnam. Also of interest are the very high values for 1998–99 and the reduction in 2000.

In the majority of provinces, including all of those in the western part of the Mekong Delta, the area of reported rodent damage has increased steadily through the 1990s (Figure 3a). This increase appears to have begun somewhat earlier in some areas than in others, e.g. An Giang and Kien Giang show a steady increase since the early 1990s, while Bac Lieu in the south shows a dramatic increase in the area damaged since 1997. These differences reflect the spatial pattern of land reclamation for intensive rice growing in the Mekong Delta, most notably the progressive blocking of saline intrusion that has allowed intensive rice production across large areas of Soc Trang and the Bac Lieu area of former Minh Hai province.

Three provinces in the core of the delta (Long An, Dong Thap and Tien Giang) show a very different historical pattern, with a major peak in rodent damage in 1993–94 and another in 1998–99 (Figure 3b). These provinces have a longer history of intensive rice cropping, and they also experience heavy seasonal inundation (Figure 1). The period of reduced rat damage in 1995–97 corresponds with three successive years of heavy rainfall in the Mekong River Basin and widespread flooding, which was terminated by the widespread droughts and reduced Mekong outflows associated with the 1997–98 El Niño (McPhaden 1999). Song Be province to the east of the Mekong Delta shows a similar but lower two-peaked pattern of rat damage (Figure 3b).

A third major pattern, featuring a strong peak in rat damage during the El Niño years, is observed in three provinces to the east of the Mekong Delta proper (Figure 3c). These provinces share considerable areas of elevated ground where rainfed rice systems predominate.

Two provinces do not seem to fit into any of these general patterns. Tay Ninh, situated in the hinterland of Ho Chi Minh City province had consistently high reports damage other than for one low point in 1999. Ben Tre, at the mouth of the delta, reported small areas of rat damage with a peak in 1999.

The substantial and systematic variations in rodent damage appear to reflect the contrasting landscape ecology of different parts of the Mekong Delta and adjacent region. In part, these contrasts relate to the differing hydrological conditions that exist between the inland, inundated, region of the delta compared with the slightly more elevated and better draining coastal and eastern zones.

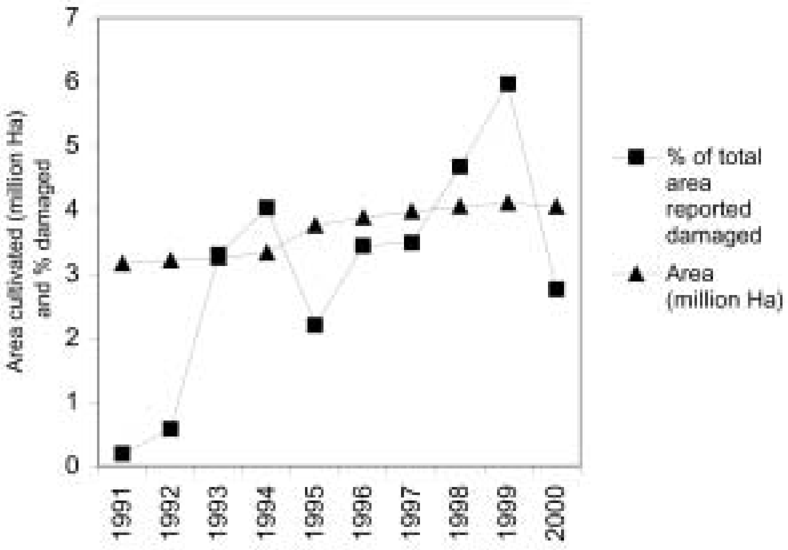

Figure 2. Recent historical trends in the area of cultivated rice in the Mekong delta region of Vietnam and in the proportion of total area reported as damaged by rats.

