We have determined the ideal size range for a TBS for farmers (G.R. Singleton and Sudarmaji, unpublished data), but not the optimum spatial distribution of these in the landscape. Although there was much variation between seasons in the extent of the halo of protection provided to crops by a TBS+TC, we recommend that a 25 × 25 m TBS would significantly reduce rat damage in the surrounding 10–20 ha of rice crop. Therefore, at a village level we suggest that one TBS+TC would be sufficient for every 15 ha of rice crop. This recommendation has not been tested.

The spatial distribution of physical methods for controlling rat numbers is an important issue given the ability rats have to re-colonise areas where their densities have been reduced. In rice fields, rats move hundreds of metres in a night, especially once the developing crop reaches the booting stage (Singleton et al. 1994; P. Brown, pers. comm.). To reduce this ability of rats to compensate for control activities, management needs to be approached initially at the village level and then at the district level. A good extension program with strong grower participation is fundamental for a community-based control campaign to be successful (FAO 1997).

At the village level, the spatial distribution and number of TBS sites will not simply be determined by the area of land under rice production. Important considerations will be how rat populations respond to:

- the heterogeneity of the habitat (the seasonal dynamics in habitats where rats can take safe refuge and/or breed);
- the degree of asynchronous planting of rice crops; and
- the variety of other crops grown in the area.

This information requires detailed studies of the population ecology and behaviour of *Rattus argentiventer* and good documentation of farming practices. There are some data available on the first two dot points. For instance, banks along the margins of rice fields and the banks of the major irrigation canals provide important habitats for rats to take refuge in during non-breeding seasons, and for rats to nest and breed in after the crop reaches the maximum tillering stage (see Leung et al., Chapter 14). Also, the breeding season of *R. argentiventer* is linked to the reproductive stage of the rice crop (Lam 1983; Murakami et al. 1990). Therefore, asynchronous planting of neighbouring crops will extend the breeding season of rats. Although we require more detailed knowledge of the population ecology and biology of *R. argentiventer*, what we already know has had an important influence on the development of management strategies for this species. Our efforts to manage this species would be considerably strengthened if we had a better understanding of the processes that influenced whether a rat did or did not enter a trap of a TBS. Towards this end, we need to develop a better awareness of the behavioural responses of rats to a TBS+TC and of the factors that may influence this response.

Concluding Remarks

In closing, the biggest hurdle facing the successful use of physical methods for managing rodent pests is the ability of rodent populations to compensate for reductions in population size through immigration, increased survival and/or better breeding performance. The early studies of Davis (1953) clearly demonstrated the ability of rat populations to recover to original levels following poisoning operations. Similarly, H. Leirs (pers. comm.) has shown that a 50% reduction in a *Mastomys natalensis* population, through the use of chemical rodenticides, has little impact on the yield loss of crops. However, sustained harvesting of rats from a population can lead to the collapse of that population, presumably because of a decline in the age structure of the breeding population (Davis and Christian 1958). Together, these studies indicate that one-off uses of physical control, especially when rodent densities are high, may have little to no impact on rat populations. In contrast, sustained use of physical control methods over an appropriate spatial scale may be both cost effective and environmentally sustainable.

Two methods which warrant further study are the use of TBS+TC and the targeting of bounty seasons at appropriate times of the year. The timing of the latter needs to be dictated by our understanding of the population biology of the rat rather than the phenology of the crop. For both methods, success will revolve around coordinated, synchronised actions at a village or district level and their ability to be adopted as part of an integrated approach to rodent management (see Singleton 1997; Leung et al., Chapter 14, for discussion of other actions).

How the use of physical barriers plus traps has evolved in our endeavours to manage the rice-field rat highlights the imperative of having sound ecological studies in progress before embarking on broad scale management programs of a rodent pest (Leirs et al. 1996; Singleton 1997). Further population studies of rodent pests are planned for Indonesia, Vietnam and Lao PDR, and they will complement our progress towards optimising the use of trap barrier systems and trap crops.

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9. Ecological Management of Brandt's Vole (*Microtus brandti*) in Inner Mongolia, China

Wenqin Zhong, Mengjun Wang and Xinrong Wan

Abstract

Brandt's vole (*Microtus brandti*) is a serious rodent pest in the grasslands of Inner Mongolia. Poison baiting is the traditional approach to controlling Brandt's vole in this region. Although this sharply reduces the density of voles, the remaining resident animals have high reproductive and survival rates, leading to rapid recovery of the population. Poison baiting also causes other problems such as environmental pollution and secondary poisoning of natural predators. Therefore, a new non-polluting, economically efficient technique, offering effective long-term control, is urgently required for the management of Brandt's vole. In this paper, we investigate the potential of an ecological strategy in managing Brandt's vole in the grassland of Inner Mongolia.

We found the main factor facilitating infestation by Brandt's vole in the grassland is overgrazing by livestock. The density and height of vegetation strongly influence the habitat selection of Brandt's vole. With heavier grazing pressure by livestock, the height and cover of vegetation are reduced and the plant composition is changed, resulting in high quality food and shelter for voles and consequent increases in their population densities. The density of voles was low where the height of vegetation was >190 mm but high where vegetation height was 30–130 mm. Fencing and pasture management could be used in some areas to reduce vole problems by increasing the height of grass.

In Inner Mongolia, local herdsmen fence pasture in June to increase herbage for harvesting in autumn or for grazing by livestock in winter. The grasses grow slowly and poorly under this traditional fencing management because extensive grazing suppresses the germination and growth of grasses that would otherwise occur due to high rainfall and warm temperatures in May. These grasslands then become more vulnerable to vole infestation. A new fencing management of removing livestock from pastures in the middle of May, rather than later in June, was examined using a series of experimental exclosures in Taipus Qi, Inner Mongolia, from 1986–1990. The densities of Brandt's vole populations in the experimental exclosures were reduced sharply and the grass yields increased greatly compared to the exclosures under the traditional fencing management. Over the next three years, the average investment:income ratio was 1:7. This new ecological management is very promising for solving the Brandt's vole problem in the Inner Mongolian grasslands.

Keywords

Brandt's vole, overgrazing, ecological management, Inner Mongolia

INTRODUCTION

BRANDT'S VOLE (*Microtus brandti*) is a major rodent pest in the grasslands of Inner Mongolia, especially in the typical steppe of the Xilin Gele region. It can cause problems in an area of up to 20 million ha or 75% of this region. The populations of Brandt's vole fluctuate remarkably, with positive feedback indicated by 2–3 years of low density after a period of high density. Each vole can eat 40 g of fresh plant material per day and in high-density years, with up to 1,384 individuals/ha, 15–44% of grass production can be consumed by voles (Zhang and Zhong 1981). The diet of Brandt's voles is similar to that of sheep and cattle (Wang et al. 1992), so it is an important competitor of livestock.

Brandt's voles live in social groups and dig complex burrow systems with up to approximately 5,616 holes/ha in high-density areas (Zhong et al. 1985b). Because voles excavate large amounts of soil, they accelerate erosion and desertification in grasslands.

Poison baiting is the traditional approach to controlling Brandt's vole in the Inner Mongolian grasslands. Although this sharply reduces the density of voles, the remaining resident animals have high survival rates because there are more resources available to them (Dong et al. 1991). The pregnancy rate increases and voles become mature earlier, leading to the rapid recovery of the Brandt's vole population (Yang et al. 1979; Zhou et al. 1992). Its relative abundance in the rodent community recovers within four months (Hou et al. 1993). Chemical control is applied nearly every year but pest problems also occur each year in a 'pest outbreak → chemical control → pest outbreak' cycle. This approach is not only expensive and fails to provide a long-term solution, but it also results in heavy environmental contamination. A new non-polluting, economically efficient technique, offering effective long-term control, is urgently required for the management of Brandt's vole. Major advances will depend on ecological studies (Barnett 1988).

The habitat of rodents is determined by many attributes of the plant community, such as the distribution and spatial pattern of plants, the proportions of edible and inedible plant species, and changes in phenology, biomass, cover and species composition. All of these influence the composition and dynamics of rodent communities. On the other hand, the animals' activities also change the vegetation.

We have investigated the number of species and the diversity and heterogeneity of plant and rodent communities in five types of steppe in the grassland of Inner Mongolia (Zhou et al. 1982). The results showed that the rodent and plant communities are closely connected (Table 1). The diversity index of the rodent community is correlated with the diversity index of the plant community ($r = 0.972$, $p < 0.01$) and that the heterogeneity index of the rodent community is also correlated with that of plants ($r = 0.905$, $p < 0.05$). Also, we have investigated the plant–rodent community in different stages of the same type of grassland (Wang et al. 1997; Table 2). The changes in the α-diversity index of the plant community and rodent

Table 1.
Species number, diversity and heterogeneity of plant and rodent communities in five types of steppe. *H* is the Shannon-Wiener index: $H = -\Sigma P_i \ln P_i$, where P_i = is the proportion of species *i* in the community. *J* is an index of evenness: $J = H/\ln S$, where *S* is the number of species in the community (Zhou et al. 1982).

Type	Rodent community			Plant community of steppe		
	No. of species	*H*	*J*	No. of species	*H*	*J*
1	7	0.9611	0.4939	39	1.7443	0.4761
2	6	1.2841	0.7167	37	2.2265	0.6166
3	9	1.4898	0.6780	40	2.4981	0.6772
4	8	1.6348	0.7862	26	2.5621	0.7864
5	5	0.8106	0.5037	26	1.8158	0.5573

Table 2.
Comparisons of the α-diversity index between plant and rodent communities along a grazing gradient in two types of steppe. The impacts of grazing were classified as: I = no grazing, II = moderately degraded pasture, and III = heavily degraded pasture. (From Wang et al. 1997.)

Season	Community	*Aneurolepidium chinense* steppe			Season	Community	*Stipa grandis* steppe		
		I	II	III			I	II	III
Spring	*Rodent*	0.2095	0.1515	0.0	Spring	*Rodent*	0.0	0.3909	0.4224
	Plant	1.2015	1.1638	1.0860		*Plant*	0.9798	1.0289	1.0410
Autumn	*Rodent*	0.3729	0.1682	0.1283	Autumn	*Rodent*	0.0	0.3195	0.3280
	Plant	1.3929	1.2290	1.1621		*Plant*	1.2238	1.2253	1.3524

community show the same trend. The diversity of plants reflects food availability for rodents, heterogeneity is a measure of the distribution of food, and height and cover are important spatial factors to which rodents are sensitive. The result is that changes in any of these plant community indices correspond to changes in the abundance and distribution of rodents.

In Inner Mongolia, the number of livestock has been increasing year by year. The number of livestock has increased 2.64 times in recent decades, with corresponding land degradation reaching 27.5% of all the Inner Mongolian grassland area (Ren et al. 1989). The pressure of grazing has resulted in degeneration and desertification of large areas of grassland as well as increasing salinity of soils. The plant community has responded with an increase in the proportion of dicotyledons and a general decrease in the production and biomass of vegetation. The successional changes in the plant community have been matched by changes in the composition of the rodent community.

Figure 1 summarises the sequence of changes in the plant–rodent community in degraded grassland in Inner Mongolia (Zhong et al. 1985a).

	Plant community	Grazing	Rodent community
(a)	*Aneurolepidium chinense* *Stipa krylovii*		*Cricetulus barabensis* *Citellus dauricus* *Ochotona daurica*
		Lightly over-grazed ↓	
	Artemisia frigida *Aneurolepidium chinense* *Cleistogenes squarrosa*		*Ochotona daurica* *Cricetulus barabensis* *Citellus dauricus*
		Heavily over-grazed ↓	
	Artemisia frigida *Potentilla acaulis* *Cleistogenes squarrosa*		*Microtus brandti*
		Excessively over-grazed ↓	
	Planta annua		*Meriones unguiculatus*
(b)	*Stipa krylovii* *Artemisia frigida* *Cleistogenes squarrosa*		*Citellus dauricus* *Ochotona daurica*
		Lightly over-grazed ↓	
	Stipa krylovii *Artemisia frigida* *Cleistogenes squarrosa*		*Ochotona daurica* *Citellus dauricus*
		Heavily over-grazed ↓	
	Heteropappus altaicus *Artemisia frigida* *Salsola collina*		*Microtus brandti*
		Excessively over-grazed ↓	
	Planta annua		*Meriones unguiculatus*

Figure 1.
The impact of grazing by livestock on the plant–rodent communities at (a) Xilin Hot (43°25'N, 116°41'E; annual precipitation 350–400 mm) and (b) the Kelulun River (49°25'N, 116°42'E; annual precipitation 250–300 mm) in the typical steppe of Inner Mongolia (from Zhong et al. 1985a).

In degraded grasslands, the biomass of families in the Compositae, Rosaceae and Chenopodiaceae increase, all of which are the preferred food of the Daurian pika (*Ochotona daurica*) (Zhong et al. 1983). The vegetation of this stage also provides suitable cover and food for storage for the Daurian pika (Wang et al. 1998). With heavier grazing pressure, the height and cover of vegetation is reduced, the availability of food and shelter becomes unsuitable for the pika, its abundance decreases and its dominant position is taken by Brandt's vole. This degenerative stage is the preferred habitat of Brandt's vole and populations increase quickly and reach high densities (Zhong et al. 1985b). With excessive grazing, soil becomes susceptible to erosion and *Planta annua* becomes the main component of the plant community. Brandt's vole is displaced by the Mongolian gerbil (*Meriones unguiculatus*) and eruptions of this species can occur (Xia and Zhong 1966; Zhong et al. 1983).

Degradation of grassland is facilitated by the digging and feeding activities of Brandt's vole. Groups of voles occupy complex burrow systems. They often excavate soil when they repair their burrows, especially when constructing 3–4 storerooms per burrow system in autumn. As each storeroom is about 1.1 m long and 120 mm high, large volumes of new soil are mounded on the soil surface beside burrow entrances. Burrow systems can have up to 36 holes covering some 14 m^2, of which 9 m^2 can be covered by fresh soil (Zhang and Zhong 1981). Around the burrow systems, the production of fine-grazing grasses such as *Aneurolepidium chinense*, *Stipa grandis* and *Cleistogenes squarrosa* decreases by 20%, 86% and 83%, respectively, and *Artemisia scoparia*, *Artemisia frigida*, *Carex duriuscula* and *Keoleria cristata* increase to 60% of total plant production. The result is that Brandt's vole facilitates the degeneration of pasture for livestock.

Habitat Selection of Brandt's Vole

There are no recorded cases of rodent pest problems in natural grassland or in areas subject to low grazing pressure. Outbreaks of Brandt's vole usually occur only in degraded pasture.

In natural pasture, the location of water sources, such as rivers, influences the grazing pressure of livestock. In one study (Zhong et al. 1985a) pasture within 3 km of a river suffered excessive grazing pressure. The area 3–8 km from the river showed moderate degradation, while the area 8–13 km from the river showed slight degradation. In the Kelulun River region, the production of herbs was 36% or 53% lower, and the density of Brandt's vole 3.6 or 0.9 times higher, in a heavily degraded area compared to a moderately degraded area (Zhong et al.1985a; Table 3).

Other research has reported a similar relationship between the density of Brandt's vole and the condition of the plant community (Liu 1979). A further investigation was conducted in a livestock resting site that was no longer used (Zhong et al. 1985b). Table 4 shows that in May 1974 low plant cover was associated with a high density of Brandt's vole, indexed by the number of holes/ha, whereas in August an increase in the height and cover of plants, mostly through rapid growth of *Aneuro-lepidium chinense* and *Allium anisopodium*,

Table 3.
The relationship between the density of Brandt's vole and the utilisation of the pasture in a terrace of the Kelulun River (Zhong et al. 1985a). The abundance of holes with signs of recent animal activity was used as an index of the density of voles. (Holes were covered with soil and checked 24 hours later. Re-opened holes were classified as active). The botanists' standard definitions were used for the degree of degradation.

Distance from river (km)	State of the pasture	Area of investigation (ha)	Density of Brandt's vole (active holes/ha)	
			June 1974	July 1975
1–3	Heavy degeneration	1.5	8.67	883.33
4–8	Medium degeneration	5.3	1.89	471.41
>20	Slight degeneration	4.0	0.0	0.0

Table 4.
Influence of vegetative change on the density of Brandt's vole at a resting site recently abandoned by livestock (Zhong et al. 1985b).

Time	Abandoned resting site			Normal grazing site		
	Vegetation			Vegetation		
	Height (cm)	Cover (%)	Voles active (holes/ha)	Height (cm)	Cover (%)	Voles active (holes/ha)
May	–	<5	972	–	10	204
August	40–50	95	0	15–20	30	84

A. bidentatum and *A. tenuissimum* after high summer rainfall, corresponded to a sharp decrease in the density of holes. Apparently, the low vegetative cover in May was due to grazing by voles, but by August voles would have dispersed to avoid high, dense vegetation.

Another study was carried out in 1982 by Zhong et al. (1985b). The vegetation and the density of holes used by Brandt's vole were monitored in a fenced area (*A*) that excluded livestock but allowed free access by rodents. The exclosure was compared to an area with normal grazing by livestock (*B*) and to a livestock resting site (*C*). The results are shown in Table 5. The density of Brandt's vole was inversely related to the height and cover of vegetation. The sites were ranked $A > B > C$ for plant biomass and $A < B < C$ for the relative density of voles. Parts of sites *A* and *B* were only 120 m apart, well within the range of movements of Brandt's vole, but the relative density of voles reached 5,616 holes/ha in C (Zhong et al. 1985b) and the density in *B* decreased by 33% to 84%. The distance from *A* to *B* was about 120 m, and from *B* to *C* about 500 m.

The biomass of *A. chinense*, which is Brandt's vole's preferred food (Wang et al. 1992), was higher in *A* than *B* and *C*. This suggests that food is not the main factor influencing habitat selection by Brandt's vole. More important factors appear to be

Table 5.
Comparisons of the density of Brandt's vole, indexed by the number of burrow holes/ha, and vegetation condition in areas with different use by livestock (Zhong et al. 1985b). Data are given as the mean (*X*) and the standard error (*SE*). *n* is the sample size.

Study site	Density of voles	Vegetation			
		No. of species/m^2	Height (cm)	Cover (%)	Biomass (g/m^2)
	n = 6 *X* ± *SE*	n = 20 *X* ± *SE*	n = 5	n = 5	n = 5 *X* ± *SE*
A. exclosure	700 ± 196	16.05 ± 0.47	30 – 35	57	190 ± 17
B. normal grazing	2063 ± 345	14.35 ± 0.51	13.6 – 16.4	46	102.9 ± 4.3
C. resting site	3661 ± 406	10.25 ± 0.51	5.4 – 7.4	33	53 ± 11
t-test	*A*<*C**	*A*>*C**	*A*>*C**	*A*>*C**	
*(*p* < 0.01)	*C*<*B*#	*C*<*B**		*C*<*B**	*C*<*B**
#(*p* < 0.05)	*A*<*B**	*A*>*B*#		*A*>*B**	*A*>*B**

the height and cover of vegetation, with voles preferring areas with sparse, low vegetation. It is likely that high, dense vegetation hinders the social behavior of Brandt's vole such as communication for feeding, mating and cooperative defense against predators (Xinrong Wan, unpublished data).

Although these studies indicate that both the height and cover of vegetation influence vole's habitat selection, it is not yet clear which one is the most restrictive factor. A study of the relationship between vegetation condition and the density of voles was carried in 1998. We chose 18 sites at random in Taipus Qi, Inner Mongolia, where we investigated the density of Brandt's vole and measured cover and height of vegetation at each site (Table 6). There was a significant negative correlation between the height of vegetation and the density of Brandt's vole ($r = -0.636$, $p < 0.01$), but there was no significant relationship between cover and the density of voles ($r = -0.128$, $p > 0.05$). These data suggest that there is an inverse relationship between the density of voles and the height of vegetation in areas where vegetation cover is in the range 28–75%.

Fenced areas were used to limit access by livestock in summer to allow recovery of pasture and the conservation of forage for winter grazing. Because the enclosures should improve the condition of vegetation, they should influence the density of Brandt's vole. This hypothesis was tested using five large enclosures in the Xilin Geluo and Zhe Limo region in 1987, with each enclosure more than 130 ha (Zhong et al. 1992). Table 7 indicates the condition of the vegetation and the density of voles inside and outside the exclosures during the course of the experiment.

The height of vegetation is significantly, negatively correlated with the density of Brandt's vole ($r = -0.708$, $n = 9$, $p < 0.01$) but there is no obvious relationship between plant cover and the density of voles

Table 6.
Comparison of the density of Brandt's vole and the vegetation conditions in its habitat. Data are given as the mean (*X*) and the standard error (*SE*).