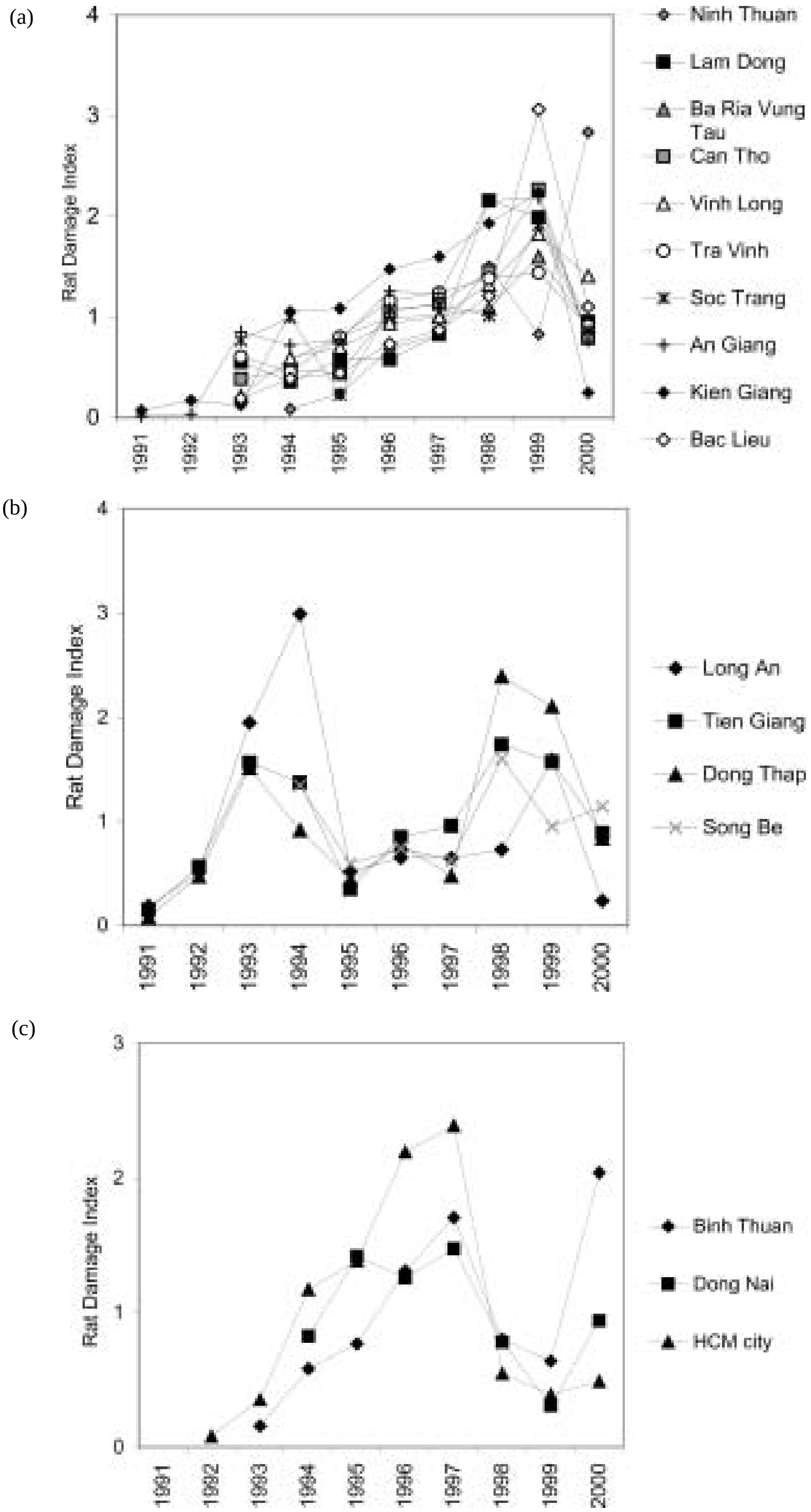

Figure 3. Recent historical trends in rodent damage in various geographic subregions of the Mekong Delta area, as indicated by the rat damage index (see Methods): (a) trends in ten predominantly western and southern provinces of the Mekong Delta proper; (b) trends in three inland provinces of the Mekong Delta proper and one to the east (Song Be); and (c) trends in three provinces to the immediate east of the Mekong Delta.

The contrasting histories of rodent damage also appear to reflect differences in cropping history between the provinces. Areas of the delta that have been cleared and drained for rice production over the last decade typically show a marked increase in the extent of rodent damage, as do areas that have converted from an annual wet-season crop to a more intensive pattern of two or three consecutive crops as a result of improved control of saline intrusion or simply improved access to irrigation water. In contrast, areas of the delta that have supported dense human populations for longer periods typically do not show any simple increase in rodent damage through the last decade, but rather, more complex patterns such as the possible link to flooding intensity.

Rodent species and communities of the lower Mekong Delta

All available information on rodent community structure in the Mekong Delta and areas to the immediate east is summarised in Tables 1 and 2. As reported previously by Brown et al. (1999), *R. argentiventer* is the dominant species in most parts of the Mekong Delta proper. A random sample of rats purchased from a rat-meat 'factory' in Soc Trang consisted of >95% *R. argentiventer*, while in Bac Lieu, the dominance of this species was probably even greater (the higher percentage of *B. indica* in our voucher sample is due to deliberate selectivity to sample for zoonoses; Singleton, Smythe et al., this volume).

Our studies indicate a lower regional diversity than reported previously by Brown et al. (1999), with eight species confirmed and one or two others potentially present. Previous records of *Rattus koratensis*, *R. germaini*, *R. rattus*, *R. flavipectus* and *R. nitidus* are here treated as reflecting phenotypic variation within one or more members of the *Rattus rattus* complex. As discussed by Aplin, Chesser and ten Have (this volume), the Mekong Delta supports what appears to be an endemic Southeast Asian species of this group and it may also host populations of the introduced 'Oceanian' black rat. *R. germaini* and *R. flavipectus* are synonyms of *R. rattus* in the broad sense (Musser and Carleton 1993). *R. nitidus* and *R. koratensis* (more properly known as *R. sikkimensis*) are valid species of *Rattus* (Musser and Carleton 1993) but neither was encountered during our studies, nor were they mapped for this region by Lunde and Son (2001). Records of *B. bengalensis* reported by Brown et al. (1999) probably represent a mix of *B. savilei* and some immature *B. indica*. We have encountered *B. savilei* only in Ho Chi Minh City and Binh Thuan provinces and are confident that the species is either rare or absent from the greater part of the delta proper. True *B. bengalensis* is found on the Indian subcontinent, east to central Myanmar (Aplin, Frost et al., this volume).

R. losea was more abundant than *R. argentiventer* in two provinces: Kien Giang in the far west and Ho Chi Minh City (Cu Chi district) in the east. This species is moderately abundant in Tien Giang province, especially at Cay Be village. As noted by Sang (1998) for Kien Giang, these sites share significant areas of upland that do not become inundated during normal flooding events. *R. losea* is rare in Soc Trang and Bac Lieu, and appears to be absent from Binh Thuan. The species is present in the coastal lowlands of central Vietnam and is abundant in the Red River Delta of northern Vietnam (Brown, Tuan et al., this volume). The northern and southern populations are morphologically and genetically distinct and may represent subspecies or sibling species (K. Aplin, T. Chesser and J. ten Have, unpublished).

The other *Rattus* species (*R. exulans*, *R. norvegicus* and members of the *R. rattus* complex) are nowhere particularly abundant, except perhaps *R. rattus* in Ben Tre (Table 1). However, higher abundance for this species reported by Brown et al. (1999) may reflect some confusion between this species and either *R. argentiventer* or *R. losea*. *R. norvegicus* was encountered rarely but in a variety of contexts, from small towns to rice fields at considerable distance from any town or buildings.

Bandicota species generally accounted for less than 5% of captures in areas sampled by Brown et al. (1999) and Sang (1998). From examination of the live rat-meat samples, we estimate that they are even less abundant in Soc Trang and Bac Lieu. All specimens examined to date from within the Mekong Delta proper have been referable to *B. indica*, the larger of the two species found in Vietnam.

Table 1. Relative abundance (%) of various rodent species across nine provinces in the Mekong Delta, based on live-trapping as described by Brown et al. (1999). *Rattus* species are regrouped as described in Methods.

Species	Kien Giang	Minh Hai	An Giang	Can Tho	Dong Thap	Vinh Long	Long An	Tien Giang	Ben Tre
Bandicota spp.	2.8	1.4	2.2	5.2	4.0	0.4	6.7	4.6	3.0
R. argentiventer	28.4	57.3	68.6	67.8	69.7	75.4	63.4	72.0	50.2
R. exulans	1.8	0.3	2.4	1.3	0.7	0.8	2.5	3.3	1.8
R. losea	45.9	18.7	12.8	10.5	11.0	8.9	8.9	5.3	9.8
R. norvegicus	3.4	3.8	1.2	1.5	2.3	1.2	1.3	2.7	2.5
R. rattus complex	11.9	17.5	11.2	13.6	12.3	13.3	17.2	10.5	30.9
Mus spp.	5.9	1.0	1.6	0	0	0	0	1.5	1.7

Table 2. Relative abundance (%) of various rodent species obtained through live-trapping (*) and opportunistically across six provinces, as described in Methods. Data for Kien Giang province (Hatien district) are from Sang (1998).

Species	Kien Giang*	Tien Giang* (Cay Lay)	Tien Giang* (Cay Be)	Tien Giang	Soc Trang	Bac Lieu	Ho Chi Minh City	Binh Thuan
Bandicota indica	3.5	1.1	11.3	0	1.2	17.7	7.7	41.4
B. savilei	0	0	0	0	0	0	2.6	37.0
Rattus argentiventer	37.6	75.5	51.6	79.5	95.2	77.2	23.1	19.1
R. exulans	2.8	0	0.8	1.3	0	0	2.6	0.6
R. losea	45.3	18.2	33.1	3.8	2.4	1.3	51.3	0
R. norvegicus	0.5	2.2	2.4	7.7	1.2	1.3	0	1.9
R. rattus complex	8.7	3.1	0.8	7.7	0	2.5	2.6	0
Mus caroli	–	0	0	0	0	0	10.3	0
Mus sp.	1.0	–	–	–	–	–	–	–
No. in sample	966	79	124	78	83	79	39	162

In Tien Giang, this species made up 11.3% of captures at Cai Be, but only 1.1% at Cai Lay, sampled at the same times of year. Further east, in Ho Chi Minh City province (Cu Chi district) and in Binh Thuan, both *Bandicota* species were collected in approximately equal numbers. Aplin, Frost et al. (this volume) give details of the distribution and breeding activity for both species. As with *R. losea*, the strong impression is that both *Bandicota* species favour areas where there is considerable local relief; presumably for *Bandicota* spp. this relates to the size of their burrow systems.

Mus species are poorly represented in all of the collecting undertaken so far. However, farmers do not seem to regard them as a major pest and they may be genuinely uncommon in most areas. Specimens of *Mus caroli* were dug from burrows in Cu Chi district.

These observations suggest that landscapes characterised by regular, deep inundation favour populations of the rice-field rat, *R. argentiventer*, over other rodent species. Even so, there are indications that populations of this species also decline annually and sharply over the period of inundation (Brown et al. 1999). Data presented here on rodent damage through the period 1991–2000 suggest that extreme flooding events, such as occurred over several years in the mid-1990s, may lead to a reduction of crop damage during the subsequent dry season. This might be due to flooding of elevated areas that normally function as refugia for *R. argentiventer.*

Conclusion

The general ecological and historical observations made here enable us to frame a number of specific hypotheses that now need to be tested through more detailed studies of spatial and temporal patterning in rodent communities, rodent densities and crop damage, and through well-designed manipulative experiments. These are:

- that rodent distributions and local diversity across the region are correlated with frequency and depth of floodwater inundation;
- that high local rodent diversity, maintained by areas of upland habitat, suppress the rate of population increase of the rice-field rat through competition for resources (especially nesting sites);
- that areas of regular, prolonged inundation, with associated low rodent diversity, provide an opportunity for the rice-field rat to assume dominance within the local rodent community;
- that low-frequency, high-magnitude flooding events lead to a general collapse of local rodent populations, with a slower rate of recovery than under normal conditions; and
- that areas with continuous rice cropping will support higher and less-variable rodent densities than areas where cropping is interrupted by flooding or prolonged periods of fallow.

Each of these hypotheses is testable; moreover, in each case, the outcomes would provide valuable insights into the complex relationship between landscape ecology, environmental variability, rodent community ecology and agronomy. Gaining these insights is necessary if we are to succeed in developing sustainable, non-chemical solutions for rodent control under the variable conditions offered by the Mekong Delta.

Acknowledgments

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Relationship between rodent damage and yield loss in rice in the Mekong Delta, Vietnam

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Abstract. The rice-field rat, *Rattus argentiventer*, is an important pre-harvest pest of irrigated rice in the Mekong Delta of Vietnam. This species is difficult to trap and little, therefore, is known about the association between population densities of this rat, damage to tillers, and yield loss. We examined the relationship between rodent damage to rice and yield loss at three different stages: seedling (15–20 days after sowing; DAS), tillering (35–40 DAS) and booting (55–60 DAS). Rats confined in small enclosures (3 × 3 m) within the rice crop, for 2 days or for the entire cropping season, were used to generate damage to the crop. The crop was able to compensate for rat damage at the seedling stage. At both the tillering and booting stages, damage to the crop was strongly associated with rodent density, and yield was highly negatively correlated ($r > 0.94$) with rodent damage. There was no compensation by the rice crop to rodent damage at the tillering or booting stage. The lack of compensation at 35 DAS is early compared with the few previous studies reported elsewhere in Asia and may be because a fast-growing (90 days) variety of rice was used in this study compared to slower-growing varieties (110–120 days) in previous studies. Our results raise the important question: how early during tillering do rice crops lose their capacity to compensate for damage caused by rats? This study examined also the use of sweet potato on small bamboo sticks as a simple index of rodent density. The method provided a good indicator of low population densities of rats up until the rice crop began to ripen (day 70 in a 90-day growing season). After this, the rats strongly preferred rice to sweet potato. However, this simple index was unable to distinguish between the range of rodent densities (one to six rats per 100 m^2) in this study.

Introduction

Rodents are the most important mammalian agricultural pests at the global level. Rats damage and destroy many crops pre-harvest, are a major pest for grain stored post-harvest, and are a major forest pest because of their debarking activity of broadleaved trees. Too little is known worldwide about the amount and value of damage inflicted annually by rodents (Rennison and Buckle 1987). In 2001, in Asia alone, it was estimated that just pre-harvest damage by rats removes enough rice to feed 180 million people for a year (Singleton 2001). This same study reviewed rodent impacts pre- and post-harvest in rice-dominated agro-ecosystems and concluded that they are the major single pest in these systems, typically causing annual losses pre-harvest of 5–20% (see also Geddes 1992). The significance of rodents in Asia is further emphasised by the statistics that rice provides 35–60% of the total food energy for the three billion people living in Asia and more than 90% of the world's rice is produced and eaten in Asia (Kush 1993).

Rodents are also carriers of a variety of diseases that can infect both humans and livestock. These diseases are of great social and public-health importance. However, their socioeconomic importance has not been properly evaluated (Mills 1999).

The main pest species of rats in the south of Vietnam (Mekong Delta) are the rice-field rat (*Rattus argentiventer*), the black rat (*Rattus rattus*), the lesser rice-field rat (*Rattus losea*), the Norway rat (*Rattus norvegicus*), and the Polynesian rat (*Rattus exulans*). Minor pest species are house mice (*Mus* spp.) and the bandicoot rat (*Bandicota indica*). Since 1990, the average rice-growing area severely damaged by rats in the Mekong Delta has been around 100,000 ha per year, with loss in rice production of about 10–15% (H.V. Chien, unpublished data). However, these losses vary considerably from season to season and year to year.

This study was carried out in Tien Giang province from 2000 to 2001 in order to study the relationships between:

(a) rodent population density and damage to rice tillers;
(b) the number of tillers damaged and yield loss at three stages of rice growth (seedling, tillering and booting); and
(c) a simple index of rat activity and rat density.