Height of vegetation (cm) (*X* ± *SE*)	Cover (%) (*X* ± *SE*)	Density of Brandt's vole (Animals/ha) (*X* ± *SE*)
12.92 ± 0.89	36.40 ± 2.11	308.31 ± 21.36
13.82 ± 0.95	52.00 ± 2.55	339.36 ± 23.31
10.95 ± 0.42	40.00 ± 2.24	396.85 ± 30.14
11.38 ± 0.61	53.00 ± 1.22	419.20 ± 13.29
16.52 ± 0.76	34.40 ± 2.20	193.80 ± 12.87
19.92 ± 1.29	70.00 ± 3.54	92.64 ± 10.86
11.99 ± 0.64	29.20 ± 1.48	233.60 ± 21.37
12.84 ± 0.69	61.00 ± 2.33	528.88 ± 24.22
68.84 ± 1.91	74.60 ± 3.26	2.40 ± 1.17
8.92 ± 0.58	36.00 ± 2.45	306.38 ± 12.46
3.62 ± 0.29	46.00 ± 1.87	464.56 ± 47.00
7.32 ± 0.47	30.00 ± 1.58	407.36 ± 26.37
4.68 ± 0.70	41.00 ± 2.45	577.60 ± 23.90
11.68 ± 0.37	28.20 ± 1.11	220.65 ± 21.79
7.72 ± 0.68	61.00 ± 1.87	191.04 ± 17.93
9.60 ± 0.28	29.20 ± 1.52	239.42 ± 16.93
7.53 ± 0.36	54.50 ± 1.89	585.44 ± 38.38
11.48 ± 1.10	66.00 ± 3.67	416.20 ± 35.04

($r = -0.304$, $p > 0.05$). This result is supported by the data in Table 8 which show the rate of change in the height of herbs (e.g. *A. chinense*) and the percentage changes in the density of voles.

There is a significant coefficient of correlation between these two variables of –0.917 indicating a very significant correlative relationship. The conclusion is that the density and height of vegetation in the habitat of Brandt's vole strongly influences its social behaviour; i.e. an increased height of vegetation decreases the fitness of Brandt's vole so that the population density of the vole decreases sharply. This suggests that fencing and pasture management could be used in some areas to reduce problems caused by Brandt's vole. As a guide, the density of voles was low where the height of vegetation was >190 mm but high where vegetation height was 30–130 mm.

The suppressive effect of vegetation growth on the abundance of Brandt's vole takes effect from spring to autumn. However the most important factor influencing the survival of voles in winter is their store of food (Zhong 1996). As *A. frigida* is the largest component (44–71%) of stored food (Zhou et al. 1988), pasture management such as fencing that diminishes production of *A. frigida*, will also reduce the over-winter survival of voles.

Table 7.

The density of Brandt's vole and the condition of vegetation inside and outside livestock enclosures (Zhong et al. 1992). Data are given as the mean ± the standard error, *n* is the sample size, and I and O indicate measurements inside and outside the exclosures, respectively.

Exclosure		Cover of vegetation (%)			Height of vegetation (cm)			Density (voles/ha)		
		n	I	O	*n*	I	O	*n*	I	O
A	June	5	36.40 ± 2.11	36.00 ± 2.45	5	12.92 ± 0.89	8.92 ± 0.58	6	308.31 ± 21.36	306.38 ± 12.46
	September	5	52.00 ± 2.55	46.00 ± 1.87	5	13.82 ± 0.95	3.62 ± 0.29	5	339.36 ± 23.31	464.56 ± 47.00
B	June	5	40.00 ± 2.24	30.00 ± 1.58	5	10.95 ± 0.42	7.32 ± 0.47	6	396.85 ± 30.14	407.36 ± 26.37
	September	5	53.00 ± 1.22	41.00 ± 2.45	5	11.38 ± 0.61	4.68 ± 0.70	5	419.20 ± 13.29	577.60 ± 23.90
C	June	5	34.40 ± 2.20	28.20 ± 1.11	5	16.52 ± 0.76	11.68 ± 0.37	6	193.80 ± 12.87	220.65 ± 21.79
	September	5	70.00 ± 3.54	61.00 ± 1.87	5	19.92 ± 1.29	7.72 ± 0.68	5	92.64 ± 10.86	191.04 ± 17.93
D	June	10	29.20 ± 1.48	29.20 ± 1.52	10	11.99 ± 0.64	9.60 ± 0.28	10	233.60 ± 21.37	239.42 ± 16.93
	September	10	61.00 ± 2.33	54.50 ± 1.89	10	12.84 ± 0.69	7.53 ± 0.36	10	528.88 ± 24.22	585.44 ± 38.38
E	August	5	74.60 ± 3.26	66.00 ± 3.67	5	68.84 ± 1.91	11.48 ± 1.10	4	2.40 ± 1.17	416.20 ± 35.04

Table 8.
The proportional change in the height of herbs and percentage decease of the vole population density in the exclosure in comparison to outside. From Zhong et al. 1992. Calculated from Table 7.

Exclosure	A		B		C		D		E
Time	June	September	June	September	June	September	June	September	August
	Times change in height of herbs								
	1.45	3.82	1.50	2.43	1.41	2.58	1.25	1.71	6.00
	% change in vole density								
	-0.63	26.95	2.58	27.42	12.17	51.51	2.43	9.66	99.42

Ecological Management of Brandt's Vole

In Inner Mongolia, local herdsmen fence off pasture in June to increase herbage for harvesting in autumn or for grazing by livestock in winter. However damage is still caused by Brandt's vole in some areas because fencing is not properly maintained to exclude livestock. High rainfall and warm temperatures in May can promote early pasture growth that may be useful in suppressing vole populations. The effect of removing livestock from pastures in the middle of May, rather than later in June, was examined using a series of experimental exclosures in Taipus Qi, from 1986–1990 (Zhong et al. 1991). Exclosure I was fenced from the middle of May, the control exclosure was fenced from June (according to the local custom) and a third area (III) remained unfenced throughout the experiment. Both fenced areas were opened to grazing from 3 September through to May (exclosure I) and June (exclosure II) of the following year. Sheep were stocked at 1.62 animals/ha during the grazing period. There were no differences between exclosures I, II and III in the vegetation and the density of Brandt's vole prior to the experiment.

In 1987 rainfall was 289.59 mm, 30% below average. In autumn, the height, cover and biomass of vegetation were higher in exclosure II than in exclosure I , and in the period from spring to autumn the rate of increase of the vole populations was 0.62 in exclosure I compared to 1.99 in exclosure II and 2.11 in exclosure III (Table 9). The autumn density of voles was 4.6 times higher in exclosure II than I. The experiment demonstrated that exclusion of livestock from pasture half a month earlier in mid-May increased biomass of grass by 40% and decreased the density of Brandt's vole by 78%. Comparing exclosure II and III, the increased grazing on the latter site resulted in the height, cover and biomass of vegetation being reduced by 70%, 12% and 55%, respectively, but there was no significant difference in the density of Brandt's vole. There appeared to be a significant threshold between 120 and 160 mm in the suppressive effect of vegetation height on the abundance of voles, and the traditional time of fencing in June was too late to allow vegetation to exceed this threshold.

The study was continued in 1988 and 1989 (Table 10). The year of 1988 was a wet year, with 339.8 mm of rainfall from May to August, 17.33% more than normal. The height, cover and biomass in the exclosure I were 95%, 10% and 80% higher than that outside exclosure, respectively. The density of Brandt's vole inside the exclosure was 2.24 times lower inside than outside the exclosure; the difference was significant ($p < 0.01$).

In 1989, 158.7 mm rain fell during the period from May to August, which was 45% less than average and the height, cover and biomass of vegetation was 35%, 22% and 139% higher in the exclosure than in the grazing area, respectively. Because of the aridity, the height of the main herb layer was about 144.2 mm, less than the critical value of 160 mm. The density of Brandt's vole in the exclosure was 16.85 animals/ha, not significantly different from the density of 33.74 animals/ha in the grazed area ($t = 1.68$, $p > 0.05$), and both were under the threshold for causing damage. Therefore, although no damage occurred in 1989, the data from the exclosure experiment in that year and from other years with different climatic conditions demonstrated the simultaneous effects of producing more grass and suppressing Brandt's vole.

After the ecological measurements, many colonies of Brandt's vole disappeared, their complex burrow systems were abandoned, and herbs grew quickly around these areas forming patches different from the surrounding area. These patches, or 'mosaics', were classified as two types: mosaic I where a burrow system was abandoned during May or June in the current year and mosaic II where the burrow system was abandoned in the previous year. Herbs growing in mosaics were big and tall (see Table 11). Vegetation cover in mosaics I and II was 1.1 and 1.07 times greater than in the non-burrow areas, respectively, and the

Table 9.

The impact of different grazing treatments on vegetation indices and the density of the Brandt's vole population. The experiment was conducted from spring to autumn in 1987 using three experimental areas: (I) livestock excluded from mid-May, (II) livestock excluded from June, and (III) free access to livestock (no fencing). Data are given as the mean ± the standard error and n is the sample size. The rate of increase of the vole population over the period from spring to autumn is calculated as $r = \ln(N_{t+1}/N_t)$ where N_t is the density at time t.

Treatment	Area (ha)	Vegetation in autumn			Density of Brandt's vole/ha		Rate of increase
		Height (cm)	Cover (%)	Above-ground biomass (g/m^2)	Spring	Autumn	
I	93	16.96 ± 0.43	73.50 ± 1.07	342.44 ± 16.42	63.00 ± 5.48	116.95 ± 36.32	0.62
		$n = 10$	$n = 10$	$n = 10$	$n = 10$	$n = 10$	
II	99	12.84 ± 0.69	61.00 ± 2.33	245.28 ± 12.12	73.41 ± 8.41	535.50 ± 25.43	1.99
		$n = 10$	$n = 10$	$n = 10$	$n = 8$	$n = 8$	
III	80	7.53 ± 0.36	54.50 ± 1.89	157.90 ± 6.00	69.39 ± 12.82	571.10 ± 38.32	2.11
		$n = 10$	$n = 10$	$n = 10$	$n = 8$	$n = 8$	

Table 10.
The impact of different grazing treatments on vegetation indices and the density of Brandt's vole population during 1998 and 1989. Data are given as the mean ± the standard error. *n* is the sample size and the rate of increase is calculated as in Table 9.

Year	Study site	Vegetation in autumn				Density of Brandt's vole/ha			
		n	Height (cm)	Cover (%)	Biomass (g/m^2)	*n*	Spring	Autumn	Rate of increase
1988	exclosure	30	27.59 ± 0.77	87.70 ± 1.37	785.87 ± 24.31	10	77.41 ± 4.40	38.04 ± 9.80	- 0.71
	unfenced	15	14.12 ± 0.64	80.13 ± 2.76	436.56 ± 26.22	10	99.97 ± 5.15	123.42 ± 12.46	0.21
1989	exclosure	30	14.42 ± 0.62	58.67 ± 1.24	129.23 ± 10.08	10	9.02 ± 2.08	16.85 ± 3.97	0.62
	unfenced	15	10.64 ± 0.44	47.67 ± 1.61	54.00 ± 5.74	10	14.00 ± 1.64	33.74 ± 9.25	0.88

Table 11.
Vegetation indices in mosaics I and II (see text) and in an area with no vole burrows. Data are given as the mean ± the standard error and *n* is the sample size.

Type	Cover of vegetation (%)	*Chenopodium aibum*		*Aneurolepidium chinense*		Biomass of other plants
		Height (cm)	Biomass (g/m^2)	Height (cm)	Biomass (g/m^2)	
Mosaic I	97.00 ± 1.22	85.52 ± 1.71	910.00 ± 85.58	45.72 ± 2.76	350.00 ± 41.76	530.00 ± 53.76
(*n* = 5)						
Mosaic II	94.00 ± 1.00	49.40 ± 2.77	94.00 ± 33.65	46.04 ± 1.04	970.00 ± 87.31	280.20 ± 89.96
(*n* = 5)						
No burrows	87.70 ± 1.37	0	0	27.59 ± 0.77	121.87 ± 11.72	664.00 ± 26.45
(*n* = 30)						

biomass of *A. chinense* in mosaics I and II was 2.87 times and 7.96 times that of the biomass in the non-burrow area, respectively. Productivity of a mosaic could exceed the productivity of the surrounding area in three months, with a considerable increase in the biomass of fine grazing grass such as *A. chinense* in the mosaics.

The ecological management of the vegetation was economically efficient with an increase of 530 kg/ha of dry matter produced in 1987 and an investment:income ratio of 1:7. 1988 was a wet year, with 1,753 kg/ha more dry herbs harvested, and the investment:income ratio was 1:8.8 (Zhong et al. 1991). By comparison, 1989 was the worst drought year in 29 years. Productivity was increased by 123 kg/ha at harvest that year and the investment:income ratio equaled 1:2.7. Over the three years from 1987–89, the average investment:income ratio was 1:7. In summary, good ecological management not only stopped the damage caused by Brandt's vole but also enhanced the productivity of the grassland.

Discussion

Heavy grazing pressure by livestock causes degradation of grassland in Inner Mongolia, with different rodent pests occurring at each different degenerative stage. At the same time, the rodents' devouring and digging activities aggravate the degradation of the grassland, i.e. there is positive feedback between damage caused by rodents and the degeneration of grassland that can lead ultimately to desertification (Figure 2). Coordinated management of livestock, grasses and rodents is required to break this vicious cycle.

The main aims of an ecological approach to controlling rodents in grasslands are economic benefits, minimal or no use of rodenticides to avoid chemical contamination of the environment, and a long-term solution brought about by decreasing the carrying capacity of rodents. To achieve this, we have studied the ecological management of both *M. brandti* and *O. daurica* simultaneously (Zhong 1996) from 1991 to 1996.

Detailed ecological studies of pest species are needed before ecological management is applied: the life history of a pest species must be understood for identifying weak links. For example, stored food is the most important factor influencing the survival of rodents during the long and cold winters in the grassland of Inner Mongolia. Decreasing the available storage food for rodents could

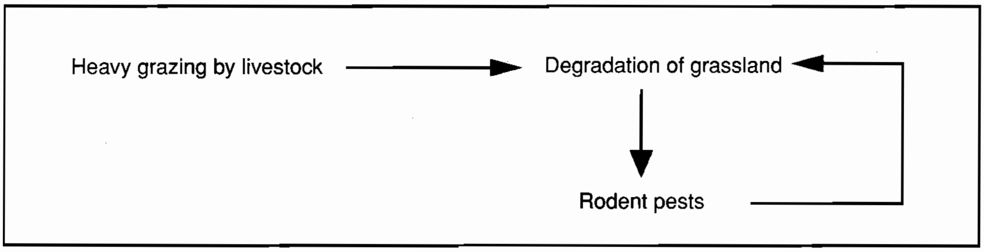

Figure 2.
Schematic diagram showing the interactions of livestock and rodents in grasslands. Overgrazing by livestock can degrade grasslands to a level that will be maintained indefinitely by rodent pests.

remarkably suppress the growth of rodent populations (Zhong 1996).

We used exclosures to adjust the pressure and duration of grazing by livestock. This resulted in the recovery of degraded grassland and a decline of the density of Brandt's vole. This result could be achieved in other ways. The cost of building fences could be saved by moving herds of livestock alternately between different areas based on well designed grazing plans, effectively employing 'formless exclosures'. As well, irrigation and the use of fertiliser are effective means of accelerating the recovery of degraded grassland (Zhong 1996). Rapid recovery of vegetation can quickly suppress Brandt's vole, preventing future degradation with economic savings in the long term.

The need for livestock to have access to water results in uneven grazing pressure and degradation of grassland near rivers. Grazing pressure near rivers can be reduced by digging wells to change the pattern of herding livestock and make full use of grass resources distant from rivers.

Dicotyledons are the main component of rodents' stored food for winter. Fencing to exclude livestock can decrease the biomass and proportion of dicotyledons in the plant community. In addition, we sowed monocotyledon seeds to increase the proportion of fine-grazing grass in fenced areas, with encouraging results (Zhong 1996). Another practice is to plough the grassland. Roots of *A. chinense* and *S. grandis* are extensive and easily cut to promote tillering. The result is an increase in the biomass and proportion of these fine-grazing grasses in the plant community (Zhong 1996).

Future research will be directed towards the strategy of ecological management at the landscape level. Myllymäki (1979) reviewed the landscape characteristics that could create conditions favourable for rodent plagues, and others that tend to prevent outbreaks. Some references suggest that characteristic changes of landscape would influence movement, competitive interaction, predation etc. of mammals in this habitat (Lidicker 1995).

Our approach to ecological management is not simply habitat modification. The main features of habitat modification are removal of basic life needs (food and water) from rodents and rodent proofing (Fitzwater 1988) using techniques such as clearing weeds quickly after crops are harvested, spraying 2,4-D herbicides to reduce pocket gopher's (*Thomoys talpoides*) favourite food and hence decrease their activity (Keith et al. 1959), planting buffer crops which pests prefer and setting up physical barriers. These techniques can eliminate rodent pests but may have deleterious effects on other vertebrate species that share the same habitat (Howard 1988), and they are usually expensive. Ecological management comes from systematic view, based on ecological studies, using natural forces to target weak links in the life history of a pest species. The aim is to take careful consideration of relationships with other species and the environment, while using existing equipment to save money and exploring new ways to enhance production.

Although we have achieved effective ways to manage Brandt's vole and the Daurian pika simultaneously (Zhong 1996), many improvements are still demanded.

Future study will continue to apply ecological principles to pest management.

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10. Biological Control of Rodents — the Case for Fertility Control Using Immunocontraception

Lisa K. Chambers, Malcolm A. Lawson and Lyn A. Hinds

Abstract

Managing rodent pests on a broad scale using lethal methods is not an appropriate long-term strategy given their extraordinary breeding capacity and high mobility. Moreover, environmental, animal welfare and ethical concerns regarding the use of poisons and trapping has decreased the acceptance of mortality methods in recent times. Another reason for avoiding lethality is that it may promote a strong selective pressure for resistance to the lethal agent, be it a disease or a chemical. The addition of fertility control, specifically immunocontraception, to the armoury currently available to control rodent pests, is discussed in this chapter. Fertility control aims to reduce a specific population size by reducing the number of young produced and recruited into the population.

Existing fertility control techniques (e.g. steroids, synthetic hormones) are flawed because they require repeated administration to maintain the sterility level of the population, they have undesirable physiological and behavioural side effects and they are not specific to the target animal. Delivery of these sterilising agents is logistically difficult, time-consuming and expensive and therefore they are not suitable for controlling field populations of rodent pests that are often widespread and cryptic in their habits. An immunocontraceptive vaccine, either distributed in bait or disseminated in a species-specific viral vector, is a new tool that could be used to reduce the productivity of pest populations. The various components of this approach and 'proof of concept' laboratory experiments conducted in house mice in Australia are described. It must be recognised that to critically evaluate the efficacy of a viral-vectored immunocontraceptive agent requires a multi-disciplinary approach with a strong ecological and epidemiological focus. Only then can the impact of this control technique be assessed at the population level.

Keywords

Immunocontraception, biological control, rodents, viral-vectored, fertility control, genetically manipulated organism, murine cytomegalovirus, zona pellucida, ectromelia virus, reproductive antigens

INTRODUCTION

RODENTS HAVE gained the reputation as one of the most persistent and ubiquitous vertebrate pests affecting human populations. They cause economic problems because of the damage they inflict in agricultural systems (e.g. Caughley et al. 1994), environmental problems due to the chemicals used for their control (e.g. Saunders and Cooper 1981; Singleton and Redhead 1989), social problems associated with their close proximity to human habitation (e.g. Beckmann 1988) and health problems as carriers of zoonoses (Childs et al. 1994; Gratz 1994; also see Mills, Chapter 6). Of increasing concern is the impact of introduced rodents on the conservation of native wildlife (e.g. Wace 1986; Moors et al. 1992; Key et al. 1994; also see Dickman, Chapter 5). Rats have been reported as the major pest in rice crops in Southeast Asia (Geddes 1992; Singleton and Petch 1994), and cause significant problems in Africa (Leirs et al. 1997; also see Makundi et al., Chapter 22), Australia (Singleton and Redhead 1989; Caughley et al. 1994), China (see Zhang et al., Chapter 12) and elsewhere (Prakash 1988a; also see Buckle, Chapter 7).

Many species that become pests do so because of their reproductive potential. They often have several large litters in each breeding period, show early onset of sexual maturity and have a short life expectancy (Tyndale-Biscoe 1994). Rodent pests typically show these life history traits—for example, one breeding pair of house mice (*Mus domesticus*) is theoretically capable of producing over 600 offspring in six months and the average life expectancy in a field population is four to six months (Singleton 1989). A post-partum oestrus allows females to produce a litter every 21 days (Whittingham and Wood 1983). Therefore, curbing the reproductive potential of rodents may be a more appropriate control tactic than increasing their mortality (Singleton 1994; also see Krebs, Chapter 2).

Increasing community interest in environmental and animal welfare issues associated with conventional pest control techniques, such as poisoning and trapping, has focused interest on developing non-lethal, non-toxic alternatives (Bomford 1990). One such strategy is to focus on reducing reproduction, rather than increasing the mortality of the pest species. This is commonly referred to as fertility control.

In this chapter, we will examine why fertility control is theoretically superior in many respects to conventional methods of rodent control that rely on increasing mortality. We discuss the various methods of fertility control currently available for reducing rodent pest populations and then focus on immunocontraception, a relatively new approach to the problem of controlling wild pest populations.

Effective pest control requires a thorough understanding of the biology and population dynamics of the pest species (Howard 1967). Specifically, for effective fertility control, a reduction is required not only in the reproductive potential of the species, but also in the final population size (Bomford 1990; Bomford and O'Brien 1997) and in the potential damage inflicted (Bomford and O'Brien 1997). Thus, we emphasise in this chapter the importance of an ecological framework for considering the use of immunocontraception and fertility control in general. We also stress that although the general principle of fertility control is similar for all mammals, the particular approach may be different for each pest and needs to consider the ecological and behavioural features of each species (Cowan and Tyndale-Biscoe 1997).

Conventional Methods of Control

Control of rodent pests currently relies on increasing their mortality. For large-scale control in agricultural systems, this typically involves the use of rodenticides such as anticoagulants and acute poisons (see Meehan 1984; Prakash 1988a for reviews). In small-scale domestic control, both rodenticides and traps are often employed. These methods are easily applied by farmers or householders and there is usually an immediate effect on population size and damage caused by rodents (Table 1) (Bomford 1990).

However, these conventional control methods are obviously not always effective in the long term (Table 1) as rodent pests are still a major problem. This may be because lethal methods are often used inefficiently as an ad hoc control approach when rodent populations have already reached high densities. Another major factor is the high reproductive capacity of the pest and the ability to re-invade treated areas from surrounding untreated sites (e.g. Emlen et al. 1948; Twigg et al. 1991). Also, because these methods are often labour intensive, they are rarely applied in areas with inaccessible terrain. The expense of poison-baiting large areas long-term can also be prohibitive, particularly if damage to crops is not reduced. For example, during a mouse plague in southern Australia in 1993, the cost of one bait application to 46,000 ha was approximately A$319,500 (Kearns 1993).

Table 1.
Advantages and disadvantages of rodenticides for the control of rodent pests (after Singleton and Redhead 1989; Bomford 1990; Chambers et al. 1997 unless indicated otherwise).

Advantages	Disadvantages
Immediate effect on population numbers and damage	Development of bait shyness if sublethal dose ingested (Prakash 1988b)
Permanent control method; removes animals for the whole of their expected life span	Non-target deaths due to primary and secondary poisoning—not species-specific
Cost effective for short-term control and reduction in damage caused	Inhumane
	May pollute the environment with poison residues
	Potential re-invasion of treated areas by rodents from neighbouring untreated sites
	Ineffective over the long-term for highly fecund or mobile species (e.g. rodents) (Caughley 1977, 1985)
	Expensive to apply over large areas long-term

Fertility control has the potential to overcome some of the inadequacies of conventional control techniques and a naturally disseminating immuno-contraceptive would reduce the need for manual delivery of the control agent.

Fertility Control as an Alternative to Conventional Methods

Fertility control has been suggested as a more appropriate control strategy than enhancing mortality under the following circumstances:

- for species with high fecundity (Caughley et al. 1992; Tyndale-Biscoe 1994);
- for species with high natural mortality rates and a rapid population turnover (Stenseth 1981; Bomford 1990; Hone 1992; Barlow 1994; Barlow et al. 1997);
- when a more humane method of population control is desired (Marsh and Howard 1973; Hutchins et al. 1982; Hutchins and Wemmer 1987);
- when the effects of sterilisation exceed any increases in juvenile or adult survival due to a lowering of birth rates (Sinclair 1997); and
- for preventing or reducing population growth after some other technique has reduced numbers, particularly in long-lived species (Bomford 1990; Barlow 1994).

The last point emphasises one of the main differences between these two control strategies—increasing mortality has an immediate effect on population numbers and damage, while reducing fertility has a delayed response until natural mortality reduces population size (Barlow et al. 1997). If sterile individuals inflict as much damage as fertile individuals, sterility is of little practical value to agriculturalists. Thus, in some instances, fertility control may need to be used in conjunction with another control method.

It has been suggested that the presence of a given number of sterile individuals in the population exerts a greater, more sustained biocontrol pressure than if the same number of animals were simply removed from the population (Howard 1967). Sterile individuals fail to contribute to the next generation as well as competing for space, food and social order. This in turn reduces the reproductive success and survival of fertile individuals and continues the suppression of breeding in subordinates if dominants are sterilised (Howard 1967). Therefore, fertility control could be used as a long-term strategy for slowing a population's growth rate and hence maintaining numbers at this lower level. Modelling the relative impact of culling versus sterilisation on populations with density-independent or exponential growth rates supports this argument (Bomford 1990). However, for populations with density-dependent or logistic growth rates, the relative efficiency of sterilisation will depend on the nature of the density-dependent regulation. Populations with density-dependent mortality appear to be reduced by sterilisation more quickly than those with density-dependent recruitment (Barlow et al. 1997).

General Aims of Fertility Control

Fertility control aims to reduce population size by reducing the number of young produced and recruited into the population. This can be achieved by temporary, permanent or partial sterilisation.

A successful fertility control method therefore needs to (after Bomford 1990; Bomford and O'Brien 1997):

- cause temporary or permanent sterility leading to reduced recruitment in the population;
- be deliverable in a way that allows an adequate proportion of the target population to be treated, particularly for widespread and abundant species in areas with poor access;
- reduce the target population sufficiently to reduce damage caused by the pest species to an acceptable level (Braysher 1993);
- produce minimal side effects to the target species (e.g. behavioural changes, interference with social structure);
- be target-specific;
- be environmentally benign (Marsh and Howard 1973); and
- be cost effective compared with conventional methods of control.

In the following section, we explore the various options available for fertility control of rodents and examine how well each of these satisfy the criteria for a suitable fertility control agent for controlling wild populations.

Options for Fertility Control — Existing Technologies

Many techniques have been developed for managing or controlling the fertility of individual animals in captivity or in confined areas that are not subject to immigration. These methods include surgical sterilisation or castration, use of chemical sterilants, agonists that block the function of natural hormones, and inhibitors of lactation (Table 2). Most of these approaches are expensive and time-consuming to apply, often have undesirable side effects (e.g. chemosterilants can induce gastrointestinal problems, abnormal growth and dysfunction of the gonads), and affect non-target species. Many disrupt gonadal function and sexual behaviour. Further, their applicability and effectiveness for free-ranging populations is low due to the difficulties of delivering the sterilising agent on a broad scale and sustaining the inhibition of reproduction.

Immunocontraception for Controlling Pest Populations — the Concept

Immunocontraception uses the body's immune system to induce immune responses (circulating antibodies or cellular immune effector cells) against reproductive cells or proteins essential to successful gametogenesis, fertilisation or implantation, leading to infertility. The feasibility of immunocontraception was directly demonstrated when Baskin (1932) injected women with human sperm and no conceptions occurred during the one-year follow-up period.

Ideally, the immunocontraceptive prevents pregnancy but does not disrupt endocrine function (i.e. renders the animal infertile but not impotent) and therefore reproductive/social behaviour is unaffected. Animals continue to occupy territory,

Table 2.

Summary of potential techniques for fertility control of pest populations and assessment of their relevance for managing rodents. Sources: Singleton and Spratt 1986; Spratt and Singleton 1986; Marsh 1988; Vickery et al. 1989; Bomford 1990; Sankai et al. 1991; Gao and Short 1993; Tyndale-Biscoe 1994, 1997a; Marks et al. 1996; Becker and Katz 1997; Jochle 1997.

Technique for fertility control	Major advantages	Major disadvantages	Efficacy for rodent pest populations	
			Current	Future
Surgery	**Castration and ovariectomy**		Very low	Very low
	Permanent	Expensive and invasive		
	One treatment only, therefore costs recouped over time	Leads to behavioural changes		
	Vasectomy and tubal ligation		Very low	Very low
	Permanent	Expensive and invasive		
	One treatment only, therefore costs recouped over time	Impractical for high density field populations		
	No behavioural changes			
Disease	**For example, *Capillaria hepatica***		Field tested, but ineffective at low densities	Low
	Natural parasite of rodents	Insufficient level of persistence in Australian situation		
		Complex life cycle		
Chemicals	**Agonist and antagonists of GnRH[a] (disrupt natural hormone functions)**		Low, but untested	Low, but untested
	Both sexes infertile	Costly to administer		
		Not permanent, may only reach a proportion of the population		
		Side effects (dose dependent)		
		Not appropriate for promiscuous species		

[a] GnRH = gonadotrophin releasing hormone

[b] ISCOMs = immunostimulatory complexes.

Table 2. (Cont'd)
Summary of potential techniques for fertility control of pest populations and assessment of their relevance for managing rodents. Sources: Singleton and Spratt 1986; Spratt and Singleton 1986; Marsh 1988; Vickery et al. 1989; Bomford 1990; Sankai et al. 1991; Gao and Short 1993; Tyndale-Biscoe 1994, 1997a; Marks et al. 1996; Becker and Katz 1997; Jochle 1997.

Technique for fertility control	Major advantages	Major disadvantages	Efficacy for rodent pest populations	
			Current	Future
Chemicals	**Synthetic steroids, anti-steroids, anti-steroid receptor (e.g. Diethylstilbestrol, RU486)**		Low, but untested	Low, but untested
	Low cost	Side effects (dose dependent)		
	Bait or implant	Must be administered regularly		
		Non-target effects		
	Prolactin inhibitors (affect lactation and/or gestation (e.g. Bromocriptine, Cabergoline)		Low	Moderate
	Oral delivery	Not permanent		
	Low cost	May not be ethically acceptable as starves young or aborts foetuses		
		Must be regularly administered		
Immunocontraception	**Disseminating vector, non-disseminating vector, synthetic delivery systems (e.g. ISCOMs[b], microspheres)**		Moderate but untested	Expected high
	Long term reduction in fertility	Not yet available		
	Species-specific, humane, cost effective	May need to repeat application		
	Could be reversible	Includes use of genetically modified organisms		

[a] GnRH = gonadotrophin releasing hormone
[b] ISCOMs = immunostimulatory complexes.

maintain social status and may suppress the fecundity of subordinates. Such an approach is potentially species-specific, considered humane and could be cost effective in the long term (Tyndale-Biscoe 1994).

Unlike vaccines directed against infectious diseases, immunocontraceptive vaccines are directed against 'self' proteins that would not normally be recognised as foreign (Alexander and Bialy 1994; Jones 1994; Dunbar 1997). Therefore, the 'self' antigen to be used in the vaccine must be presented in a 'foreign' or 'non-self' form to elicit an immune response. In 1987, a new approach to fertility control was conceived—the concept that viruses could be used to deliver immunocontraceptives (Tyndale-Biscoe 1994) (see Figure 1). This could be achieved by delivering the immunocontraceptive vaccines through the agency of a virus or other contagious agents that spread naturally through the target pest population. Similarly, a non-disseminating agent in baits could be used to provoke an appropriate immune response.

Since 1992, this approach has been under development at the Cooperative Research Centre for Biological Control of Vertebrate Pest Populations (Vertebrate Biocontrol CRC) and its successor the Pest Animal Control CRC based in Canberra, Australia. The Centre's mission is "to contribute to the better management of Australia's biodiversity by limiting growth of vertebrate pest populations through fertility control".

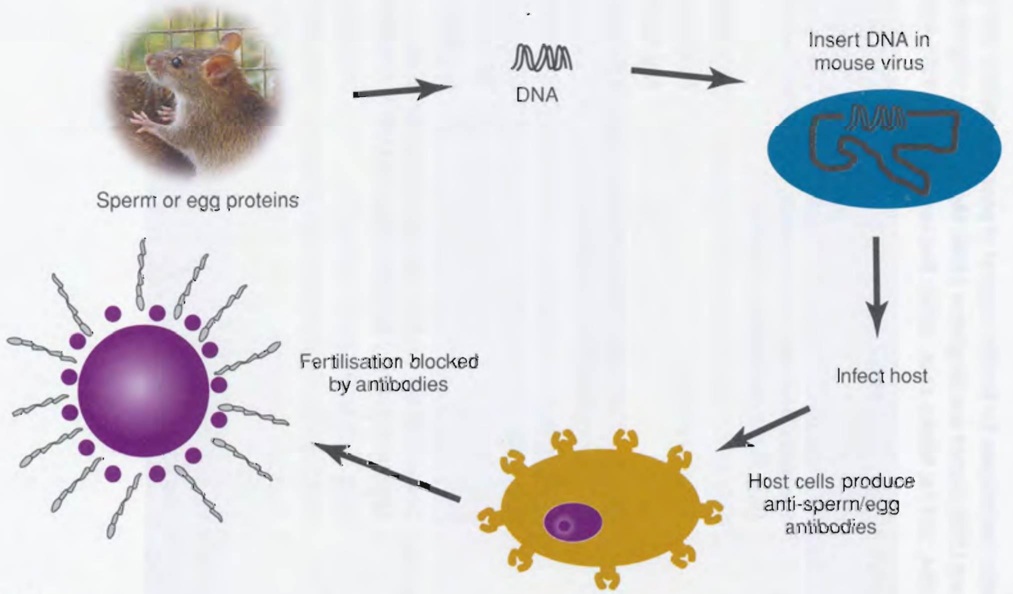

Figure 1.
The concept of viral-vectored immunocontraception. Genes encoding a reproductive protein(s) are incorporated into the genetic structure of a species-specific virus. This virus infects the host, expressing the reproductive protein(s) as well as viral proteins on the surface of infected cells. The host's immune system produces antibodies against the reproductive protein(s), as well as the virus, and these spread to the reproductive tract where they bind to either the egg or the sperm and block fertilisation. Redrawn with permission from the Vertebrate Biocontrol CRC.

Immunocontraception—Its Components

The choice of reproductive antigen(s)

Fertility control agents may be of two types: anti-gonadal or anti-gametic. By targeting the gametes there is likely to be less disruption of other reproductive functions, but sustained immune responses may be more difficult to achieve because the gamete proteins are produced in small quantities at specific sites and are not highly immunogenic (Alexander and Bialy 1994). Initial studies by many groups have focused on sperm proteins as candidate antigens. The view was that male antigens might be able to induce significant immune responses in the female reproductive tract because they were not expected to be auto-antigens in females. The potential of sperm proteins, such as SP-10 and testis-specific lactate dehydrogenase (LDH-C4) has been explored in humans, baboons and pigs (Goldberg and Shelton 1986; Herr et al. 1990a,b) and PH-20 in guinea pigs (Primakoff et al. 1988). Initial research in the Vertebrate Biocontrol CRC also focused on sperm antigens (Bradley 1994; Holland and Jackson 1994; Tyndale-Biscoe 1994). However, after several sperm antigens had been tested by direct immunisation without effects on the fertility of female rabbits or foxes (Bradley et al. 1997; Hardy et al. 1997; Holland et al. 1997), attention turned to the female gamete antigens, specifically the zona pellucida proteins forming the extracellular coat of the oocyte.

In the mouse, the zona pellucida comprises three non-covalently linked glycoproteins, ZPA, ZPB and ZPC, which are expressed by the growing oocytes in the ovary. ZPC is the receptor for sperm binding at the time of fertilisation (Florman and Wassarman 1985; Rosiere and Wassarman 1992). Passive immunisation with monoclonal antibodies to ZPC inhibit fertilisation in vivo (East et al. 1984, 1985), and active immunisation with synthetic peptides which include a B-cell epitope of ZPC also induce infertility for periods from 0–8 months (Millar et al. 1989; Lou et al. 1995). For these reasons, mouse ZPC (also known as ZP3) was the first candidate antigen to be tested in a mouse viral-vectored system.

Many of the zona pellucida proteins and sperm proteins show high identity between species (Harris et al. 1994; Bradley et al. 1997; Holland et al. 1997; Jackson et al. 1998). Therefore a key challenge is to identify or engineer the antigen to be species-specific. This may be achievable using specific peptides or epitopes. The difficulty then becomes whether such small peptides have the ability to block fertility. The use of epitopes alone or in combination with immunomodulatory molecules (such as cytokines or T-cell help epitopes) to enhance the species-specific immune responsiveness to these antigens are currently being investigated (Dalum et al. 1997; Ramsay and Ramshaw 1997).

Delivery of the immunocontraceptives

The delivery of an anti-fertility vaccine to populations of wild animals over large areas poses a number of unique problems. It is essential to consider the distribution of the species under study, whether large-scale or localised control is desired, and any possible consequences for non-target species. Another factor is the genetic heterogeneity of the wildlife population, which is certain to generate significant individual variability in the immune responses to a vaccine (Klein 1979). Effective application of any vaccine requires that a high level of immunity can be achieved amongst individuals exposed to the vaccine (Alexander and Bialy 1994). As mentioned previously, it may therefore be necessary for the antigen(s) to be presented in conjunction with other highly immunogenic carrier proteins (e.g. cytokines and immunomodulatory molecules) to maintain a contraceptive level of immunity. In addition, multiple antigenic determinants could be included within a vaccine to stimulate a broad range of immune responses.

The three main delivery systems under development are (i) non-disseminating genetically modified organisms (GMOs) in baits, (ii) synthetic delivery systems and (iii) disseminating GMOs such as viruses or bacteria. For many rodent pests, particularly those that are native species, bait delivery may be the method of choice for political, social, economic and ecological reasons.

Non-disseminating agents

Non-replicating GMOs, such as attenuated *Salmonella*, are currently being developed and tested (Bradley 1994; Bradley et al. 1997). Selected mutant strains of *Salmonella* have the advantage that they are avirulent without decreasing their immunogenicity and they are not infective. Furthermore, the introduction of a 'suicide' plasmid into this system would have the added advantage of degrading the foreign deoxyribonucleic acid (DNA) and would make it more acceptable because the bait-delivered product would contain no foreign genetic material (Knudsen et al. 1995; Tedin et al. 1995).

Various gram negative bacteria (*Escherichia coli, Salmonella typhimurium, Vibrio cholerae, Klebsiella pneumoniae* and *Actinobacillus*) can be engineered to carry a gene (PhiX174 geneE) which, when induced, causes lysis and release of the cytoplasmic contents of the bacteria. This process produces a non-living vaccine delivery system. These bacteria can also be engineered to carry other genes (e.g. encoding reproductive proteins). After lysis, the 'ghost' bacteria contain only membrane-associated recombinant antigen. Bacterial ghosts are cheap to produce, can be stored for long periods and can contain multiple antigenic determinants that are present in a highly immunostimulatory environment (Szostak et al. 1996). Such features make bacterial ghosts an attractive delivery system for immunocontraceptive antigens. However, it remains to be seen whether these preparations produce immunity to reproductive antigens after oral delivery.

Synthetic delivery systems

Synthetic delivery systems for antigens include ISCOMs (immunostimulatory complexes—e.g. Quil A, cholesterol, phospholipid constructs), microspheres (polylactide-coglycolide polyphosphazenes), and liposome emulsions (Davis 1996).

The current high costs of production mean these systems are only suitable for human and companion animal vaccination and not for broad-scale application to a wildlife population. Nevertheless, the per unit production cost will decrease as these systems become more popular and production technology improves.

Disseminating GMOs

These currently have the greatest theoretical potential for use as vectors for immunocontraceptive agents. A viral vector could potentially overcome problems associated with the distribution of an immunocontraceptive to control wild populations (Bomford 1990). The advantages of a viral-vectored immunocontraceptive agent over a bait-delivered immunocontraceptive agent are summarised in Table 3. Clearly the selection of a viral vector requires careful consideration of its properties. The current vector of choice for delivery of a mouse immunocontraceptive is mouse cytomegalovirus and it possesses most of the essential and desirable characteristics required (Table 4), although additional research is required to confirm some of its features.

Viral-Vectored Immunocontraception (VVIC) — Laboratory Progress

Ectromelia

Ectromelia virus (ECTV: family Poxviridae, genus *Orthopoxvirus*) causes the disease known as mousepox and is a pathogen of laboratory mice (Fenner and Buller 1997). It is closely related to vaccinia virus and was investigated as a useful model system for the development of viral-vectored immunocontraception (VVIC). A recombinant ectromelia virus, with a thymidine kinase negative phenotype, expressing ZPC was constructed and then used to infect female inbred laboratory mice of the BALB/c strain, which are highly susceptible to mousepox (Jackson et al. 1998). Fertility was assessed by pairing females with males from three weeks post-infection and monitoring for

Table 3.
Viral-vectored versus bait-delivered immunocontraceptives (after Bomford 1990; Shellam 1994; Chambers et al. 1997)

Advantages of a viral-delivered immunocontraceptive
A replicating virus may induce a stronger immune response and greater immunological memory.
An infective agent can potentially spread a reproductive protein rapidly through a population.
A self-perpetuating, infectious agent is ultimately cheaper than baits which must be manually applied.
A viral vector is a species-specific carrier.
Overcomes problems associated with bait aversion or bait shyness.
Overcomes the precise timing necessary for bait delivery relative to the target animal's breeding cycle.
Reduces wastage associated with inadvertent multiple baiting of some individuals.
Advantages of a bait-delivered immunocontraceptive
More acceptable to the public than the use of a disseminating genetically modified organism.
Easier regulation of control activities—can be readily withheld or withdrawn from use.

Table 4.

Essential and desirable properties for a virus which will act as a vector of an immunocontraceptive agent for the biological control of rodents (after Shellam 1994). Does murine cytomegalovirus (MCMV) meet these requirements?