Materials and methods

Study site

Two series of experiments were conducted in 2000 and 2001 at the Southern Regional Plant Protection Center, Chau Thanh district, Tien Giang province in the Mekong Delta region of southern Vietnam. Up to three irrigated rice crops are grown in this region each year. The variety of rice used in the various studies was IR 9729-67-3. The rice was directly seeded at a rate of 200 kg/ha and had a 90-day growing period. The study animals were *Rattus argentiventer* and were in a weight range of 150–200 g.

Experiment 1: the effect of damaged tillers on yield loss

This was evaluated at three stages of rice growth: seedling stage (15–20 days after sowing; DAS), tillering stage (35–40 DAS), and booting stage (55–60 DAS).

For each stage, there were three treatments and three replicates over plot sizes of 3 × 3 m and following a randomised complete block design (RCBD). The treatments were two, three and four male rats per plot, with one set of control plots (no rats). Each treatment plot (n = 30, 3 treatments × 3 crop stages × 3 replicates, plus 3 control plots) was fenced by plastic to a height of 1 m, with 3 m between plots. For each treatment, rats were released for two nights, and then they were caught by hand and killed.

Experiment 2: evaluation of the incidence of tiller damage during the rice cropping season

There were five treatments plus one control and three replicates of each. The study followed a randomised complete block design (RCBD). In this experiment, the plot sizes were 10 × 10 m and rats were maintained in fenced plots (n = 15, plus 3 controls) for the entire cropping season. The respective plots contained: 1 male rat only; 1 female rat only; 1 male and 1 female rat; 2 male and 2 female rats; 3 male and 3 female rats; and no rats in the control.

Assessment of crop damage and yield

The percentage of damaged tillers was calculated using equation (1). Yield was estimated by multiplying the weight of mature rice grains per panicle by 1000 and by the number of panicles per m^2. The actual yield was estimated by weighing rice harvested per plot at a grain moisture content of 14%.

Assessment of rat activity

Signs of rat activity were assessed at 15-day intervals. Twenty pieces of sweet potato held by bamboo sticks 50 mm above the ground were added to each plot. The percentage of pieces gnawed by rats provided an index of activity.

Statistical analysis

Least standard errors, correlation indices and linear regressions were calculated using the statistical software packages SPSS and IRRISTAT.

Results and discussion

Experiment 1

Seedling stage (15–20 DAS)

In the treatment plots, rodent damage to tillers ranged from 23–76% and yields from 4.00–4.30 t/ha. There were no significant yield differences between treatment and control plots (Table 1). Yield decrease was highest at 4% in the treatment that had four rats. However, there was no significant correlation between damage and yields (Table 2; r = –0.414 ns).

The association was modelled by the simple linear functional form of the equation:

$$Y = 4.0975 - 0.00048X \qquad (2)$$

Where, (Y) represents yield loss and (X) represents damage to tillers.

Therefore at the seedling stage (15–20 DAS), the rice plants compensate even when damage was as high as 76%.

Tillering stage (35–40 DAS)

In the treatment plots, rodent damage to tillers ranged from 18–47% and yields from 1.65 to 2.85 t/ha. There were significant yield differences (P < 0.05) between treatment and control plots (Tables 1 and 2). Yield loss was negatively correlated with rat density (r = –0.945). Yield loss was highest (52.9%) when there were four rats per plot (4.4 rats/m^2 or 4444 rats/ha).

The estimated linear regression between yield loss (Y) and damage to tillers (X) was:

$$Y = 3.8446 - 0.049X\text{, with } X_{\min} = 18 \text{ and } X_{\max} = 47 \qquad (3)$$

Therefore at the maximum tillering stage of the rice crop, there was no productive compensation by rice plants—damaged tillers produced new growth, but these were non-productive tillers.

End of booting stage (55–60 DAS)

On the treatment plots, rodent damage to tillers ranged from 19–33% and yields from 1.40 to 2.50 t/ha. There were significant yield differences (P < 0.05) between treatment and control plots (Tables 1 and 2). Yield loss was negatively correlated with rat density (r = –0.995).

$$\text{Damaged tillers (\%)} = \frac{\text{Total number of damaged tillers in treated plot}}{\text{Total number of tillers in the control plot}} \times 100 \qquad (1)$$

Table 1. Incidence (%) of tillers damaged by rats over two nights and actual yields at three stages of rice growth.

Number of rats	Seedling stage		Tillering stage		Booting stage	
	Incidence (%)	Yield (t/ha)	Incidence (%)	Yield (t/ha)	Incidence (%)	Yield (t/ha)
2	26	4.30	19	2.40	20	1.65
2	23	4.15	18	2.65	19	2.50
2	28	4.00	26	2.30	20	1.95
3	41	4.10	23	2.85	25	1.90
3	34	4.05	27	2.50	27	1.50
3	38	4.15	32	1.75	22	1.95
4	76	4.05	47	1.65	19	1.65
4	54	4.00	45	2.05	29	1.75
4	56	4.05	38	2.25	33	1.40
Control	00	4.20	00	4.20	00	4.20

Table 2. Actual yields and percentage of yield decrease compared with control plots. Note: numbers followed by the same letter are not significantly different at the 5% level.

Number of rats	Seedling stage		Tillering stage		Booting stage	
	Yield (t/ha)	Yield decrease (%)	Yield (t/ha)	Yield decrease (%)	Yield (t/ha)	Yield decrease (%)
2	4.15a	1.2	2.45b	41.7	2.03b	51.7
3	4.10a	2.4	2.40b	42.8	1.78b	57.6
4	4.03a	4.0	1.98b	52.9	1.60b	61.9
Control	4.20a	0.0	4.20a	00.0	4.20a	00.0

The estimated linear regression between yield loss (Y) and damaged tiller numbers (X) was:

$$Y = 4.0375 - 0.0934X, \text{ with: } X_{\min} = 19 \text{ and } X_{\max} = 33 \quad (4)$$

Therefore, at the end of the booting stage of the rice crop, there was no productive compensation by rice plants to rodent damage.

Together, these results confirm previous observations that rice crops are able to compensate for rat damage inflicted early to the crop provided the tillers are able to re-grow (Buckle et al. 1985; Singleton et al. 2002). However, these previous studies suggested that the rice crops were able to compensate, at least partially, for rat damage until the maximum tillering stage. There was no compensation demonstrated in this study at the tillering stage. We qualify this by referring to productive growth; there may have been some compensation by rice plants in the weight of seed produced from the undamaged tillers. The lack of compensation at a relatively early stage of production may be because a fast-growing (90-day) variety of rice was used in this study compared to varieties with 110 to 120-day growing seasons in the previous studies. Our results raise the important question: how early during tillering do rice crops lose their capacity to compensate for the damage caused by rats?