Essential properties		MCMV
• Species-specific and naturally infects target species	√	Native murids will be tested to verify this
• Readily transmitted in target species	√	Seroprevalence >90% in wild mice (Smith et al 1993)
• Insertion of foreign gene is stable and does not affect viral growth or transmission	√	Insertion sites identified (Manning and Mocarski 1988); recombinant constructed with beta-galactosidase gene. More research required on effects on transmission
• Stimulates long lived immune response and immunological memory	?	
• Recombinant virus can be introduced and maintained in the presence of existing immunity	?	Wild mice have been found with up to four strains; infection with multiple strains can be achieved in the laboratory (Booth et al 1993). Epidemiology of this needs to be examined in wild mice
• Panel of isolates available	√	
• Epidemiology of infection understood and site of viral growth known	√	Virus persists in submaxillary gland Weak knowledge of epidemiology outside laboratory
• Approval by regulatory authorities likely	√	Already in Australia

Desirable properties		MCMV
• Virus is already in the country	√	(see Smith et al. 1993)
• Virus establishes persistent and non-lethal latent infection	√	
• Good local immunoglobulinA response which does not interfere with transmission	√	
• Mechanism for any genetically determined host resistance is known	√	Ability of subsequent infections to stimulate immune response not known
• Genetically determined host resistance does not interfere with infection or transmission	√	
• Mechanism of transmission known	√	Close contact; sexual and via saliva
• Virus is sexually transmitted	√	Enhances species-specificity
• Knowledge of the epidemiology of infection and transmission of natural virus variants	?	
• A DNA rather than an RNA virus (greater genetic stability)	√	

evidence of pregnancy and birth of litters. Two major experiments were conducted, one to assess the immediate effects on fertility and the second to test the duration of the effects.

The immediate effects on fertility were a reduction in the number of litters produced by females infected with ECTV–ZPC compared to uninfected controls or females infected with recombinant ectromelia virus (ECTV-602) expressing a non-reproductive marker protein, *LacZ* (Table 5). The effects on fertility were long term, with mice infected with ECTV–ZPC infertile for periods of 5–9 months while those infected with ECTV-602 remained fertile. Mice became fertile as the anti-ZPC antibodies in the serum decreased, but when they were re-infected with the recombinant virus, antibody titres to ZPC increased and the animals returned to an infertile state (Jackson et al. 1998). Therefore, this study provided the first demonstration of VVIC in laboratory mice.

Examination of the ovaries of infertile females revealed two possible mechanisms for infertility. Half of the animals showed disruption in folliculogenesis, with an absence of mature follicles and oocytes as well as large clusters of luteinised cells (Jackson et al. 1998). There was no observable oophoritis. The remaining animals showed normal ovarian development of follicles and ovulation; antibody localisation studies indicated binding of ZPC antibodies to these oocytes, suggesting that after ovulation, sperm would not be able to bind and result in fertilisation (Jackson et al. 1998).

Murine cytomegalovirus

Ectromelia virus is not present naturally in the Australian environment and therefore, for ethical, political and social reasons, is not an ideal candidate for release as a viral vector of an immunocontraceptive agent. Moreover, its lethality would select for resistance more rapidly than a non-lethal agent. Other research is being conducted using murine cytomegalovirus (MCMV) which is highly prevalent in Australian mouse populations and possesses the desirable properties of a vector (Table 4) (Singleton et al. 1993; Smith et al. 1993; Shellam 1994). This large DNA virus (230 kb, ~200 genes) is a member of the Betaherpes-virinae sub-family of the Herpesviridae. It

Table 5.
Infertility in BALB/c mice infected with either recombinant ectromelia virus expressing zona pellucida glycoprotein C (ECTV–ZPC) or recombinant ECTV expressing a non-reproductive marker protein (ECTV–602) compared with uninfected controls (after Jackson et al. 1998), SE = standard error.

Ectromelia virus infection	No. of mice with litters/total mice	No. of implantations (mean ± SE)		Litter size (mean ± SE)	
		Animals with litters	All animals	Animals with litters	All animals
None	10/10	9.5 ± 0.8	9.5 ± 0.8	6.6 ± 0.8	6.6 ± 0.8
ECTV-602	12/15	8.5 ± 0.9	6.8 ± 1.1	7.3 ± 0.7	5.8 ± 1.0
ECTV-ZPC	4/13	2.5 ± 0.7	0.8 ± 0.4	1.8 ± 0.3	0.5 ± 0.2

shows strict species-specificity (Hudson 1994) and establishes a persistent infection in the salivary gland with latent infection apparently associated with ubiquitous elements such as macrophages (Koffron et al. 1995; Pollock et al. 1997), rather than with organ-specific cells (e.g. hepatocytes). Infection requires close contact and the virus is believed to be transmitted via secretions such as saliva and sexual secretions (see Shellam 1994).

Recombinant MCMV has been constructed by inserting the mouse ZPC gene into the immediate early 2 (*ie2*) gene. The effects on fertility of infecting with recombinant MCMV expressing either ZPC or a non-reproductive marker gene (*LacZ*) were assessed for several different inbred strains of mice (BALB/c, A/J, C57BL/6, ARC/s) with varying susceptibility to infection with MCMV (Grundy et al. 1981; Allan and Shellam 1984). Recombinant MCMV–ZPC induced a long-lasting, high-titred antibody response to ZPC in all mice tested. The fertility of uninfected controls was also determined. BALB/c females ($n = 9$) infected with recombinant MCMV–ZPC produced no litters for 200 days after infection, while the uninfected controls and the MCMV–*LacZ* infected group produced approximately 250–350 pups during the same period (Figure 2). The response was similar in A/J females although the overall productivity of this strain was lower. Contraceptive effects of lesser magnitude were observed in C57BL/6 and ARC/s strains. The ovaries of recombinant MCMV–ZPC infected females showed histological changes but the mechanism of infertility remains under investigation.

These results (M. Lawson et al., unpublished data) demonstrate that recombinant MCMV expressing the ZPC gene can elicit an immunocontraceptive response in mice. This response occurred in the absence of high levels of replication of the recombinant virus, since very low levels of virus were found in the salivary glands of mice relative to controls. Research is continuing on ways to enhance this response in less susceptible strains of mice as well as to demonstrate the transmissibility and competitiveness of the recombinant virus when confronted with prior MCMV infection in wild outbred mice (see next section).

Epidemiological Considerations

Manipulating the genetic structure of a virus to incorporate an immunocontraceptive antigen may effect its transmissibility, persistence and species-specificity. Thus, it is important to examine the epidemiological consequences of such a manipulation from both an ecological and a viral engineering perspective. The key questions that need to be addressed are:

- What is the transmission rate of the wild-type virus and the recombinant sterilising virus? Do they differ? If so, why?
- Do the characteristics of viral infection such as the immune response and site of replication differ between the wild-type and recombinant virus?
- What is the threshold population size required to maintain the viral infection at a specified prevalence? What influences this?

- Can a recombinant strain of the virus establish and generate an immune response in a rodent population that may have a pre-existing infection with the wild-type virus? Is the order of infection important?
- What is the persistence of the virus in the environment?

Many of these questions are difficult to test in wild populations, particularly for the recombinant viruses where thorough testing under contained conditions is required before release into a field population. A crucial experiment will be to examine if the impact of the sterilising, recombinant virus on breeding affects the transmissibility of the virus.

Experiments will be conducted to address these questions using large (2 m × 2 m) cages to house a simulated 'population' of mice. These cages are

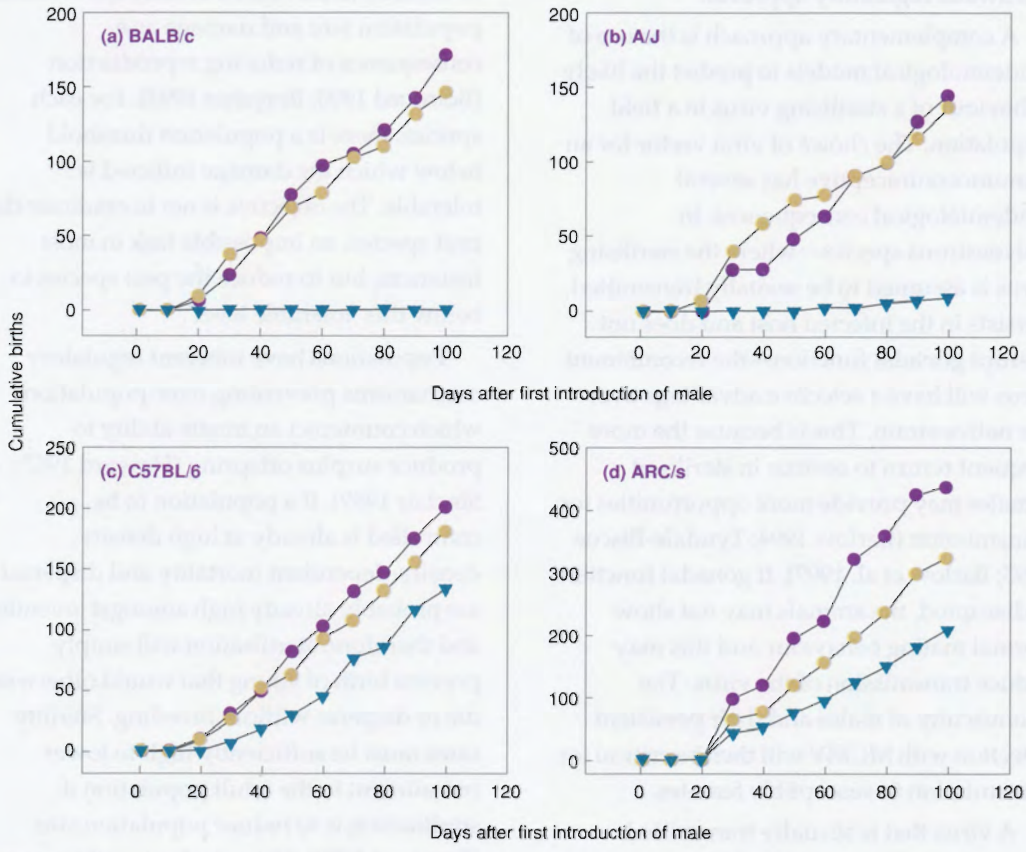

Figure 2.

Cumulative births in different strains of mice infected with either recombinant murine cytomegalovirus–zona pelucida glycoprotein C (MCMV–ZPC) (▼), or recombinant MCMV–*LacZ* (a non-reproductive marker protein gene (●) compared with uninfected controls (●). Groups of nine females were infected with 2 × 10^4 pfu (plaque forming units) of tissue culture-derived virus 21 days prior to the introduction of males to the breeding cages. Each cage contained three females and one male. Groups were checked for births several times per week.

internally complex so that mice can avoid each other within the cage if required. Uninfected mice will be released into this cage, a number of mice infected by intraperitoneal inoculation and the spread of the virus monitored. Further studies of MCMV in wild populations will still be necessary to assess the relevance of these cage results. The use of a virus strain expressing an innocuous, non-reproductive marker gene would be useful in this instance but awaits regulatory approval.

A complementary approach is the use of epidemiological models to predict the likely behaviour of a sterilising virus in a field population. The choice of viral vector for an immunocontraceptive has several epidemiological consequences. In polyoestrous species—where the sterilising virus is assumed to be sexually transmitted, persists in the infected host and does not disrupt gonadal function—the recombinant virus will have a selective advantage over the native strain. This is because the more frequent return to oestrus in sterilised females may provide more opportunities for transmission (Barlow 1994; Tyndale-Biscoe 1995; Barlow et al. 1997). If gonadal function is disrupted, the animals may not show normal mating behaviour and this may reduce transmission of the virus. The promiscuity of males and their persistent infection with MCMV will then be critical for transmission to susceptible females.

A virus that is sexually transmitted increases the chances of the VVIC agent contacting only the target pest population compared with a contagious or insect-borne virus. However, spatial modelling suggests that a sexually transmitted virus would be at a disadvantage when compared with a virus spread by insect vectors, as the requirement for close contact could potentially limit the rate of spread of the virus (G.M. Hood, unpublished data). These considerations need to be balanced when determining which viral vector is most appropriate in each pest control situation.

Ecological Implications

Immunocontraception can only be judged to be successful for rodent control if it reduces population size and damage as a consequence of reducing reproduction (Bomford 1990; Braysher 1993). For each species, there is a population threshold below which the damage inflicted is tolerable. The objective is not to eradicate the pest species, an impossible task in most instances, but to reduce the pest species to below this 'tolerable level'.

Populations have inherent regulatory mechanisms preventing over-population which counteract an innate ability to produce surplus offspring (Howard 1967; Sinclair 1989). If a population to be controlled is already at high density, density-dependent mortality and dispersal are probably already high amongst juveniles and therefore, sterilisation will simply prevent birth of young that would otherwise die or disperse without breeding. Sterility rates must be sufficiently high to lower recruitment to the adult population if sterilisation is to reduce population size (Bomford 1990). This emphasises the importance of gaining some understanding of the factors regulating populations and how these are affected by fertility control.

Fertility control may interact with other population processes to enhance the overall effect on population numbers. For example, if a pest species is prevented from increasing its reproductive rate, predation may be able to maintain their population at a low level (Sinclair 1997). This may apply to house mouse populations in Australia in which avian predators are capable of regulating the population when mouse densities remain low but can not maintain this regulation when mouse densities increase to high levels (Sinclair et al. 1990).

Several ecological questions need to be addressed when assessing the potential of a particular immunocontraceptive agent:

- What proportion of a wild pest population needs to be sterilised to significantly reduce growth rate and population size? And can a delivery system be developed that will reach the required proportion of the population?
- Is the maintenance of social structure important and does it affect the efficiency of the immunocontraceptive?
- Is compensation a likely factor that could reduce the efficacy of an immunocontraceptive?

A further question is whether density-dependence plays a role in modifying the efficacy of a given sterility level. Will the proportion of sterilised individuals need to be increased in a high-density compared with a low-density population to have the same impact? Is compensation density-dependent? Some of the implications for density-dependent regulation on the applicability of sterilisation to control populations have been discussed in a previous section.

Level of sterility required

Modelling

Mathematical models have been used to estimate the level of fertility control required to produce a significant reduction in population size. Knipling and McGuire (1972) modelled the effects of permanent sterilisation of females or both sexes versus killing similar numbers in a rat population. Their model predicted that by sterilising 90% of both sexes, this had a greater effect than killing 90% of rats. However, they assumed that if 90% of males don't breed, 90% of females would not breed. In a species such as rodents with a promiscuous mating system, this is an invalid assumption (Kennelly et al. 1972; Pennycuik et al. 1978). There was also no allowance for compensatory changes in immigration and dispersal.

N. Stenseth et al. (unpublished data) have modelled empirical field data from populations of the multi-mammate rat *Mastomys natalensis*, in eastern Africa. The model simulated a permanent decrease in reproductive rate of this species and found that long-term reductions in population density were attained if between 50 and 75% of females were sterile.

A simple demographic model using life-history information obtained from laboratory, enclosure and field studies was used to examine the proportion of mice to be sterilised to produce a significant decrease in population size in enclosure populations (Chambers et al. 1997). This simulation was a useful precursor to a manipulative experiment (described below), assisting with experimental design and indicating the types of data that needed to be obtained. The model examined two levels of sterilisation (67% and 75% of females) and compared the outcome against a non-sterilised population. The simulation found that both the 67% and 75% levels of sterility were sufficient to reduce population size and growth rate, relative to the unsterilised population (Figure 3).

However, models often overestimate the effectiveness of an immunocontraceptive as they are generally based on higher levels of fertility control than can be practically achieved in the field. They also tend to ignore or underestimate factors that may reduce the effects of fertility control, such as compensatory changes in behaviour, survival or fecundity (Bomford 1990). The latter applies to all of the models described above.

Manipulative experiments

Manipulative experiments can be used to examine empirically the sterility level suggested from mathematical models. Experiments involving surgical sterilisation allow the degree and nature of sterilisation required to reduce population size to be examined (Kennelly and Converse 1997). For example, when females in populations of house mice housed in outdoor enclosures (Figure 4) were surgically sterilised at a level of 67%, this significantly reduced population size. Over 18 weeks, populations were reduced from a mean abundance of 221 mice in two control populations to 104 mice in four sterilised populations (Chambers et al. 1999).

Kennelly et al. (1972) sterilised 85% of males in a Norway rat population and found no effect on population size when compared with an unsterilised population, confirming that the development of an immuno-contraceptive for males in a species with a promiscuous mating strategy is not effective.

Social structure

Many studies of wild mammals have shown that reproductive success is closely linked to an animal's rank in the social hierarchy. Lower ranking animals either do not breed or fail to rear their young to independence (Wasser and Barash 1983; Abbott 1988). Caughley et al. (1992) highlighted the need to have some understanding of the social structure and mating system of the species to be controlled by fertility control. They showed via modelling that for most scenarios, sterilisation would reduce population growth, irrespective of mating system or social structure. However, where the sterilisation of a single dominant female releases subordinates from breeding suppression, sterilisation actually enhanced the overall productivity of the population. This emphasises the need to sterilise individuals without compromising their social position (Chambers et al. 1997). This would maintain the breeding performance of subordinates at a low level, preventing compensation by these individuals for the reduction in population growth (Caughley et al. 1992; Barlow 1994; Tyndale-Biscoe 1994; Cowan and Tyndale-Biscoe 1997).

The importance of maintaining hormonal competence in surgically sterilised females in reducing the overall productivity of populations has been examined for mice housed in near-natural outdoor enclosures (Chambers et al. 1999). Female mice were either ovariectomised (hormonally incompetent) or tubally ligated (hormonally competent) at the rate of 67% per population

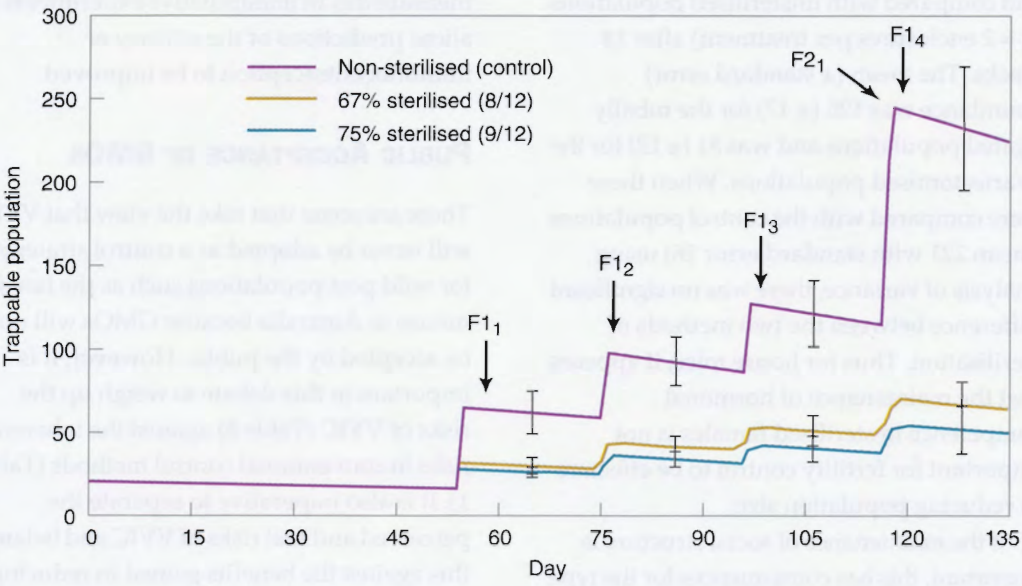

Figure 3.

Demographic model predicting the trappable population of mice housed in outdoor enclosures after 0%, 67% and 75% of females have been sterilised (see Chambers et al. 1997 for details of the model). Each plot is the mean (± standard deviation) of 10 runs of the model. $F1_1$ to $F1_4$ indicates when F1 generation litters (those produced by the founding population of mice) will enter the trappable population. $F2_1$ indicates when the first litter of the F2 generation (produced by the $F1_1$ litter) enters the trappable population (adapted from Chambers et al. 1997).

(a) **(b)**

Photos: G. Singleton, CSIRO.

Figure 4.

Outdoor enclosures used for manipulative experiments examining the effectiveness of fertility control to reduce mouse population abundance and rate of increase. Each enclosure is 15 m × 15 m in area and is protected from predators by wire mesh fencing. Mice are prevented from burrowing into or out of the enclosures by metal fences that are buried to a depth of 800 mm. Food and water are provided ad libitum. (a) Ground-level view; (b) Aerial view.

and compared with unsterilised populations (n = 2 enclosures per treatment) after 18 weeks. The mean (± standard error) abundance was 126 (± 17) for the tubally ligated populations and was 81 (± 12) for the ovariectomised populations. When these were compared with the control populations (mean 221 with standard error 26) using analysis of variance, there was no significant difference between the two methods of sterilisation. Thus for house mice, it appears that the maintenance of hormonal competence in sterilised females is not important for fertility control to be effective in reducing population size.

If the maintenance of social structure is important, this has consequences for the type of immunocontraceptive antigen to be used (Chambers et al. 1997). Some of these antigens are known to cause oophoritis or ovarian dysfunction that may affect the release of hormones controlling reproduction and social position (Skinner et al. 1984; Kirkpatrick et al. 1992; Rhim et al. 1992).

Compensation

If fertility is reduced, the average population size is also reduced, but only under certain conditions. If juvenile or adult survival improves with lower fertility or territoriality limits populations, the effects of lower birth rate will not change population size unless such reduction exceeds the effects of these processes (Sinclair 1997). If sterile individuals have increased survival, they may cause more damage than non-sterile animals (Bomford 1990).

As was discussed earlier, modelling the effects of fertility control on wildlife populations often ignores the effects of compensation. Therefore it is important to measure this in manipulative experiments to allow predictions of the efficacy of immunocontraception to be improved.

Public Acceptance of GMOs

There are some that take the view that VVIC will never be adopted as a control strategy for wild pest populations such as the house mouse in Australia because GMOs will not be accepted by the public. However, it is important in this debate to weigh up the risks of VVIC (Table 6) against the inherent risks in conventional control methods (Table 1). It is also imperative to separate the perceived and real risks of VVIC and balance this against the benefits gained in reducing the damage caused by the pests (Chambers et al. 1997). The strategy adopted by the Vertebrate Pest Animal Control CRC is that research should proceed incrementally with public discussion at each step so that its potential use can be weighed against the risks (Tyndale-Biscoe 1997b).

The risks of VVIC are discussed in detail in Tyndale-Biscoe (1994, 1995), Guynn (1997) and Williams (1997) and are summarised in Table 6. Most relate to the issues of public acceptability of GMOs and maintaining the species-specificity of the recombinant virus.

How species-specificity is achieved will depend on the target animal, the ecosystem, the delivery system, local non-target species and, in general, the aims of the fertility control program (Stohr and Meslin 1997). The important question to address is if a VVIC encounters a non-target species, will this cause infertility even though no productive infection occurs? Species-specificity operates at three levels: the viral vector, the reproductive protein and social factors governing the spread of the VVIC agent (Tyndale-Biscoe 1994). Ideally, all of these levels of specificity should be satisfied.

Public acceptability will be heavily influenced by the media's interpretation of this technology (Williams 1997) as well as by international debate and agreement on its safety (Oogjes 1997; Stohr and Meslin 1997; Williams 1997).

Apart from the issues associated with the use of a GMO, public acceptability also encompasses animal welfare issues. Although it is generally agreed by animal welfare groups that immunocontraception is a more acceptable form of control than the current lethal methods (Oogjes 1997; Singer 1997), there are other biological issues that need to be considered. For example, Guynn (1997) expressed concern over sterilised females experiencing an abnormal number of oestrous cycles and thus expending more energy. The use of long-term field trials should give some indication of behavioural changes experienced by sterilised and non-sterilised individuals. For example, Williams and Twigg (1996) found during the first year

Table 6
Risks and benefits of viral-vectored immunocontraception (VVIC).

Risks	Benefits
Public concerns about genetically modified organisms (Regal 1986; Molak and Stara 1987; Siddhanti 1987)	Environmentally benign
Possibility of non-target species infection (national) and infection of target species in another ˇountry where it may be a desirable part of the fauna (international) (Tyndale-Biscoe 1995)	More humane than conventional methods of control; supported by animal welfare groups (Oogjes 1997; Singer 1997)
Possibility of pathogens broadening their host range after genetic modification (Regal 1986; Kurtz 1987; Tiedje et al. 1989)	Species-specific
Potential for behavioural/hormonal disruptions to cause ill effects in sterilised individuals; other animal welfare/ethical issues such as potential mortality in utero (Guynn 1997)	Can be used in terrain where pest species would be inaccessible to instigate conventional control methods
Irretrievable once released	More appropriate for highly fecund pest species as it targets reproduction (Bomford 1990; Tyndale-Biscoe 1994, 1995)
Virus may infect laboratory colonies	May be active long- or short-term and therefore have the potential to be a flexible tool for population management
VVIC may select for animals with poor immune systems, therefore favouring immunodeficient animals and thus increasing their susceptibility to pathogens (Guynn 1997; Nettles 1997)	Presence of sterile individuals in the population may exert a much greater biological control pressure than if the same number of fertile animals were removed (Howard 1967)
Legal implications with respect to federal and state registration requirements (Guynn 1997).	Self-disseminating 'release and forget' strategy

of a sterility trial on wild rabbit populations that sterilised females had higher survivorship and body weights than unsterilised females.

Conclusion

Ecologically-based pest management requires the application of a suite of strategies to manage pest species. New approaches, such as fertility control, will become one of these strategies and thus must not be seen as a replacement for conventional methods of control. Where damage mitigation is the objective for population reduction, the short-term use of lethal approaches may still be appropriate. However, it is the prolonged use of such techniques that should be discouraged.

Fertility control techniques that are currently available are not logistically appropriate for wildlife populations. They are expensive and/or invasive, require repeated dosing to maintain sterility levels and often have side effects that lead to behavioural changes. They are also difficult to administer on a broad-scale. Immunocontraception, and in particular viral-vectored immunocontraception, aims to overcome many of these shortcomings by being a naturally disseminating, species-specific fertility agent. However, one disadvantage of this method is the public acceptance of the use of a GMO. Therefore, it is important that the risks of new methods of control, including GMOs, are fully assessed through experimental trials and public debate. These risks should be viewed in the context of control methods which are currently available—i.e. non-specific, fatal poisons. This may mean that these new methods will not be available for broad scale release for at least another decade. However, the potential rewards of this technology will be well worth the longer-term investment.

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11. Urban Rodent Control Programs for the 21st Century

Bruce A. Colvin and William B. Jackson

Abstract

Urban rodent control in the 21st century must focus on a program approach that is both strategic and comprehensive (i.e. proactive rather than reactive). This includes an integrated pest management approach that incorporates long-term planning, scheduling, data management and mapping capabilities. It also must include greater partnership among municipal agencies, private pest control companies and community groups. Central to program success will be coordination, communication and accountability among all program participants. Cost-effectiveness will be achievable but predicated on effective administrative management, training, and understanding of the ecological and political complexities of urban environments. Greater focus on sanitation enforcement, infrastructure maintenance and construction will be essential for long-term removal of causal factors. The long-term goal must be an effective and sustainable program.

Keywords

Urban, integrated pest management (IPM), rodent control, commensal rodent, sanitation, infrastructure

INTRODUCTION

THE PRINCIPLES of urban rodent control have been well researched and described in this century. However, substantial problems continue to persist and grow in many metropolitan areas, as well as in small municipalities. Although the science and technology have been established (Jackson 1982; Frantz and Davis 1991), the failure appears most evident at the point of implementation. Success is not predicated on a control tool, but rather on coordinated efforts supported by technical leadership at the local level.

Telle (1969) in Germany and Myllymäki (1969) in Finland described the principle of establishing a 'rat-free town'. The goal was to have less than 1% of the premises showing signs of rat activity. Drummond (1970) in England stressed the idea and importance of a program approach for managing urban rat populations (Drummond et al. 1972, 1977; Drummond 1985). Examples of successful and coordinated programs are few, but include Budapest, Hungary (Gacs et al. 1977; Bajomi and Sasvari 1986), Kuwait (Al Sanei et al. 1986), and Denmark (P. Weile 1998, pers. comm.). All of these have included an emphasis on sanitation and environmental management.

The primary difference between urban and agricultural rodent control is that the urban environment is relatively diverse and stable, requiring consistent application of control measures, since food and structural resources are consistently available. On the other hand, in open agricultural settings, the environment is relatively homogeneous and subject to disruptions, and resources used by rodents and control efforts tend to be seasonally timed. Habitat manipulation is readily feasible in urban areas for limiting growth of rodent populations and to prevent over-dependency on rodenticide. In contrast, with agricultural situations there may be limited opportunity for habitat manipulation and thus greater emphasis frequently is given to trapping and rodenticide use. The basic ecological and organisational principles of rodent control programs, however, are transferable between urban and agricultural environments.

Urban rodent control in the United States (US) typically is implemented in a limited or disjointed fashion, rather than being comprehensive or coordinated. Programs commonly are reactive rather than proactive. Reasons for this include limited funding, training, political and technical support, and organisation (Howard 1984). The political and scientific interest in urban rodent control in the US currently is low, although the need appears to be great.

Commensal rodents are those described literally as 'feeding at our table'. They include species such as Norway rat (*Rattus norvegicus*), roof rat (*Rattus rattus*), and house mouse (*Mus musculus*). In Asia, they also can include species such as the lesser bandicoot rat (*Bandicota bengalensis*) and Polynesian rat (*Rattus exulans*). Commensal rodents have been associated with a variety of diseases, contamination and destruction of stored foods, structural damage, and other aspects of environmental deterioration (Gratz 1994; Lund 1994). They frequently display remarkable adaptive behaviour in urban environments.

Urban infrastructure is ageing, congestion is increasing, and urban habitat is expanding worldwide. These factors accentuate the growing need for effective rodent control programs, for public health, economic and aesthetic reasons. Additionally, expectations of urban residents and businesses for quality-of-life improvements and effective public health management will continue to grow. The result will be more sanitation problems to be managed in more densely populated urban centres, and these urban environments will increasingly require re-design and construction to support human population levels and business economies.

The purpose of this chapter is to describe strategies and issues for implementing urban rodent control programs, while considering both ecological and administrative components. This includes a historic US perspective with transition to future opportunities worldwide.

Historical Background

The 'Modern Rodent Control Era' began with the advent of World War II, as urban destruction and concern for food supplies (both quality and quantity) forced attention to rodent control. This included the need for more effective rodenticides and better understanding of rodent biology. (The term 'ecology' had not yet been applied to this issue.) Federal funds in the US supported related research and development projects.

Initial efforts focused at the School of Hygiene and Public Health of the Johns Hopkins University in Baltimore, Maryland. The rodenticide ANTU was brought forth there, and Compound 1080 resulted from a massive synthesis and evaluation program by the federal government. These rodenticide baits were far more effective than the arsenic and phosphorus baits in use at that time. (It was not until the next decade that warfarin would leap into the marketplace as a 'miracle' rodenticide, following the 'miracle' insecticide, DDT.)

The 1940s and early 1950s at Johns Hopkins University were times of active research on basic elements of rat behaviour, later serving as the foundation of control approaches and future urban programs worldwide. Calhoun (1948, 1963) performed detailed studies of the sociology of the Norway rat, providing new research approaches for studying the social behavior of semi-confined rodent populations. Basic studies of Norway rats in the residential blocks of Baltimore followed by Davis and others (Davis et al. 1948; Emlen et al. 1948, 1949; Davis and Fales 1949, 1950; Davis 1953). Those studies documented for the first time the reproduction, movement, and many other life history components (now referenced as 'ecology') of urban rat populations. Parallel studies on aspects of commensal rodent biology also occurred in the United Kingdom during the same time era (Chitty and Southern 1954).

From the fundamental studies at Johns Hopkins University came the notion of relating a logistical growth curve (sigmoid curve) to changes in rodent populations (Figure 1). Such a mathematical expression could then be used to predict population growth and as a tool for understanding how to strategically manage rodent populations. By lowering the carrying capacity of the environment, the rate of population increase could be dampened and population declines achieved (Davis and Jackson 1981).

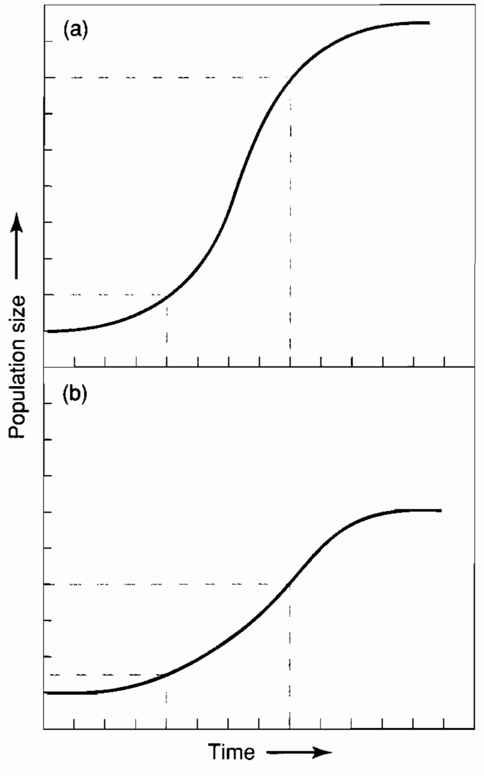

Figure 1.
Sigmoid curves depicting the rate of change and growth of rodent populations over time, (a) without environmental (sanitation) management and (b) with environmental management to reduce carrying capacity. The two dashed lines on each graph show the passing of the same amount of time on the horizontal axis, while on the vertical axis there is a dramatic increase in the population size during the second time period. The most economic and effective strategy is to manage populations at the low end of the sigmoid curve under reduced carrying capacity (b).

Populations then could be more effectively 'managed' at the low end of the population growth curve. Baltimore officials cooperated and set up a demonstration area in which no rodenticides would be used, but intensive enforcement of environmental standards would be substituted. Specific regulations were passed and sanitation police were hired. Outdoor toilets, board fences, old cars and other rubbish were removed. Proper storage and handling of refuse was enforced. With this regimen, the outside rat population was virtually eliminated from this residential area. However, the program was not maintained because of the need for intensive (i.e. expensive) site management and the lack of political and personal will to maintain environmental standards. Yet, the logistical model as a management tool had been demonstrated successfully and, to one degree or another, became the basis of future management efforts in the US and elsewhere (Figure 2).

During World War II, the US Public Health Service set up programs in the Communicable Disease Center (CDC) in Atlanta, Georgia, for training personnel in the control of various disease vectors met in military activities. In post-war years, such training programs expanded to include state and municipal personnel. Equipment was provided for state agencies as well. Handbooks covering a wide variety of vector and sanitation topics were developed, and many remain as the prime resource documents available today (Pratt and Johnson 1975; Pratt and Brown 1976; Pratt et al. 1976; Scott and Borom 1976; Davis et al. 1977). However, the involvement of CDC in technical support for urban rodent control programs faded by the early 1980s and personnel once active have retired.

Universities were slow to pick up the challenge of urban rodent ecology and control. The Johns Hopkins program faded when the core staff left by the late 1950s.

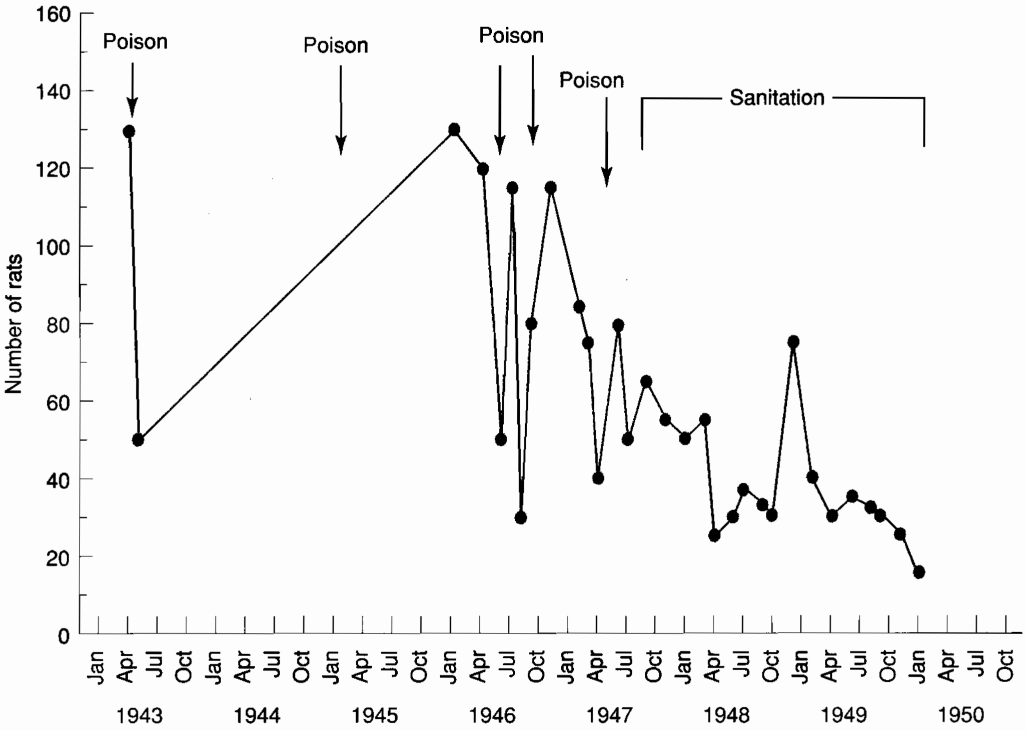

Figure 2.
Changes in Norway rat abundance in Baltimore following poisoning and sanitation improvements (Jackson 1998). The population increase during late 1948 was attributable to a strike by garbage collectors that temporarily increased food resources (carrying capacity) for rats.

Most mammalian researchers considered urban pest rodents not 'worthy' of basic research and the urban environment a distasteful setting for studying mammalian ecology. This left entomologists as the source of much information for pest control curricula, and they commonly did not want to bother with rodents or approached them as 'furry cockroaches'.

Two universities, Bowling Green State University in Ohio and the University of California at Davis, developed effective vertebrate pest curricula in the 1960s and 1970s. This included undergraduate and graduate instruction and research programs. Designations such as 'economic biology' were typical, and research continued the kinds of efforts first begun at Johns Hopkins University. This included basic behaviour but also, by the 1970s and 1980s, a focus on genetic resistance to anticoagulant rodenticide, secondary poisoning hazards, and development of new rodenticides, traps and bait stations. Many personnel currently providing leadership on vertebrate pest management in the US came from these two university programs. However, by the late 1980s these programs also began to fade and ended as faculty retired.

The Federal government, through the US Public Health Service, supported research on genetic resistance to warfarin (first-generation anticoagulant rodenticide) during the 1970s (Jackson et al. 1988). During that same era and into the early 1980s, $12.8 to $15.0 million dollars annually were provided for state and local efforts specifically for implementing urban rodent control programs. These programs involved a standardised approach of environmental management, including target areas, systematic surveys, education, sanitation improvements and baiting. The goal was to progressively shift blocks of premises to a maintenance condition with subsequent monitoring for re-infestation. This federal program assisted more than 100 communities (Jackson 1984, 1998). However, in the early 1980s, specific designation of federal funding for urban rodent control ended, and subsequently many local programs were greatly reduced and eventually became less structured.

The US Fish and Wildlife Service, through regional and state programs in the 1960s–1980s, stimulated and supported efforts at universities as related to vertebrate pests. This included some technical support on urban rodents, although most of their effort was directed at predators, birds and field rodents. In the mid 1980s, these programs were transferred by the US Congress to the US Department of Agriculture (USDA). With that change, control of urban rodents was specifically excluded from the USDA scope of services, although rodent infestation of stored grain and croplands remain within their area of concern.

Today in the US, technical support for urban rodent control is very limited. Active research programs do not exist on the federal, state or university level. Most States and municipalities have limited knowledge and skill in urban rodent control, resulting in limited effectiveness when programs are implemented. Urban (and suburban) rodent control could be described as a composite of work by householders, licensed pest control operators and municipal agencies (Kaukeinen 1994), but without defined coordination. Most efforts by local health departments are reactive, in response to citizen complaints about infestations or rat bites. Their efforts typically involve use of anticoagulant baits within a limited area (e.g. at the site of a complaint or perhaps a few city blocks).

The Boston Model

The basic research of the 1940s–1950s, the program approaches described in the 1960s–1970s, and the technical advances of the 1970s–1980s were combined in 1990 in Boston, Massachusetts. The unique opportunity to establish a truly comprehensive and properly designed rodent control program had arisen from the start of an 11-billion-dollar highway construction project funded by the Federal Highway Administration (Colvin et al. 1990). This involved reconstruction of the urban infrastructure along a seven-mile route, including utility systems and an 8–10 lane highway to be built underground.

Key to the program design was a centralised approach with well-defined responsibilities and firm accountability. The primary management function was performed by personnel (biologists) skilled in technical aspects of rodent control, yet also with contract management, public relations, engineering, scheduling, and computer-based mapping and data management skills. The second component of the program was the municipal functions, performed by the Inspectional Services Department, the Code Enforcement Police, the Water and Sewer Commission, and the Public Works Department. The third component involved pest control contractors who performed poison baiting, trapping and monitoring. The fourth component was public participation, championed by community leaders and organisations. These various components were integrated to maximise the skills and participation of each group within the total program.

Work tasks assigned to each municipal agency were based on their existing scope of services. For example, the Inspectional Services Department was assigned standardised surveys of premises, enforcement of State Sanitary Code and public education. The Code Enforcement Police dealt with violations of City sanitation ordinances. The Water and Sewer Commission assisted by cleaning catch basins and providing access to sewer manholes. The Public Works Department helped by making infrastructure repairs and maintaining trash receptacles in public areas. Most of these municipal tasks focused on environmental change to reduce rodent habitat.

The program was an integrated pest management (IPM) approach covering about a seven-square-mile area. It was tailored to the need of each neighborhood based on surveys of sanitary conditions and rodent activity at surface and subsurface levels. Where problems were chronic, IPM methods and monitoring were applied more intensely. The program included an extensive public outreach and education campaign involving community meetings, diverse literature, videos, door-to-door contact and school presentations. The education campaign recognised cultural differences among neighbourhoods, and literature was prepared in multiple languages.

Sanitation was given heightened attention on more than 10,000 premises in the project area. The Code Enforcement Police performed ticketing daily, and the Inspectional Services Department cited property owners to hearings and court for chronic sanitary code violations. In locations highly susceptible to infestation, residents and businesses were given refuse containers after signing a contract to maintain and use them. Property owners and businesses were held responsible for maintaining their property in an acceptable condition, including hiring their own pest control contractor if needed. City personnel conducted baseline and periodic surveys on private properties, and these surveys helped ensure maintenance of environmental improvements. The objectives were to reduce the environmental carrying capacity for rodents and also to prevent their dispersal.