Experiment 2

Yields of rice per plot were highly negatively correlated with rodent density (Table 3).

The relationship between indices of rat activity based on the percentage of pieces of sweet potato gnawed and known rodent density was not the same for all stages of the rice crop. There were consistent differences at all stages between one rat present and two to six rats present. However, only at 30 DAS was there a significant positive association with rodent density (Table 3).

Overall, indices of rat activity from 30–60 DAS were high, and then rapidly decreased once the crop was at the ripening stage. These results were not influenced by different growth rates of the rat populations within each plot because the average recruitment per plot was 6.7, 5.3 and 4.7 rats for 1, 2 and 3 pairs of rats, respectively, and the young were pre-weanlings. An expected result was a decrease in yield with rat density (Table 3). The finding that sweet potato is a good indicator of low densities of the rice-field rat up to the ripening stage of the rice crop is important because this species of rat is difficult to trap (Leung et al. 1999). However, this simple index was unable to distinguish consistently between the known rodent densities. Further studies across a wider range of population densities are warranted.

Table 3. Signs of rat activity (% sweet potato eaten) during the cropping season and actual yields in each of the plots (DAS = days after sowing, CV = coefficient of variation). Note: numbers followed by the same letter are not significantly different at the 5% level.

Treatment	30 DAS (%)	45 DAS (%)	60 DAS (%)	75 DAS (%)	85 DAS (%)	Yield (t/ha)
1 male	11.67a	30.00ab	53.33b	33.33b	11.67ab	3.87b
1 female	15.00ab	31.67ab	50.00b	40.00b	10.00ab	4.00b
1 pair	35.00bc	48.33b	66.67bc	45.00b	16.67ab	2.80c
2 pairs	45.00cd	68.33b	76.67bc	68.33c	23.33b	2.10d
3 pairs	58.33d	71.67b	81.67c	73.33c	21.67b	1.53d
Control	00.00a	00.00a	00.00a	00.00a	00.00a	4.87a
CV (%)	42.60	57.70	25.10	27.70	72.90	10.70

Conclusions

In short-maturing irrigated rice crops in Tien Giang province, damage by rats was compensated for at the seedling stage, but not at the tillering and booting stages. There was strong compensatory growth by rice plants when damage occurred during tillering, but this growth did not result in productive seed. There was a strong association between damage to tillers and reduction in crop yield.

Sweet potato was a good indicator of rodent activity up to the ripening stage of the crop. Thereafter, the rats preferred the rice to the sweet potato.

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The rodent density–damage function in maize fields at an early growth stage

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Abstract. The relationship between the population density of *Mastomys natalensis* and percentage crop damage at planting of maize was determined in experimental maize fields in Morogoro, Tanzania. The experimental design was completely randomised with 21 plots of size 70 × 70 m. We determined rodent density using the capture–mark–release (CMR) technique in each of the plots. The best model for the data was determined using Akaike information criterion values in order to establish the relationship between rodent density and rodent damage. The relationship between rodent density and rodent damage is sigmoidal ($r^2 = 0.55$, $n = 44$, $p = 0.001$).

Introduction

The problem of rodent damage in agriculture is complex because almost any crop can be the target of rodent attack (Taylor 1972; Fiedler 1988). Dramatic rodent outbreaks have been reported in many countries where intensive and extensive cultivation of agricultural crops is undertaken (Singleton and Redhead 1990). Such outbreaks, particularly in cereals such as rice, maize, wheat and barley, have caused serious losses and widespread food shortages (Walker 1990). Damage ranges from negligible destruction to total crop loss. For example, regional reports from Lindi in Tanzania showed that yield loss due to rodents was 85,108 tonnes (i.e. 71,236 for cereal and 13,872 for pulse crops) in 1989/90 (Mwanjabe et al. 2002). These losses could feed 290,669 people in Lindi (i.e. 700 g/person/day for cereals and 100 g/person/day for pulses).

For decisions to be made about rodent control in any cropping system, the density of rodents must be estimated. However, little is known about rodent density–crop loss relationship functions. It has been reported that there is a positive correlation and linear relationship between rodent density, damage, and yield loss in fields of rice at maturity in Southeast Asia (Walker 1987, 1990). While it is theoretically and widely assumed that there is a positive linear relation between the number of rodents and damage, in practice this may not be so, since the damage curve always reaches a necessary asymptote of 100%.

The current study was carried out to determine and describe the rodent density–crop loss functions in maize fields in Morogoro, Tanzania. Here we present the data about damage occurring just after maize seeds have been planted.

Materials and methods

Location of experimental fields

Field experiments were carried out in two locations at Sokoine University of Agriculture, Morogoro, Tanzania. The first location is 510 m above sea level (asl), 6°50'S, 37°38'E, within the university farm. The second location (Solomon Mahlangu Campus) is 480 m asl, 6°46'S, 37°37'E. The area has a bimodal rainfall patterns with a 'short rain season' in October–December and a 'long rain season' from March–June. The study was conducted during the long rain seasons in 1999, 2000 and 2001. The exact timing of the field observations depended on the date of sowing, which was in turn dependent on the timing of rainfall.

Density of rodents and agronomic practice

Twenty-one maize fields, each 70 × 70 m, were used in the study. The size of the plots corresponds to the field size in smallholder farms in Tanzania. The plots were located a minimum of 80 m apart or, in four cases, were fenced. The plots were experimental fields of other ongoing studies with different treatments manipulating the level of predation, dispersal, land management or cropping system. Details of those experiments are less relevant here, but the important point is that through these treatments we could make observations in fields with a considerable range of rodent densities. The rodent population size in each field was estimated with closed-model capture–mark–recapture estimates (estimator Mh in CAPTURE; White et al. 1982) based on sessions of three consecutive trapping nights with 49 Sherman live-traps at fixed trapping points in a square trapping grid with 10 × 10 m mesh size in each plot. We estimated population size before ploughing and after planting and used the average of both estimates as a measure of rodent density at planting in each field.

All fields received similar standard agronomic treatments, i.e. early ploughing, application of triple superphosphate (TSP) fertiliser (20 kg P_2O_5/ha) before planting, and nitrogen fertilisers (40 kg N/ha) twice as a top dressing three weeks after sowing and booting stages. Three maize seeds (variety Staha) were planted per hole, with a planting spacing of 90 cm × 60 cm. Weeding was carried out twice.

Assessment of crop damage

Crop damage assessment was carried out at the seedling stage, 10 days after planting. We used a non-stratified systematic row-sampling technique, described by Mwanjabe and Leirs (1997), where sampling units were maize rows, four rows apart, leaving out the two outer rows. The assessor walked along maize rows across the plot, counting seedlings at each hole. Since three seeds had been planted per hole, we calculated the difference between observed and expected number of seedlings, and expressed the difference as a percentage damaged.