Trapping and poisoning were performed on both surface and subsurface levels in all public areas, and as a supportive measure on some private properties. Engineering drawings and information were used to 'three-dimensionally' dissect the infrastructure. About 1,500 sewer and other types of utility manholes were baited using pulsed-baiting methods on a seasonal basis (Colvin et al. 1998). Census and monitoring tools were used extensively to detect and closely monitor for low levels of activity (non-toxic census baits, tracking tiles, night-time visual surveys and tracking with snow cover). Night-time observations were essential for targeting control resources and identifying sanitary problems that only appeared after dark (e.g. plastic rubbish bags left out on sidewalks).

Administrative elements were emphasised as part of the IPM program. Contract specifications for both pest control contractors and municipal agencies were developed (Colvin et al. 1992). This provided a basis for accountability and performance. Program elements were centrally scheduled, to maximise timing and geographical distribution of resources. Data management and mapping using a geographic information system was important for efficiency of operations (Von Wahlde and Colvin 1994); this included tracking of events over the entire project area, historic patterns of problems and poison placements in utility systems. Standardised data sheets were used to collect information for program planning and analysis. Data sheets also helped ensure that personnel were performing their assigned tasks. Cost containment was predicated on maintaining a proactive rather than haphazard or reactive approach.

An important administrative element that characterised the dynamics of the program was a referral system. All members of the program team were cross-trained to identify program issues, even though the particular issue might involve a task assigned to another team member (agency or contractor). If a pest control contractor observed a sanitary problem on private property, the contractor could refer that observation through the centralised program office to the city agency responsible for enforcement. Similarly, observations by a city agency of a rat infestation needing treatment could be referred to a pest control contractor assigned to the particular geographic region. All referrals were tracked on a database to ensure they were followed through.

The program also entailed habitat modification beyond basic rodent-proofing of structures (i.e. sealing of holes and entry points). Landscaping within the project area was evaluated and factors conducive to rodent activity were identified (Colvin et al. 1996). Rodent-proofing principles were then incorporated into design specifications for final surface restoration and landscaping. For example, rat abundance in landscaped areas was associated with the amount of coverage by shrubbery. Plots with massed needled evergreens were most susceptible to infestation, in contrast to plots with broad-leafed evergreens and deciduous shrubs. Numerous property owners and businesses re-designed their existing landscaping, reducing densely planted needled-evergreens and giving greater emphasis to stone mulch, shrubbery spacing, refuse containers, maintenance, and trees and shrubs that did not produce excessive fruit. Varieties that grow in vase-like, rather than mounded, shapes provided more openness within landscaped areas.

Results of the control program can be characterised in several ways. Brick sewers with pipe diameter <61 cm in residential areas had the highest subsurface rat activity;

up to 38% of those manholes were active at the program start (baseline). Bait consumption and the number of active sewer holes were 96% and 87% below baseline, respectively, when seasonal baiting was last initiated in 1997. The Code Enforcement Police in 1996 were issuing 67% fewer tickets for sanitation violations than in 1991, even with intensified efforts. About 375 properties were identified with rat activity during baseline surveys; by 1997, control efforts were needed on about ten of those properties (<4% of those originally identified). Another 25–30 properties required close monitoring to detect potential re-infestation. Referrals by the program's pest control contractors to the City for resolution of sanitary problems and rat activity on private property declined from a high of 153 in 1993 to 13 in 1995 and 20 in 1996 (87% reduction). Visual night-time surveys for rat activity declined from a localised average event of 104 sightings per hour (range 19–500) to incidental observations within the project area (>99% reduction). These 'real world' statistics collectively demonstrated that the program approach was effective.

Throughout the program, phone calls from the public concerning complaints about rodents and sanitation remained relatively constant, independent of the obviously positive environmental changes that were occurring. However, the magnitude of problems identified by the public grew less as the program continued. The relatively constant input from the public was a positive event, since it demonstrated sustained participation by the communities. This was achieved through the consistent presence of program staff in the neighbourhoods, timely and effective response to public concerns, involvement of community leaders, and repetitive positive feedback to political entities by program managers and the public. Neighbourhood 'cleanup days' evolved with the participation of residents and businesses, and awards and recognition were given. The pattern of success, involvement, and commitment broke the public scepticism that commonly degrades the opportunity to sustain an urban rodent control program.

The Boston model had several elements that proved crucial for success. Foremost was a true partnership among City agencies, community groups, and contracted management and pest control firms. The model demonstrated that a blend of municipal and privatised functions worked well and could succeed, but only with technical leadership, open sharing of information, consistent communication among team members, and trust. It had to be one team focused on an IPM strategy, with excellent diversity of skills and accountability on the part of each team member. Weekly meetings within various program groups and quarterly team meetings enhanced training and communication.

Future Opportunities

The future of urban rodent control is not limited by science and technology; it is limited by politics and bureaucracies. Personnel management, budgets, contracts, news media, legal proceedings and political agendas were not factored together when Davis and others performed the original ecological research in Baltimore, but they must be today for the science of rodent control to be implemented. When Davis (1972) summarised rodent control in context of future strategies, he expressed frustration with the political impedance of urban rat control and use of short-term solutions. He reaffirmed the need to focus on basic biological principles (i.e. reducing carrying capacity) and the need for competent administrators.

Urban programs need to be consistently and strategically managed rather than politically cyclic in their implementation and focus. Lethal measures need to be intensive rather than simply cropping populations and spurring higher reproductive rates that occur with lower competition. In other words, many urban programs function today on the steep slope of the sigmoid growth curve (Figure 1). A temporary lowering of the number of animals is achieved by a punctuated control effort, but subsequently a sudden population rebound occurs. This sudden perturbation of rodents often is misinterpreted as a 'new' population of colonists. Whereas in reality, the population may never have been effectively controlled to start with and has simply responded reproductively as the sigmoid curve predicts.

There must be a commitment to long-term management of the urban environment and an organisational structure to achieve closure of issues day-by-day. This type of preventative approach is actually a more cost-effective (economical) approach long-term than chronically reacting to crises and public complaints. Of course, any program also must have the capability to respond quickly to sudden problems and emergencies (e.g. disease, rat bites or localised outbreaks).

Rats need to be viewed as an 'indicator species' of environmental quality (or degradation), and programs need to focus on causal factors for species success rather than simply being reactive and poison dependent. The goal must be to manage populations at the low end of the sigmoid growth curve by reducing carrying capacity and giving greater emphasis to surveillance monitoring and sanitation controls. A behavioural shift from rat hunting to environmental management and monitoring is needed. This represents an ecologically-based strategy.

The kind of organisational management and IPM methods demonstrated in the 1990s in Boston should become the foundation of program implementation in the 21st century. An effective program will include centralised leadership, partnerships among participants, sound definition of work scope, assigned responsibilities, mapping and data management capabilities, and education of policy makers. A program approach should be comprehensive in scope and structure, and inclusive in terms of participants (Figure 3).

An emphasis on the engineering and structural maintenance of urban environments, to reduce pest habitat and permanently lower carrying capacity, is critically needed as part of public health management. Rodent control should be incorporated into both urban planning (design) and urban maintenance if a truly proactive program is desired. Municipalities also should require rodent control for major construction projects, since by their nature they create rodent habitat during the

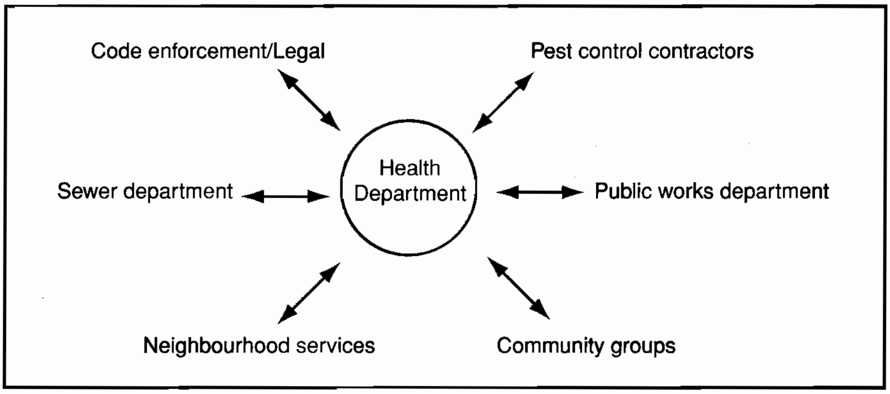

Figure 3.
A flow chart that illustrates a centralised, inclusive and organised approach to managing an urban rodent control program.

construction phase. Biologists need to become more familiar with design engineering and urban infrastructure, and work with engineers and architects.

Basic research and stewardship on the use of refuse containers, recycling programs, and refuse management and containment should be a priority. A shift from focusing primarily on rodenticide and traps (reactive approach) to sanitation management (proactive approach) is needed in urban environments. This includes use of rodent-proof containers (rubbish bins, dumpsters, refuse compactors and grease containers), public education campaigns, reduction of refuse volume, and uniform refuse containers and pickup times. Foremost, there must be effective and enforceable sanitation laws and practices established. For example, keeping lids securely closed on containers, not using plastic bags alone for refuse storage, avoiding placement of refuse outside overnight the day before collection, and timing necessary night-time collections to minimise the number of hours that refuse is exposed.

Inclusion of subsurface environments (sewers), currently ignored by most municipalities, must become a fundamental part of urban rodent control programs (Figure 4). Subsurface populations function as reservoirs that can chronically re-infest surface areas and 'elevate' disease organisms. Effective training on subsurface baiting and control is needed worldwide and will have to be incorporated into comprehensive training necessary for the success of any program.

Use of rodenticide in the future will have to be more carefully planned and implemented than typically occurs in most cities today. The spread of genetic resistance, including the recent involvement of second-generation anticoagulant compounds (MacNicoll et al. 1996), presents a significant concern for the future of urban rodent control and public health management. Rodenticide, rather than habitat management, too often is the primary approach used today by municipalities. This provides short-term resolution but may result in long-term problems.

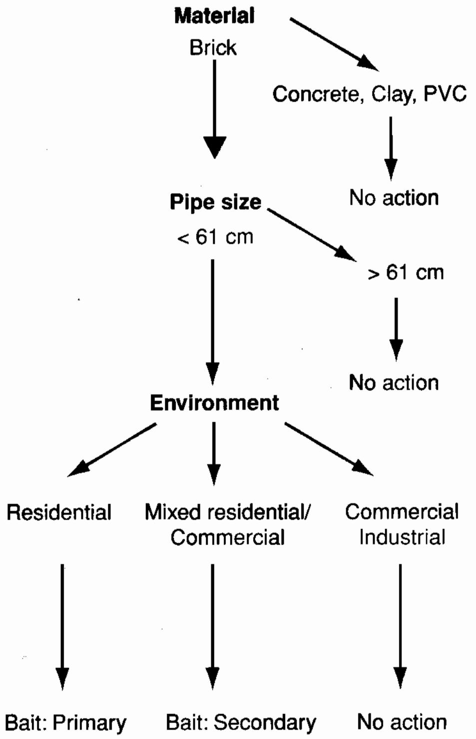

Figure 4.
An example of how to strategically implement and prioritise a sewer baiting campaign (Colvin et al. 1998).

Excessive use of rodenticide, while allowing sanitary problems to remain, presents a condition for rapid reproduction by survivors and the perpetuation of genetic qualities favourable to resistance. The strategy for lowering the potential for resistance must be to focus on environmental management and the wise use of rodenticide.

Diversity of skills should be sought when establishing a rodent control team. For example, a creative approach for public education may require the involvement of public relations and marketing experts. Teachers, lawyers, engineers, contract administrators, computer scientists, property managers, architects and social workers must be made part of the immediate or extended team to maximise program effectiveness.

A rodent control program should have an 'action plan' that defines program elements and implementation. The action plan should describe: program organisation, staff responsibilities, training, legal requirements and enforcement capabilities, contracted services, schedules, sanitation management, infrastructure design and maintenance, mapping and data management, lethal measures (including subsurface), public education and outreach, community organising, surveys and monitoring, and administrative elements.

Whether in a developed or developing nation, the ecological and organisational principles associated with urban rodent control are largely the same. The difference may be the extent of program resources available; however, it can not be assumed today that a developed nation automatically has an advantage regarding program implementation. Large, developed cities can provide more habitat, have greater bureaucracy, but have no better technical knowledge than found in smaller cities or cities in developing nations. The beginning point for all is the establishment of qualified staffing and training, political and budgetary commitment, enforceable sanitation laws, and defined responsibilities and program goals. Implementation of the IPM plan follows, encompassing surveys, public education, sanitation programs, baiting/trapping, structural improvements, community involvement, scheduling and monitoring.

Technical leadership is a serious constraint for urban rodent control today, and this needs to be overcome through involvement of universities and federal and state agencies. Field personnel on the municipal level need to base their efforts on facts rather than myths. To assist them, they need technical support that is accessible, knowledgeable and practical. In that regard, research biologists must help resolve any technical gaps concerning control methods and local ecological factors. They also must learn to partner directly with municipal personnel and translate the science of rodent control for the 'real world', so programs can be better designed, implemented and sustained.

The history of urban rodent control and the 'lessons learned' in recent years present a 'road map' for future success. However, without political support and effective administration, implementation of urban rodent control programs will continue to be limited and public health and economic impacts will result. The ecological and political arenas of the urban environment are complex and interrelated, and urban rodent control programs can only be implemented effectively when both of those subjects are mastered.

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Section 3

Case Studies in Asia and Africa




12. Rodent Pest Management in Agricultural Ecosystems in China

Zhibin Zhang, Anguo Chen, Zhendong Ning and Xiuqing Huang

Abstract

Rodent pests are a serious problem of agricultural production in China. Abnormal climate patterns of recent decades, with more severe droughts and warmer winters, have allowed rodents to become increasingly abundant. In the early 1980s, there was a widespread outbreak of rodents in the agricultural areas of China. Since 1986, rodent management has been listed three successive times as a national five-year-plan key project (1986–1990; 1991–1995; 1996–2000). These key projects aim to (1) collect long-term population data on major rodents and establish forecasting models, (2) understand population recovery and community succession after large scale management, (3) develop effective control techniques and strategies, and (4) set up demonstration areas to assist local governments to launch a large-scale rodent control campaign. In this paper, a brief introduction to the results of our national key projects in four agricultural regions is given. The agricultural regions and their main pest species are (i) the North China Plain, rat-like hamster (*Cricetulus triton*), (ii) the Northwest Loess Plateau, Chinese zokor (*Myospalax fontanieri*), (iii) the Dongting Lake region along the Yangtze River, oriental vole (*Microtus fortis*) and (iv) the Pearl River Delta, *Rattus rattoides*. The problems and future challenges of rodent pest management in agricultural ecosystems are also discussed.

Keywords

Rodent pest management, agricultural ecosystem, China

INTRODUCTION

On the world scale, China has the largest population (1.2 billion people), but one of the smallest average family holding of arable land (less than 0.4 ha). Grain production is listed as the top priority by the central government in China. In most areas of the countryside, farmers not only depend on grain for food, but also for earning money by selling grain to the market or to the government.

There are four key regions of grain production in China (Figure 1). The first is the North China Plain, which belongs to the middle and lower regions of the Yellow River and regions of the Huai-He and Hai-He Rivers. Wheat, corn, peanuts and green beans are the major crops. The second is the South China Plain, located in the middle and lower regions of the Yangtze and Pearl Rivers. Rice is the major crop in this region. The third is the Northeast China Plain, which is formed by the flood plains of the Hei-Long-Jiang River, Nen-Jiang River, Song-Hua-Jiang River and Liao-He River. Corn, wheat and soybean are the major crops in this region. The fourth is the Northwest Loess Plateau, located in the upper reaches of the Yellow River, where corn and wheat are the major crops.

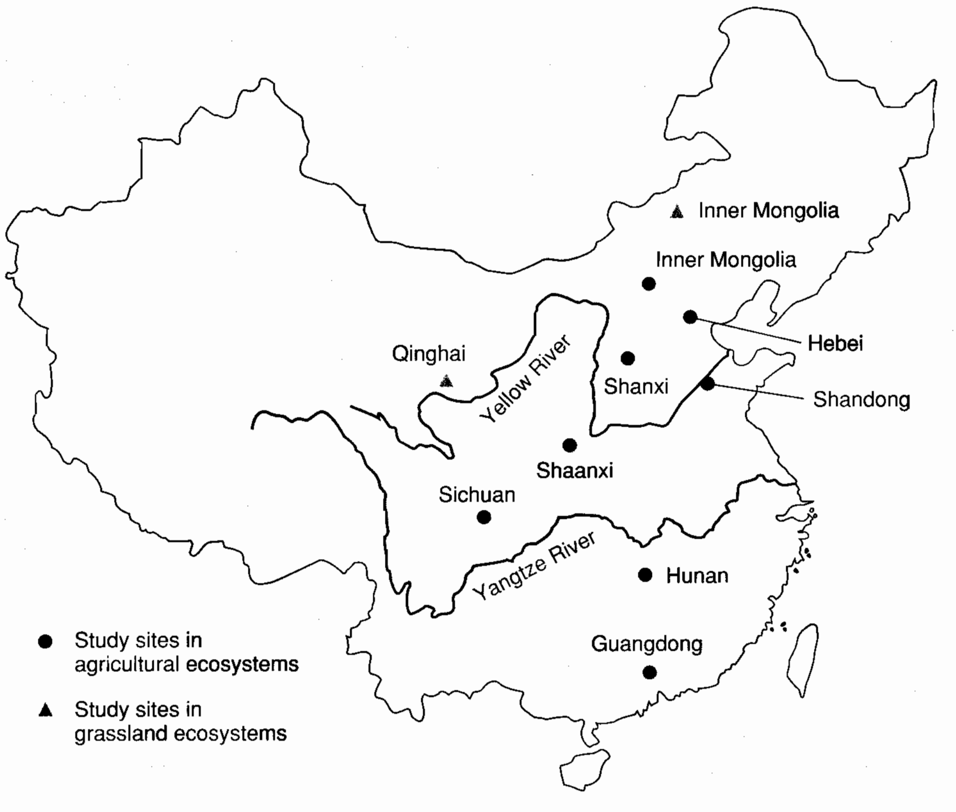

Figure 1.
Long term study sites for rodent ecology and management in China.

Although the annual grain production in China is now greater than 500 million t, in the remote areas there are still several million people who are short of grain. The government is planning to increase production by 25 million t every year during 1996–2000 by introducing new agricultural technologies. Plant protection, through management of diseases, insects, weeds and rodents is listed as the top priority in realising this goal. Since the 1980s, rodent problems have become more and more serious. Changes in climate nationally have resulted in more severe droughts and warmer winters (Wang and Ye 1992) which are two important factors influencing rodent abundance. In 1997, the Yellow River, called the mother-river of China, was without water flow for more than 100 days. Usually the river flows continually. This is indicative of the severity of the droughts that China (especially North China) is facing.

In 1982, large-scale eruptions of rodent populations occurred in the farmlands of China. The area of infested arable land was greater than 27 million ha, about 27% of the total arable land in China. The annual grain loss caused by rodents was over 15 million t. In one year, over 140,000 people contracted rodent-borne diseases (mostly epidemic haemorrhagic fever, leptospirosis and endemic typhus) (Wang 1996).

In 1983, the State Council of the Chinese Central Government issued an urgent document calling for local governments to launch a movement on rodent control in farmland and grassland. Rodent control was listed in the top three priorities for the plant protection program. Consequently, the governments of different levels put much effort and resources into rodent control. About 44% of infested areas were treated using rodenticides, and grain losses were reduced by approximately 7.5 million t (Table 1). However, since early 1993, input by governments on rodent control has been much reduced due to changes in government infrastructure and policy. Farmers have become responsible for their own rodent control with much less coordination by government.

Table 1.
The area of arable land infested by, and treated for, rodents in China from 1980 to 1993 (from Zhao 1996).

Year	Infested area (million ha)	Treated area (million ha)
1980	3.3	1.3
1981	6.7	3.3
1982	20.0	2.5
1983	21.5	9.9
1984	24.0	8.7
1985	24.8	14.5
1986	33.9	17.5
1987	39.3	17.3
1988	26.7	11.7
1989	21.3	14.7
1990	21.3	6.7
1991	20.3	13.9
1992	21.5	13.3
1993	33.3	5.0
Total	**317.9**	**140.3**

Note: data for 1980–82 were based on surveys in 18 provinces; data for 1983–87 in 20–24 provinces; data for 1988–1991 in 27 provinces; data for 1992 in 26 provinces; data for 1993 in 22 provinces.

The magnitude of the rodent outbreaks in the arable land of China in the early 1980s also led to an increased effort in rodent research. Since 1985, rodent control has been listed in three successive national five-year-plan projects (1985–1990; 1991–1995; 1996–2000) by the central government. There are approximately 100 scientists with the Chinese Academy of Sciences, Ministry of Agriculture and universities working on rodent control. Long-term study sites located in key regions of grain production were selected (Figure 1) according to level of the rodent infestation. Table 2 gives details of the locations of the study sites and the major rodent pest species in each. No sites were on the Northeast China Plain. Two study sites within the grassland ecosystem (Figure 1) were selected and the findings from research conducted at these sites are reported elsewhere in this book (Fan et al, Chapter 13; Zhong et al., Chapter 9). In 1986, another study site, which does not belong to the key regions of grain production but with local heavy rodent infestation, was selected in the south part of the Inner Mongolia Plateau. This region is a mixture of cropland and grassland. Mongolian gerbils (*Meriones unguiculatus*) cause huge damage to crops (mostly cereals and potato) in this region.

Since 1985, population surveys, assessment of rodent damage, and control techniques and strategies, have been extensively studied by well-trained scientists. Scientific staff at each of the study sites provide technical extension and advice for instigating local rodent control campaigns. In this chapter, case studies are described from four major agricultural regions, focusing on the achievements of rodent control based on biological and ecological knowledge of the target rodent pests.

Table 2.
Long-term study sites of the three successive national five-year-plan projects on rodent ecology and management in key regions in China.

Key regions	Study sites	Major pest species
North China Plain	Hebei Province Shandong Province	*Cricetulus triton* *Cricetulus barabensis*
Northwest Loess Plateau	Shanxi Province	*Myospalax fontanieri*
		Citellus dauricus
	Shaanxi Province	*Microtus mandarinus*
		Cricetulus triton
South China Plain (Yangtze River Region)	Hunan Province (Dongting Lake Region)	*Rattus norvegicus* *Microtus fortis*
	Sichuan Province	*Rattus nitidus* *Rattus norvegicus*
South China Plain (Pearl River Delta)	Guandong Province	*Rattus rattoides* *Bandicota indica*
Inner Mongolian Plateau	Inner Mongolia	*Meriones unguiculatus*

Case Studies of Rodent Management in the Major Agricultural Regions

Hamster management in the North China Plain

Agricultural systems and environments

In the North China Plain, wheat is planted in autumn (October) and harvested the next summer in June. Summer corn is planted immediately after the wheat harvest and is harvested in October. Small areas of the arable land are not planted in October. Instead, they are planted the next spring with crops such as cotton, peanuts, soybean and spring corn. Therefore there are three sowing seasons (April, June and October) as well as two harvest seasons (June and October).

The climate in this region belongs to the warm–temperate zone. It is very cold in winter and very hot in summer. The annual rainfall is approximately 400–500 mm, with 80% of the annual rainfall occurring in summer (June, July and August).

Ploughing and irrigation are two major agricultural activities in the sowing seasons. Other common activities in the fields include spreading of chemical insecticides and fertilisers, and the clearing of weeds. Most of these activities have a negative effect on rodent populations in this region. Ploughing and irrigation destroy their burrow systems, and sometimes kill the juveniles directly. The spatial distribution of burrow holes of the rat-like hamster is clearly affected by periods of intensive agricultural activities; most of the burrows are constructed in the banks or in non-irrigated or non-ploughed wastelands (small patches of trees and grasses) during this time (Zhang et al. 1997c).

In 1986 in Raoyang County, Hebei Province, the impact of winter irrigation on the habitat and distribution of the burrows of the rat-like hamster (*Cricetulus triton*) was examined. The density of burrows of the hamster in the wasteland was 67.7 holes/ha, while the density in irrigated farmland was 35.6 holes/ha (Zhang et al. 1997c). Winter irrigation of wheat is therefore crucial in reducing the over-wintering hamster population.

Reproduction patterns and population dynamics

The climate, crop plantation system and agricultural activities determine the seasonal reproduction and population dynamics of rat-like hamsters. Rat-like hamsters usually begin to reproduce in early March and finish breeding by the end of August or early September. The adult female hamsters that survive the winter produce three litters and their young of that season may in turn produce 1–2 litters. Females born in early autumn do not breed until the next spring. The litter size of the rat-like hamster ranges from 2–22 with an average of 9 or 10. The reproductive performance of hamsters is considerably affected by population density. In the peak year of 1996 (average trap success 7.7%) the average litter size of the rat-like hamster was 9.1 with a pregnancy rate of 24.8%. In the trough year of 1998 (average trap success of 1.2%), the average litter size was 9.9, with a pregnancy rate of 39.2% (Zhang et al. 1998).

For the rat-like hamster, there are two periods of high density within a year; one in spring and one in autumn. The autumn peak (e.g. in 1986) is usually larger than the spring peak (Figure 2). Heavy rains and high temperatures in summer cause low population densities by increasing the mortality rate of the hamsters. In 1986, the monthly mortality rates of rat-like hamsters were 0.19, 0.14 and 0.42 in spring, autumn and summer, respectively (Zhang et al. 1992). The high summer temperatures (possibly together with the interaction of heavy rain or changes in the photoperiod) result in a 10-day longer mean interval between pregnancies for hamsters compared to spring (Zhang et al. 1991).

Since the early 1980s, the winter has become warmer in the North China Plain and the seasonal population patterns have begun to change, with the magnitude of the spring peak similar to, or higher than, the autumn peak. Taking 1986 and 1994 as examples, the average air temperature in January in 1986 and 1994 was –3.66°C and –2.1°C, respectively; the hamster population density in January was 0.07% and 3.01%, respectively; and the mortality from the previous October to April was 0.83 and 0.56, respectively. This resulted in a higher spring peak than autumn peak in 1994 (Figure 2).

Damage and assessment

The rat-like hamster has a mean body mass of 120 g and is principally a seed-eater; 70% of the food carried in its cheek pouches is composed of crop seeds, 15% stems, roots, flowers and leaves of crops, and 15% insects (Wang et al. 1991). The main damage caused

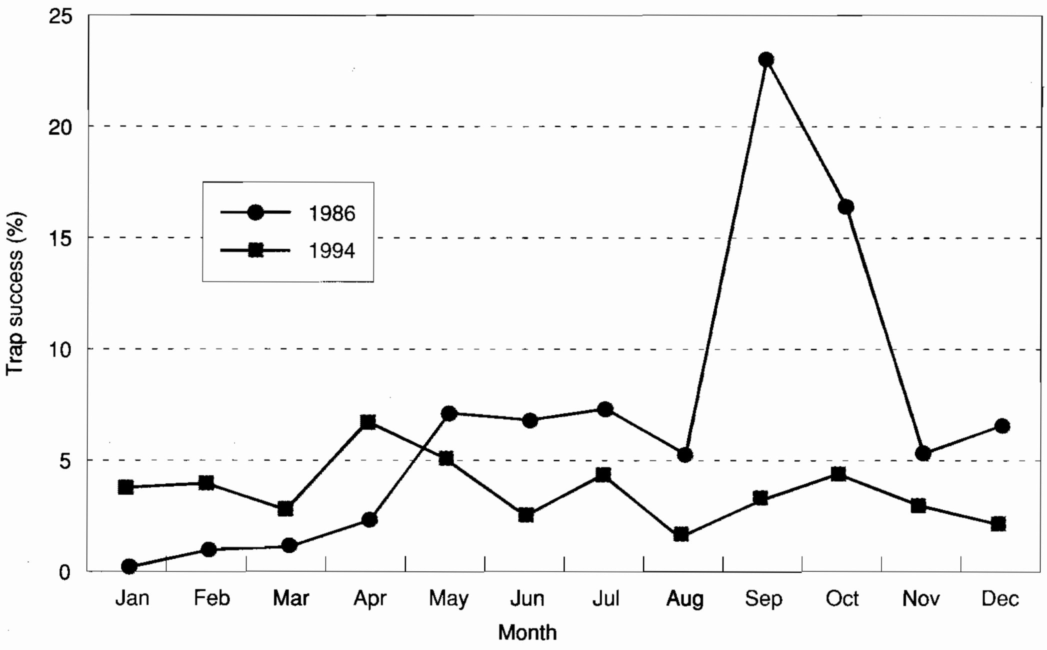

Figure 2.
Seasonal dynamics of the rat-like hamster population in 1986 and 1994 in Raoyang County, Hebei Province (from Zhang et al. 1998).

by the rat-like hamsters occurs to seeds during the sowing periods and to mature crops during the harvest periods. The rat-like hamster stores about 200 g of seed in both spring and summer, and much more in autumn ranging from 0.6–20.0 kg (n = 40) per hamster.

Peanuts, the favourite food of the rat-like hamster, suffer high levels of damage. In 1986, two enclosure experiments were conducted in Raoyang County, Hebei Province, on the depredations of the rat-like hamster to peanut crops. The first study was conducted in a 0.26 ha enclosure. At a capture success of 22%, the rat-like hamsters consumed 14.8% of the peanut crop. The second study was conducted in a 2 ha plot. At a capture success of 24%, the rat-like hamsters consumed 19.6% of the peanut crop (Zhang et al. 1998).

It is difficult to assign damage to particular species when the rodent population consists of a mix of several species. By employing multiple regression statistics, Wang et al. (1996) developed a model for estimating the damage to peanut crops by mixed populations of rodents during the sowing period (May) and the harvest period (September) in Shandong Province as below.

$$LS\% = 0.167 + 0.155D_{S1} + 0.260D_{S2} + 0.086D_{S3} \; (r = 0.981, F = 87.48, d.f. = 3,10, p < 0.001) \quad (1)$$

where $LS\%$ is the peanut loss at sowing caused by the striped hamster (D_{S1}), the rat-like hamster (D_{S2}) and the striped field mouse, *Apodemus agrarius* (D_{S3}). DS indicates the trap success (%) of the respective rodent populations in spring.

$$LA\% = 1.226 + 0.176D_{A1} + 0.456D_{A2} + 0.110D_{A3}, r = 0.959, F = 22.98, d.f. = 3,6, p < 0.001) \quad (2)$$

where $LA\%$ is the peanut loss at harvest caused by the striped hamster (D_{A1}), rat-like hamster (D_{A2}) and striped field mouse (D_{A3}). DA indicates the trap success (%) of the respective rodent populations in autumn.

Population forecasting for management

Since the most serious damage occurs in autumn, and rodent control often begins in early spring, there is a strong need to be able to forecast the population of hamsters in autumn. Based on the monitoring data from 12 years in Raoyang County and Guan County, a short-term forecasting model for the rat-like hamster was established (Zhang et al. 1998):

$$Y_A = 0.98 + 8.66X_4 \; (r = 0.96, p < 0.01) \text{ when } X_4 \leq 2.33 \quad (3)$$

$$Y_A = 18.43 - 2.14\,X_4 \; (r = 0.89, p < 0.05) \text{ when } X_4 > 2.33 \quad (4)$$

Using this model, where Y_A is the maximum trap success (%) in autumn (September, October or November), X_4 is the trap success (%) in April.

Although the autumn trap success of the rat-like hamster is highly correlated with its April trap success, the correlation is non-linear. There is a strong positive association when the April trap success is ≤ 2.3 and a strong negative association when the April trap success is > 2.3 (Figure 3).

Based on the above forecasting models, we successfully predicted the changes in population dynamics of the rat-like hamster in Raoyang County and Guan County in 1996 and 1997 (Table 3). The accuracy of prediction is defined as:

$$A = [1 - |P - O| / M] \times 100\% \quad (5)$$

where A is the accuracy of prediction, P is the predicted trap success, O is the observed trap success, and M is the maximum trap success ever observed. The accuracy of prediction in 1996 for Raoyang County and Guan County was 87% and 97.9%, respectively. In 1997 the accuracy of prediction for the same two counties was 95.2% and 90.7%, respectively.

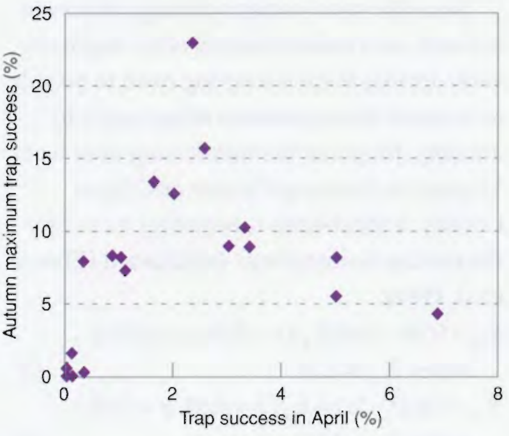

Figure 3.
The relationship between the autumn maximum trap success (%) and trap success in April (spring) in Hebei Province from 1984–1995.

Forecasting is an important step in deciding whether to launch a rodent control campaign in spring in this region. If the predicted autumn trap success is over 5%, a rodent campaign is necessary to reduce grain losses. We have observed that farmers pay less attention to damage when autumn trap success of the rat-like hamster is less than 5%. This trap success is equivalent to approximately 3–4% loss of the peanut crop.

Control techniques and strategies

The rat-like hamster is an important rodent pest in the North China Plain and farmers have developed several traditional methods of pest management. In autumn after harvest, farmers dig the rodent burrows to recover the grains stored by the rat-like hamster. Some farmers are extremely proficient at digging hamster burrows, recovering 100 kg of grain within 1–2 weeks.

The value of ploughing and irrigation is also well known by farmers for reducing hamster populations. It is common for farmers to directly kill hamsters during ploughing and irrigation.

During 1994–98, the negative impact of irrigation on the hamster population was clearly demonstrated in Shunyi District, Beijing. Shunyi used to irrigate its farmland in the traditional way, pumping water directly into farmland. This method wasted a lot of groundwater. In 1994, Shunyi swapped over from the old ditch irrigation to spray irrigation. The rodent community

Table 3.
Prediction of the population abundance of the rat-like hamster in Raoyang County and Guan County, Hebei Province, in 1996 and 1997 using the forecasting models described in the text (see also Zhang et al. 1998). *A* is the accuracy of prediction, *P* is the predicted trap success, and *O* is the observed trap success. The maximum trap success ever observed for this cropping system was 23.1

Place	1996			1997		
	P	O	A%	P	O	A%
Raoyang	7.73	8.21	97.9	7.68	5.52	90.7
Guan	12.0	9.0	87.0	9.4	8.3	95.2

changed suddenly from a striped field mouse dominant community into a rat-like hamster dominant one. The outbreak of rat-like hamster populations in Shunyi District occurred for several years after this change in irrigation system, and has resulted in tremendous losses in crop production.

In 1978, rural China experienced a reform from a community-based system to a family-based system in which each family rents a small area of land, and they decide what they plant. This has led to a patchy landscape consisting of a mosaic of different crops. This heterogeneous cropping system provides a favourable environment for hamsters by increasing their survival and breeding performance. Small plots of land in a patchy landscape are particularly vulnerable to attack by hamsters, especially those plots growing oil crops. Chemical control has little impact on rodent populations in such small plots of land because recolonisation by rats from the surrounding environment soon counteracts any local reductions in population density. In order to solve this problem, a new multiple-capture physical trap was invented (Zhang et al. 1996). The pitfall trap was designed with a magnetic trigger on its lid (Figure 4). One trap was set in each of two corn fields in Guan County in the summer of 1995. In eight days, both traps caught 20 hamsters. During the experiment, the capture success in snap-back traps of the rat-like hamster, striped hamster (*Cricetulus barabensis*) and house mouse (*Mus musculus*) was 21%, 1% and 0.3%, respectively.

Fresh wheat containing 0.005% bromadiolone (see Guo et al. 1997) was used in a rodent control campaign in Beijing. In 1997, more than 333,000 ha of farmland were treated with bromadiolone, achieving approximately a 92% kill rate (based on pre- versus post-treatment indices of abundance) in early spring. The capture success of hamster was maintained at a level less than 5% through the year, however the population recovered to its original density the next spring, and another chemical control campaign was launched in 1998 (Xihong Guo, pers. comm.).

In addition, a male chemosterilant, 1–2% α-chlorohydrin, has been tested for controlling the rat-like hamster (Zhang et al. 1997a,b). The chemosterilant was tested in Guan County, where bromadiolone only kills 70–80% of hamsters, enabling the populations to recover quickly from poisoning campaigns (Zhibin Zhang, unpublished data). Zhang (1995, 1996) suggested that a strategy of combining fertility control with chemical mortality might delay the recovery of hamster populations post-poisoning; male hamsters that do not die following the ingestion of bromadiolone would become sterile from the α-chlorohydrin.

In July of 1993 and in April of 1995, an experimental farmland site was treated with a wheat bait of 0.005% bromadiolone and 1% α-chlorohydrin. Similar surrounding farmland was selected as an untreated area. Ten days after treatment, 75% and 78% mortality were achieved in 1993 and 1995, respectively, on the experimental site. In 1994, no control measure was taken. Mortality control combined with sterilisation achieved good results. During 1995, the capture success of the rat-like hamsters on the experimental site was less than 5%, while eruptions of hamster populations occurred on the untreated site (Zhang et al. 1998; Figure 5).

Figure 4.
A new multiple pitfall trap with a magnetic trigger.

Recommended management strategies and research priorities

In the North China Plain, there are two strategies recommended for farmers to manage the rat-like hamster:

- If the hamster is causing localised problems within a farming system then the pitfall trap is recommended. One trap should be placed in the middle of a crop (in this region the average farm size is 0.25 to 0.5 ha).
- If the hamster is causing problems over a large area then broad-scale application of a wheat bait of 0.005% bromadiolone and 1% α-chlorohydrin is recommended.

Further research is required on the efficacy of bromadiolone with and without α-chlorohydrin, and on the social acceptance of using male sterility baits. Other research has begun on Chinese herbs for enhancing the effect of anticoagulants. In particular, is it possible to increase the susceptibility of hamster populations to bromadiolone and can the time until death be reduced (currently around 10 days for hamsters)?

Zokor management in the Northwest Loess Plateau

Agricultural system and environment

The Northwest Loess Plateau is one of the most undeveloped areas in China due to its harsh climate. This region has very limited

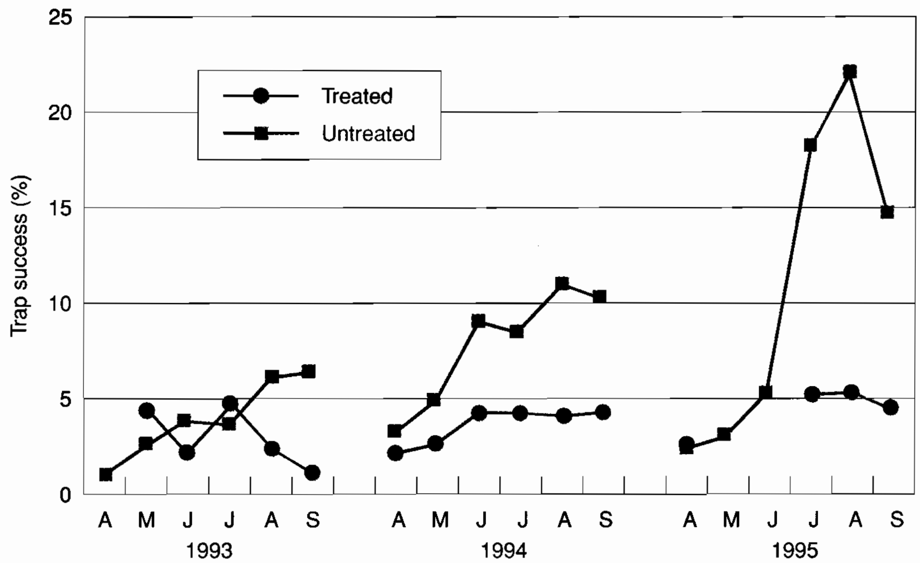

Figure 5.
Field trials of the effect of a-chlorohydrin combined with bromadiolone on the rat-like hamster population in Guan County, Hebei Province, from 1993–1995.

rainfall. Corn and wheat are commonly planted in the upper Yellow River regions. The grain production is seriously affected by rodents, particularly the Chinese zokor (*Myospalax fontanieri*). Rodent control is very important for reducing grain losses and increasing the income of farmers in this region.

Reproduction patterns and population dynamics

The Chinese zokor is a large rodent (300–650 g) that lives underground. The breeding season is from March to June, and adult females reproduce only once a year. The litter size ranges from 1–6, averaging 3.0 ± 0.4 (Zou et al. 1998). There is one annual peak in zokor numbers in June or July.

Damage and assessment

The burrowing activity of the Chinese zokor causes significant damage to crops. Zokors also take crop seedlings or seeds to their burrows for food. Winter wheat sustains high damage because zokor populations are short of other food sources during winter. Serious damage occurs to corn and sunflower seedlings in spring when zokors begin to breed and more extensive digging and burrowing take place. Zokors also horde food in autumn for over-wintering.

The degree of damage caused by zokors can be divided into five classes based on the proportion of seeds/seedlings eaten (Ning et al. 1994):

- no damage;
- proportion of seeds/seedlings eaten is 1–25%;
- proportion of seeds/seedlings eaten is 25–50%;
- proportion of seeds/seedlings eaten is 50–75%; and
- proportion of seeds/seedlings eaten is 75–100%.

The regression models between crop losses and density of zokor were established as follows (Ning et al. 1994; Chang et al. 1998):

$$L_W = -0.4462 + 0.9748X_6 \ (r = 0.9625, \ d.f. = 7, p < 0.01) \quad (6)$$

where LW is the proportion of wheat eaten by zokors (%) and X_6 is the density of the zokors in June (individuals/ha); and

$$L_C = -1.6427 + 1.1913X_9 \ (r = 0.9657, \ d.f. = 5, p < 0.01) \quad (7)$$

where L_C is the proportion of corn eaten by zokors (%) and X_9 is the density of zokors in September (individuals/ha).