Relationships between rodent density and rodent damage

In order to find out which model represented the relationship best, first the data points were presented in a scatter plot, and we identified different biologically meaningful function types (Harshbarger and Reynolds 2000). Computer software (Sigmaplot, Excel, and Table curve 2D) was used for curve fitting. We calculated Akaike's information criterion (AIC) values for those models and compared (Akaike 1973). Therefore, the model with the lowest AIC (and thus lowest parsimony) was chosen to be the best model for the relationship.

Results and discussion

Twelve models were tested for the relationship between rodent density and damage and AIC values compared (Table 1). The relationship was best described by a sigmoidal function with three parameters ($r^2 = 0.55$, $n = 44$, $p = 0.001$) (Figure 1). The function has an intercept of about 14%, which corresponds to a realistic background germination failure rate. It is obvious from the curve of the best model that even at a low level of rodent density, there is considerable damage and the rodent damage increases with increasing rodent density from the beginning. However, rodent damage reaches an asymptotic level (constant level of damage) at high rodent density (>40 animals per plot, which is equivalent to 80 animals/ha). Interestingly, a simple linear regression is almost equally good as a best model.

There is considerable variation around the curve, indicating that effects other than rodent density, e.g. rainfall, should be included in future multivariate analysis. In terms of rodent management, therefore, the results show that if populations are high, there is little point in controlling rodents unless densities can be reduced to fewer than 20 animals/ha.

Table 1. Relationship between rodent density and percentage damage at the seedling stage using Akaike's information criterion (AIC) values obtained from best fitting models.

No.	Model and its coefficients	AIC
(1)	Sigmoidal, sigmoid with three parameters	238.84
(2)	Linear regression with two parameters	240.32
(3)	Logarithm first order	240.59
(4)	Hyperbola with two parameters	240.68
(5)	Sigmoidal, logistic with three parameters	241.89
(6)	Sigmoidal, sigmoid with four parameters	241.93
(7)	Exponential rise to maximum with three parameters	242.63
(8)	Sigmoidal, logistic with four parameters	243.38
(9)	Hyperbola with three parameters	244.32
(10)	Logarithm second order	244.90
(11)	Power with three parameters	244.96
(12)	Logarithm third order	247.33

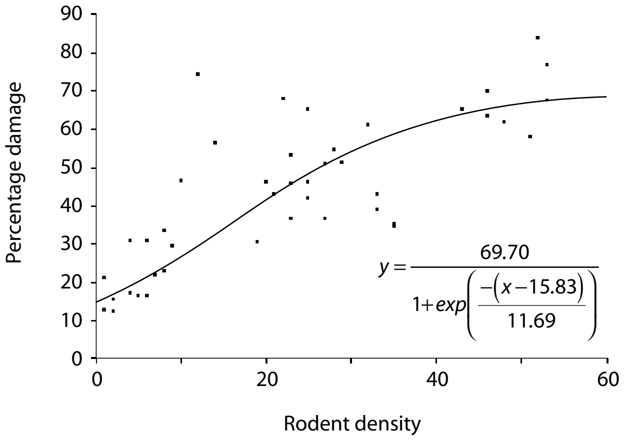

Figure 1. Relationship between the density of *Mastomys natalensis* per hectare and the percentage of damage at sowing of maize crops in Tanzania. A sigmoidal curve best described these data and accounted for 55% of the variation.

The relationship between rodent damage at planting and the actual effect on the final yield needs to be investigated further. Although compensation could occur after rodent damage, it has been reported to be minimal in maize (Myllymäki 1987). On the other hand, at low rodent damage levels, farmers may actually thin the seedlings to two seedlings per planting hole to reduce competition between plants. It is also important to note that different causes of crop loss interact and the yield response is usually variable at a given location and time (Walker 1990) due to environmental factors, e.g. rainfall. Further analysis is currently in progress.

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Commercial use of rats and the use of barn owls in rat management

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Abstract. More than 50 years experience in rat population control throughout Indonesia has not succeeded in overcoming the numerous problems associated with rats. Today, rats remain a major pest, with economic loses estimated at US$25 million per year. The intention of this paper is to offer new technologies for the utilisation of rats and provide a new paradigm for rat management.

Impacts of rodent pests and traditional methods of control

There are at least six species of rodents that cause significant losses to agricultural production in Indonesia: *Rattus argentiventer*, *R. diardi*, *R. exulans*, *R. tiomanicus*, *R. norvegicus* and *Bandicota indica* (Kalshoven 1981). Farming communities of the past and present have attempted various mechanical, chemical and biological methods to decrease these rat populations. Farmers recognise the role of snakes, predatory mammals, and predatory birds in limiting rodent populations, but predators are becoming fewer. Formerly, rats served an important role in traditional medicine and it is estimated that when this practice ceased, economic losses by rats increased.

Mechanical and chemical control methods are conducted year after year to eliminate rats. In Java, in 1961, there were major outbreaks of rodent populations in some localities, leading students of the Faculty of Agriculture, Gadjah Mada University, to develop an extension program for rat control in Bojonegoro subdistrict, Central Java. They modified a midget duster into a fumigator. This simple fumigator, '*Emposan Gama*', burned rice straw and sulfur granules, producing smoke containing CO_2 and SO_2 that was forced into rat burrows. Rats inside the burrows suffocated. This simple technology has been widely adopted in Java. Another simple technology, developed in the 1990s, is the trap–barrier system (TBS) which, together with ecologically based rodent management, is effective in decreasing damage to rice crops and in increasing yields (Singleton et al. 1998).

Despite these efforts and promising progress in reducing impacts, rats remain the most important agricultural pest in Indonesia. In a national panel discussion on rats in Jatisari, West Java, in May 2001, it was reported that total losses due to rice-field rats, *R. argentiventer*, reached US$22.5 million per year. Other commodities that suffer significant rodent damage, mainly caused by *R. tiomanicus*, are cocoa, coconut and oil palm (Sipayung et al. 1990). House rats (*R. exulans*, *R. norvegicus*, *R. rattus*) and bandicoot rats (*B. indica*) cause serious problems in traditional markets, grain stores and around houses. At this meeting, it was estimated that total annual losses due to rats to agricultural produce in Indonesia was >US$50 million.

Discussion

Integrated management

The concept of integrated pest management (IPM) was introduced to Indonesia in 1983 to promote the control of brown planthoppers in rice crops. The impact of IPM was impressive, with the use of insecticides reduced from 17,300 t in 1986 to about 3000 t in 1989.

The government of Indonesia now encourages the use of ecologically based management for the control of rodents (Research Institute for Rice 1998). However, in Central Java, 94% of trained farmers would only implement IPM to manage rodents if the government provided subsidies, particularly for chemical rodenticides (Eddy Mahrub et al. 1995).

In contrast to farmers in other regions of Southeast Asia (see Nguyen Tri Khiem et al., this volume), farmers in West Java usually do not use rats commercially. Such use of rats may be an advantage when implementing ecologically based rodent management because the additional benefit from selling rat products makes it more likely to achieve positive benefit–cost ratios. Rat skins could be used as materials for various handicrafts, while the rat body could be processed for animal feeds. In Java in 2001, we conducted a training course dedicated to commercial use of rats by farmers (20 participants from 6 provinces).

How can the attitudes of farmers regarding rats be changed from disgust to the perception of potential economic benefits? In the past, local governments paid bounties for dead rats turned in by farmers of about rupiah (Rp)200 to Rp1,000 per individual. In 2001, the Sleman subdistrict government spent Rp22,500,000 on rat bounties. Also in 2001, the General Chairman of the Indonesian Society of Farmer Groups, who attended a special discussion with farmers about rat control, estimated that it might be possible to sell animal feed produced from rat bodies for Rp10,000 per kg. This encouraged some farmers to set up home businesses producing rat pellets or rat meal as animal feed for chickens, dogs and fish. In the future, rat meat could be produced for food for human consumption. This is already practised in Central Java and North Sulawesi, but religious and personal beliefs must be overcome.

In addition, rat skins may be used for making wallets, bags or clothing. These handicrafts are marketable, either for domestic or foreign consumers. Farmers can collect and preserve rat skins in salt for 3–4 months, but specialists should do tanning to minimise the risk of environmental pollution by chemicals used in the tanning process.

Predators of rats

The promotion of predators may be another way to increase the effectiveness of ecologically based rodent management. The barn owl, *Tyto alba*, is a night active predator of rats and may prove useful for controlling rodent populations. Barn owls breed naturally in oil palm plantations (Sipayung et al. 1990; Heru et al. 2000). Artificial breeding has been successful in Java and we have established a breeding colony in a cocoa plantation in North Segayung, Batang, Central Java which has been maintained for 5 years. More than 60 progeny were produced from one of the nest boxes (S. Mangoendihardjo, unpublished data). The owls have been observed to spread about 8 km from the breeding site.

Conclusion

We suggest the utilisation of rats in assisting ecologically based rodent management to control rats in West Java. However, it is important to change the attitude of people towards the use of rats. The establishment of breeding barn owls in agricultural land in West Java is promising for their potential use in rat control. Rats should be considered as animals having economic value and the barn owl should be protected.

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The efficacy of a trap–barrier system for protecting rice nurseries from rats in West Java, Indonesia

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Abstract. The rice-field rat, *Rattus argentiventer*, causes substantial damage to freshly sown rice nurseries in West Java, Indonesia. Rice nurseries surrounded by a plastic barrier with multiple-capture rat traps (trap–barrier system; TBS), or a barrier system (BS) consisting of plastic and no traps, were compared for their effectiveness to reduce rodent impacts against untreated nurseries that did not have a barrier to rats. There were 10 replicates of each treatment and the study was conducted for one wet and one dry season. The study clearly demonstrated the substantial impact of rats on unprotected rice nurseries for the two major crops in West Java—the dry and wet season rice crops. Both the TBS and BS provided significant protection to rice nurseries. There was no rat damage in nurseries protected by a TBS in either season. In the 1996 dry season, nurseries surrounded by a BS had 7% (±2.0 se) of seedlings damaged, whilst those with no barrier had 88% (±8.1) of seedlings damaged. In the 1996/97 wet season, nurseries surrounded by a BS had 14% (±3.1) of seedlings damaged, whilst those with no barrier had 97% (±2.1) of seedlings damaged. The mean number of rats caught per day per trap in a TBS led to the recommendation of four traps per nursery in the dry season but only two in the wet season. Whether farmers opt to use a TBS or BS will depend on the weight they give to having approximately 10% of their seedlings damaged by rats versus the expense of purchasing four live-capture rat traps.

Introduction

The rice-field rat, *Rattus argentiventer*, is the most important pre-harvest pest of rice crops in West Java (Geddes 1992; Singleton and Petch 1994). These rats can damage rice tillers from transplanting to just before harvest (Singleton et al. 1998). Rats also cause significant damage to seedlings in rice nurseries before they are transplanted. In West Java, the most common method of rodent control in the rice nurseries is a physical barrier made from plastic sheeting. These barriers are erected to deflect rats from the nurseries. However, the nurseries are planted during land preparation, when food is limiting for rat populations. Therefore, these rice nurseries are prone to rat damage. When rat densities are high, farmers often have to replant their seedbeds. If a farmer has to replant then his crop will be transplanted late. This in turn can lead to high damage before harvest if rats aggregate at the late-planted crops (Jacob, Nolte et al., this volume).

The addition of multi-capture live-traps to a plastic fence (trap–barrier system) has proven a successful method of managing rodent impacts to crops after the rice has been transplanted (Singleton et al. 1998, 2002). This study examines the efficacy and benefit–cost of a trap–barrier system for controlling losses by rats to seed nurseries in a region where rice is the dominant crop. The replicated study was conducted over the two main rice-cropping seasons in West Java.

Materials and methods

The study was conducted in rice paddies of farmers near Sukamandi, West Java (6°20'S, 107°39'E) during the 1996 dry season (19 April to 12 May) and the 1996/97 wet season (13 October to 2 November 1996). In this region, the rice is sown in a small nursery 3 weeks before being transplanted into the rice paddies. There were two treatments and a control: a trap–barrier system (TBS), a barrier system without traps (BS), and no fence (control). Each had 10 replicates, separated by a minimum of 200 m. Each rice nursery was approximately 10 m × 15 m. The BS consisted of a plastic fence. The TBS consisted of a plastic fence and one multiple-capture trap made of wire mesh ($600 \times 240 \times 240$ mm) placed along each side of the fence. Each trap was located within the TBS, with its opening flush with a hole in the fence. The traps were checked in the morning of each day and all rats were removed. The number of rats caught over a period of 20 days was recorded. The fences were inspected each morning and any holes found in the fences were patched immediately to maintain the fence in good condition.

Cost of TBS and BS

The cost for materials and labour (2002 prices) to build the barriers were as follows: 50 m of new plastic, US$2.25; bamboo sticks, string and staples, US$1.9; installation, US$1.5. The four traps cost US$14. Therefore, a BS cost US$5.65 and a TBS US$19.65.

Assessment of rat damage to seedlings

Rodent damage to rice tillers is distinctive. Rats cause a clean cut near the base of the seedling at approximately a 45° angle. The percentage of damaged seedlings was assessed visually at 10 and 20 days after the rice seeds were planted. Two people independently assessed the level of rat damage and a mean of the two estimates was used.

Statistical analyses

Sex differences in the number of rats caught per season were analysed using a one-way analysis of variance. The data on tillers damaged were analysed using a repeated measures analysis of variance. Standard errors of the mean are given in brackets.

Results and discussion

1996 dry season

More males (64%) than females were caught in the TBS ($F_{1,18} = 6.84$, $P = 0.002$; Table 1). The reason for this is unclear. Perhaps male rats were more trappable following a short fallow and high disturbance of the cropping landscape during land preparation, or perhaps they simply move more and are therefore more likely to come in contact with nurseries protected by a TBS.

Despite daily observation and maintenance of the plastic fencing, rats gained access to the nurseries and they caused damage to the seedlings in the BS treatment.

There was a significant treatment effect ($F_{2,27} = 89.98$, $P < 0.001$). There was no rat damage in the nurseries protected by a TBS. In the nurseries protected by a BS, the mean percentage of seedlings damaged by rats was 7% (±2.0) after 20 days. Severe rat damage was observed in the unprotected plots; the mean percentage of seedlings damaged by rats was 88% (±8.1) after 20 days (Figure 1). There was no significant difference in damage to seedlings 10 and 20 days old ($F_{1,27} = 2.67$, $P = 0.065$).

1996/97 wet season

There was no difference in the number of males and females caught in the TBS ($F_{1,18} = 0.02$, $P = 0.902$; Table 1).

Again, there was rat damage to the seedlings in the BS treatment despite the fences being maintained as a 'barrier' with no holes during the 20 days.

There was a significant treatment effect ($F_{2,27} = 251.0$, $P < 0.001$). There was no rat damage in the nurseries protected by a TBS. There was a significant difference in damage to seedlings after 10 and 20 days ($F_{1,27} = 25.68$, $P < 0.001$) (Figure 1). This suggests that perhaps rice seedlings less than 10 days old are more attractive to rats than those 11–20 days old. In the nurseries protected by a BS, the mean percentage of seedlings damaged by rats was 14% (±3.1) after 20 days. Severe rat damage was observed in the unprotected plots; the mean percentage of seedlings damaged by rats was 97% (±2.1) after 20 days (Figure 1).

Economics and efficacy of the different treatments

The major cost was the purchase of new live-capture traps. The time to process rats caught by the TBS was minimal compared to the average of 10 h (1.3 days of labour) over the 20 days to check and maintain the TBS or the BS. The daily labour cost is approximately rupiah (Rp)15,000, so it only cost Rp20,000 (≈US$2) to maintain the respective fences over the 3 weeks.

In West Java, seed nurseries clearly need to be protected from the severe impact of rats. Where there was no barrier erected to protect the nurseries, farmers had to replant new seed in each season when high losses were suffered. A TBS or BS provided substantial reductions in rodent damage. In determining whether to use a TBS or a BS to protect the rice nursery, farmers need to weigh the extra cost of new traps against losses of about 7 to 14 % of their seedlings. Recommendations on the number of traps per TBS are based on the number of rats caught per day per trap. In the dry season there were mean captures of up to 12 rats per trap, whereas in the wet season the mean was usually ±4 rats per trap. Therefore, the recommendation is to use four traps per TBS in the dry season and only two in the wet season for a 10 m × 20 m nursery. An added consideration for determining whether to adopt a TBS rather than a BS is that once farmers have purchased the traps they can be used for many seasons.

Table 1. Rats captured over 20 days in the trap–barrier system protecting rice nurseries of farmers near Sukamandi in the 1996 dry season and the 1996/97 wet season.

Season	Number of rats caught per replicate										
	Sex	1	2	3	4	5	6	7	8	9	10	Total
Dry	Male	33	14	15	15	13	13	33	22	24	7	189
	Female	17	12	5	10	14	4	8	17	14	5	106
Wet	Male	6	3	9	3	3	12	6	9	2	2	55
	Female	4	8	5	3	5	7	10	8	1	4	55

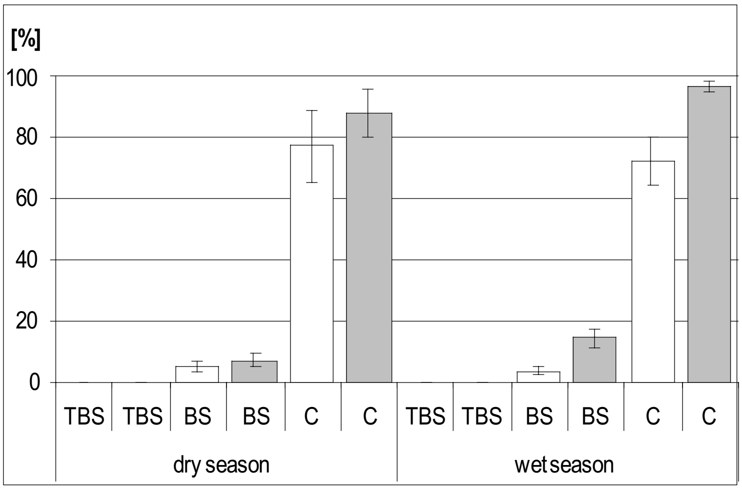

Figure 1. Rat damage (± 1 se) to rice seedlings in nurseries for three different treatments during the dry season 1996 and wet season 1996/97; damage at day 10 (unshaded), damage at day 20 (shaded). TBS = trap–barrier system, BS = barrier system, C = control with no barrier.

During the wet season one-third fewer rats were caught compared with the catch during the dry season, but rat damage was higher in the wet season. There are two likely explanations for these results. First, rats are more nutritionally stressed after the 3 months fallow at the end of the dry season (there is only a 1 to 1.5 month fallow at the end of the wet season) and therefore may be more active in their search for food. Second, rats, particularly male rats, may be more trappable during the beginning of the dry season. This could be related to there being a predominance of younger cohorts at the end of the wet season. More studies are required to distinguish between these two possibilities.

Conclusion

Rats cause substantial damage to both rice nurseries and to rice crops after they have been transplanted. A TBS that contains a rice crop transplanted three weeks earlier than the surrounding crops is effective in reducing crop losses caused by rats once the rice crop has been transplanted (Singleton et al. 1998, 2002). This is the first study to examine the efficacy for using a TBS or a BS for protecting rice nurseries against rats.

This study clearly documented the substantial impact of rats on unprotected rice nurseries for the two major crops in West Java—the dry and wet season rice crops. Both the TBS and BS provided significant protection to these nurseries. Whether farmers opt to use a TBS or a BS will depend on the weight they give to having approximately 10% of their seedlings damaged by rats versus the expense of purchasing two to four live-capture rat traps.

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