Control techniques and strategies

Because zokors live underground and do not readily take baits or enter physical traps, routine techniques like rodenticides and physical trapping are inefficient for control. A fumigant, aluminium phosphide, is commonly used to kill zokors in this region. The burrow tunnel system is very complex, therefore it usually requires about 10 pieces of the fumigant (3.3 g) to effectively fumigate a burrow. The kill rate is approximately 80% (based on pre- versus post-treatment indices of active burrows) if conducted by experts, but is generally less than 70% when applied by farmers during a rodent control campaign.

A new technique was invented in 1986, called the 'explosive paper tube' (EPT) which is specialised for controlling underground rodents (Liu et al. 1991). The EPT contains explosives of dinitrodiazo-phenol or nickel nitrohydrazino, and is triggered via a battery. The EPT is 20–30 mm long, and its diameter is 3 mm (Figure 6). The EPT is waterproof, easy and safe to carry. EPT is also cost effective and available commercially in this region.

The kill rate with EPTs is over 95% for large-scale rodent control campaigns — much better than using rodenticides. The procedure for setting an EPT is simple and requires four steps: (1) select an active burrow tunnel; (2) dig into the tunnel to place an EPT there, bury it; (3) block the tunnel with a soil ball loosely; (4) connect the two wires with a small battery (1.5 V), making a trigger which will be touched by the falling soil ball. When a zokor pushes the soil ball which blocks its tunnel, the ball will touch the trigger, and the EPT will explode under the zokor body and kill it (Zou et al. 1998).

Recommended management strategies and research priorities

The EPT has been successfully commercialised and proven very efficient for zokor control in this region. However, the trigger system is still complex, and thus needs to be improved further. A trigger system is required that does not re-use the battery and the connecting wires. This would make it easier to set the EPT in the field.

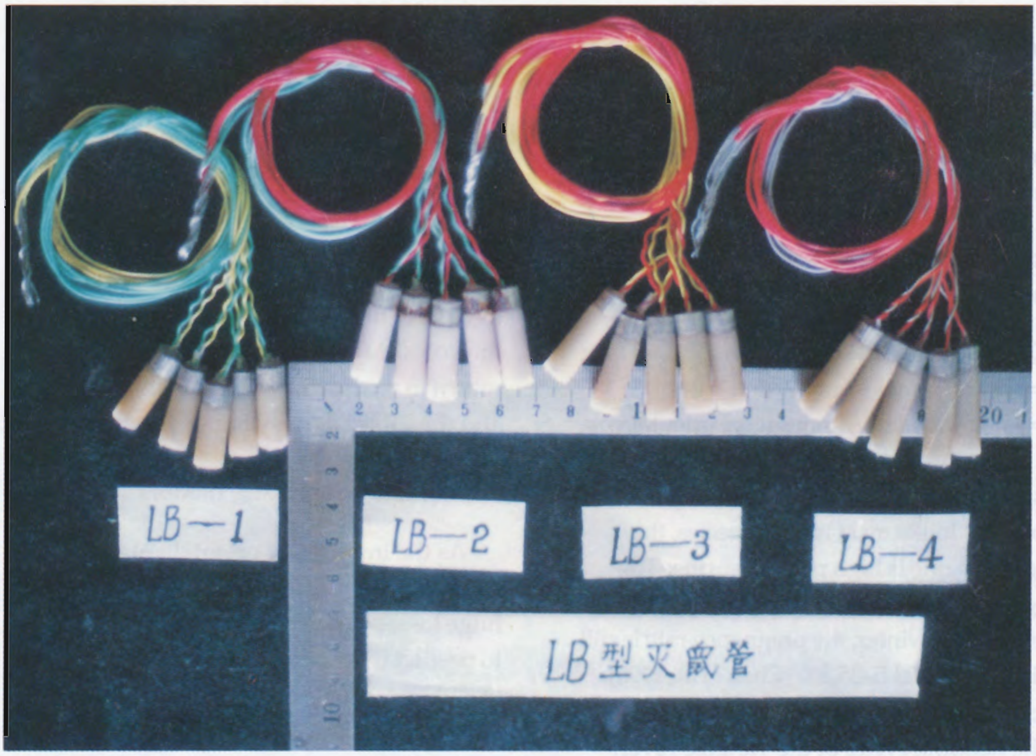

Photo: Zhendong Ning

Figure 6.
The explosive paper tube (EPT) for controlling zokors.

The EPT occasionally only injures the zokor, and has potential risk to people, especially children. From the view of humaneness and public safety, alternative control techniques need to be considered for replacing the EPT for zokor control. Two research priorities are suggested. The first is to improve the acceptance of rodenticide bait by adding an attractant. This requires detailed study of zokor behaviour and their chemical communication. The second is to find an ecological management strategy for zokor control. The Chinese zokor's favourite food are the roots of grass and crops. The clearing of weeds using herbicides in non-crop lands has shown potential for reducing zokor populations (Zhengdong Ning, unpublished data). Also, planting toxic herbs in wastelands (non-crop habitats), banks and croplands could be effective in reducing the favourite grasses of zokors and in poisoning zokors when they eat the roots of the herbs.

Vole management in the South China Plain (Yangtze River region)

Agricultural system and environment

Dongting Lake is a very large lake located in the middle of the Yangtze River. It plays an important role in regulating floods of the Yangtze River during the rainy season. The oriental vole (*Microtus fortis*) is a rodent species well adapted to the environment of

Dongting Lake (Chen et al. 1995; Wu et al. 1996, 1998; Guo et al. 1997). The voles migrate back and forth between the beaches and islands of Dongting Lake and the surrounding rice fields as the floodwaters rise and recede (see below).

Reproduction patterns and population dynamics

The adult oriental vole weighs 59.5 ± 11.3 g (n = 378) for females, and 77.5 ± 15.0 g (n = 415) for males. Although the oriental vole can breed throughout the year at Dongting Lake, its breeding is much affected by flooding. Unlike most rodent species, the pregnancy rate is high prior to spring. The pregnancy rate from February to April is 64%. Even in deep winter, the pregnancy rate is still maintained at 23.5–35.3% (Chen et al. 1998). This reproductive strategy is clearly adapted to the flooding cycles of the Yangtze River. The beach and island habitat with grass in the lake is the optimal habitat for the herbivore voles in winter. During the flooding season these habitats are flooded. Just prior to flooding, oriental voles migrate in large swarms to the surrounding farmland where their breeding is greatly reduced (Table 4). During September and October, the flooding waters recede and the voles return to the beach and island habitats for the winter (Chen et al. 1995, 1996, 1998; Wu et al. 1996; Guo et al. 1997).

The seasonal population patterns of the oriental vole in rice fields and in the grass habitats on the islands and near the beaches of the lake are affected greatly by their migration between lake habitats and the rice fields. There is a population peak in summer in the rice fields following the migration of the voles. After October, voles begin to return to the beaches and ephemeral islands, and then their density in rice fields is low.

Population forecasting models

As the invasion of oriental voles into rice fields during the flooding season causes huge losses to rice production, it is necessary to predict these population changes. Chen et al. (1998) found that the trap success (%) of voles in farmland during the flooding season is mainly determined by the duration of breeding of the vole population living in beaches in the non-flooding season and the rainfall in March. The duration of breeding in lake beaches is strongly correlated with the period when the water level of Dongting Lake is below 27.5 m. The regression model was established as follows:

$$Y = 0.0394X_1 - 0.0048X_2 - 5.02 \ (R = 0.957, d.f. = 9, F = 49.23, p < 0.0001) \qquad (8)$$

Table 4.
Reproduction of oriental voles in flooding and non-flooding seasons (from Chen et al. 1998).

Habitat	Lake beaches	Rice fields
Duration	November to May	May to October
Season	Non-flooding season	Flooding season
Number of females	185	280
Pregnancy rate (%)	51.4	20.4
Litter size	5.06 ± 0.15	5.37 ± 0.25

where Y is the trap success of voles in rice fields during the next flooding season, X_1 is the duration of breeding in lake beaches and X_2 is the rainfall in March. In 1994 and 1996, this model was used with good accuracy for predicting the trap success of voles in rice fields during the next flooding season (Chen et al. 1998).

Damage and assessment

In 1986, in the Yueyang County, 5,213 ha of rice fields were damaged by voles with grain losses of 918 t. More than 50% of the surrounding trees were seriously chewed by voles (Chen et al. 1998).

The oriental vole also spreads a serious rodent-borne disease, leptospirosis, to farmers working in rice fields. In 1979, 527 people on one state farm were infected by leptospirosis and 214 of them were sent to hospital.

The regression model between rice loss (L%) and the trap success is established by Wang et al. (1997):

$$L = 0.0674X_1 + 0.0307X_2 - 0.1627\ (R = 0.83,\ d.f. = 2,10,\ F = 11.07,\ p < 0.01) \quad (9)$$

where X_1 is the trap success of oriental voles, and X_2 is the trap success of the striped field mouse.

Control techniques and strategies

Based on the habits of migration of the oriental voles between beaches of the lake and rice fields during the flooding and non-flooding seasons, a new method for rodent control was invented in 1981 by the local farmers of Jingpen State Farm. They buried deep pots between fixed fences that were erected along the dyke surrounding the Dongting Lake. The plate fence was 500 mm high, and buried 50–100 mm into the soil to prevent immigration of voles from lake beaches to the rice fields. Pots which were 0.8 m deep and 0.3 m diameter were buried between two fences. The pots were located every 50 m along the fences. When the flooding season approached, the large swarm of voles was channelled into the pots en route to the surrounding rice fields. From 1981–1987, along the west bank of Dongting Lake (which covers two state farms and eight towns), 1,588 t of voles were captured along a total of 231 km of fence (Table 5).

Table 5.
The quantity (t) of voles captured by burying deep pots in the dyke along the west bank of Dongting Lake from 1981 to 1988 (from Chen et al. 1998).

Year	Barrier line (m)	Voles captured (t)
1981	3 050	11.00
1982	17 300	159.00
1983	43 200	58.55
1984	40 700	106.75
1985	35 450	240.50
1986	42 160	511.00
1987	47 200	501.2
1988	2 850	49.00
Total	**231 910**	**1 637**

Chen et al. (1998) later improved this technique by enclosing the banks of the dyke with a 0.5 m high brick wall at the top of the dyke, with a 80 mm overhang. This physical structure prevented the voles from entering the rice fields (Figure 7). The damage of this species has been well controlled since the construction of the rodent-proof wall. This is an example of successfully controlling rodents based on understanding their ecology, and without using chemical rodenticides.

Recommended management strategies and research priorities

The modified dyke-barrier is an efficient method for controlling voles in this region. This system also satisfies the demand for flood management, and is readily incorporated in the flood prevention program in the Dongting Lake region when the dyke needs repair. Therefore, it is important to maintain the dyke with the modified physical barrier system for vole control. Future study should focus on another pest species, the Norway rat (*Rattus norvegicus*), which causes damage in both fields and houses.

Rat management in the South China Plain (Pearl River Delta)

Agricultural system and environment

The climate in the Pearl River Delta is subtropical with an annual rainfall of 1500–2000 mm. Rice is the main crop in this region and it is planted twice a year. *Rattus rattoides* and *Bandicota indica* are two major rodent pests in the rice fields. In this region, the amount of arable land is decreasing because of industrialisation and this has created more wastelands (non-cultivated lands). In some areas, *B. indica* is becoming more abundant (He 1998).

Reproduction patterns and population dynamics

R. rattoides is a rodent of medium size. The adult body weight ranges from 100–200 g. It breeds through all seasons of the year, with two pregnancy peaks, one in June and the other in October. The pregnancy rates in January and December are very low, less than 0.6%. The average pregnancy rate ranged from 35.4–54.6% during 1987–1991 (Huang et al. 1994a). The litter size ranges from 2 to 14, averaging 6.78 ± 0.10.

Photo: Anguo Chen

Figure 7.
The modified dyke-barrier system for controlling oriental voles.

R. rattoides displays seasonal movements between different crop fields. During the growing seasons for rice (April to July; August to November) they invade rice fields. After the harvest of rice they migrate into orange and banana plantations, where they over-winter.

In winter, the average densities of rats in orange and banana plantations are 13.6% and 13.7%, respectively, while the average densities in rice fields surrounding orange and banana plantations are only 6.2% and 7.1%, respectively (Feng et al. 1990a).

Population recovery of *R. rattoides* after chemical control

The population recovery of *R. rattoides* after chemical control has been well studied in 1987 by Feng et al. (1990b). The experimental area of each treatment was 27 ha without replicates. Twenty days after use of diphacinone rodenticides in the middle of January, February, March or April, the kill rates (based on pre- versus post-treatment abundance indices) of rats were 78.5%, 91.2%, 94.8% and 70%, respectively. In the experimental area treated in mid-January, the rat population had recovered to or surpassed its original level by early July. In the other experimental areas treated either in the middle of February, March or April, the rat populations also had recovered to their original levels by July (Figure 8). Therefore, even if the kill rate during the first half-year was over 90%, populations of *R. rattoides* recovered so rapidly that another chemical control campaign was necessary to protect the autumn rice crop. Rodenticides were applied in August to protect the autumn crop, however heavy rain, strong winds and thick ground weed cover resulted in a much lower kill rate than in the first half-year. Following an August baiting campaign, populations of rats recovered to the original level, or even higher, by November (Figure 8) (Feng et al. 1990b).

Damage and assessment

In the Pearl River Delta, rice, orange, bananas and vegetable crops suffer great losses from *R. rattoides.* Rice that ripens early suffers more damage than rice that ripens later. The levels of rat damage to early, medium and late ripening rice are 5.3%, 1.5% and 0.6%, respectively. Huang et al. (1990a) reported that an adult *R. rattoides* could cause losses amounting to 3,150 g of rice in one year. Huang et al. (1990b,c) established a regression model between infestation rate of rice (L, %) and the trap success of *R. rattoides* (X, %) in 1987:

$$L = -0.27 + 0.29X \ (d.f. = 3, r = 0.998) \quad (10)$$

For assessing damage caused by a mixture of populations of several rodent species, Feng et al. (1995) established two regression models between the loss rate (%) of rice and rodent densities in 1992:

$$L_1 = -0.0990 + 0.3367X_1 + 1.4578X_2 + 0.0361X_3 \ (R = 0.976, d.f. = 5, F = 73.22) \quad (11)$$

$$L_2 = -0.4250 + 0.3781X_1 + 1.4523X_2 + 0.6639X_3 \ (R = 0.904, d.f. = 5, F = 122.24) \quad (12)$$

where L_1 and L_2 represent the loss rate (%) of early ripening rice and late ripening rice and X_1, X_2, and X_3 are the trap success (%) of *R. rattoides*, *B. indica* and the house mouse, respectively.

Control techniques and strategies

Since the 1980s, coumatetralyl and diphacinone have been widely used for controlling *R. rattoides.* Two separate chemical control campaigns are needed

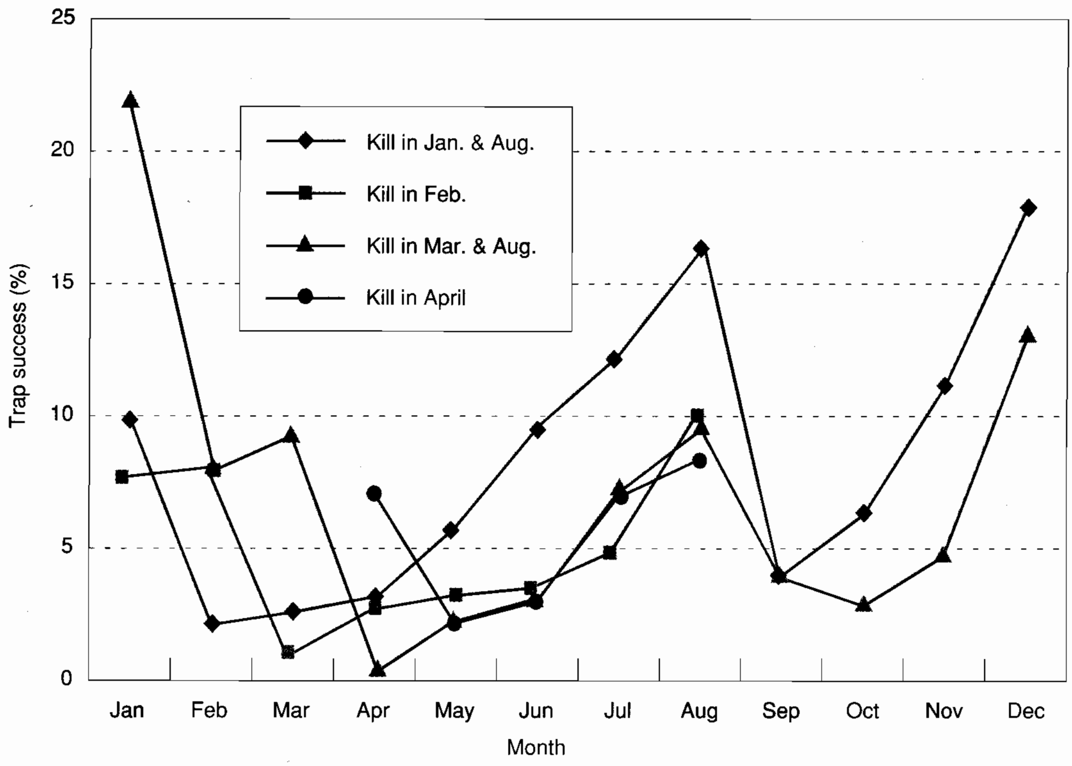

Figure 8.
Population recovery dynamics of *Rattus rattoides* after chemical control (from Feng et al. 1990b).

every year in this region in order to reduce rat damage to rice because of the rapid recovery of the rodent populations after chemical control. Therefore ecologically-based management is urgently needed as an alternative method.

R. rattoides depends much upon the ground vegetation cover in the orange groves, banana plantations, wastelands and banks of rice fields. When the ground vegetation cover in orange or banana plantations is over 60% with dry biomass of 766 g/m^2, the number of active burrow holes of *R. rattoides* is 48 ± 4.7 holes/100 m (estimated using a line transect method); when the ground vegetation cover in these plantations is less than 20% with dry biomass of 369.5 g/m^2, the number of active burrow holes of *R. rattoides* is only 2.4 ± 0.3 holes/100 m (Feng et al. 1996). Therefore, the clearing of weeds in the orange groves, banana plantations, wastelands and banks of rice fields is important for reducing the density of rat populations. Huang et al. (1994b) demonstrated that the density of *R. rattoides* was reduced from 52.0 ± 5.5 holes/100 m to 5.0 ± 1.1 holes/100 m after the clearing of weeds in rice fields and in the optimal habitats surrounding the rice fields.

Feng et al. (1996) examined whether planting some economic fruit trees with thick branches and leaves such as lychee, mango and longan in the wastelands or at the edge of rice fields could greatly reduce the weed cover, and thence reduce the rat density. After planting such evergreen fruit trees, weed biomass was reduced by 62.5–79.5% and the rat density was reduced by 77.3–89.1% (Table 6).

Recommended management strategies and research priorities

This study clearly indicates that chemical control is not a solution for sustainable management of rodent pests in this region. We recommend the strategy of combining chemical control with ecological management. In regions with high rat density, rodenticides should be used in February or March, followed by clearing of weeds in the wastelands and/or fruit tree plantations, and modifying these habitats by planting trees with thick leaves, such as lychee, mango or longan. The latter would be a more promising method of management because it not only reduces the population density of rats by reducing weed cover and their damage to crops, but also provides additional economic income for the farmers.

Problems and Possible Solutions

Since the 1980s, China has achieved promising advances in rodent pest management in agricultural systems (Zhang and Wan 1997). Firstly, acute poisons were replaced with anticoagulants. This alleviated the environmental pollution and secondary poisoning of natural predators and increased public safety.

Secondly, population ecology has been considered more than before as a basis for developing strategies for rodent pest management. Prediction of population increases and data on damage assessment have been listed as important aspects for the development of cost-effective and environmentally sensitive rodent control. The concept of ecological management is becoming much more accepted by people, even by those who were strong proponents of pure chemical control. For some of the major rodent pest species, reliable prediction models and sound damage assessment models have been established. These provide important information on when,

Table 6.

Changes in weed biomass and rat density (active holes/100 m) after planting fruit trees on the river dyke and waste hill lands in Pear River Delta. Control plots were not planted with any fruit trees (from Feng et al. 1996).

Habitat	Fruit tree type	Plots	Weeds biomass (g/m^2)	Rat density (active holes/100 m)
River dyke	Lychee	10	299.3 ± 21.5	36.3 ± 4.4
	Orange	10	354.1 ± 27.9	39.9 ± 4.1
	Control	10	945.2 ± 58.2	175.6 ± 12.0
Hill lands	Lychee	10	120.6 ± 35.9	14.7 ± 3.2
	Orange	10	187.3 ± 29.6	23.5 ± 2.7
	Control	10	589.4 ± 37.3	135.2 ± 19.3

where and how to manage rodents before launching a control campaign.

Thirdly, some new techniques for managing target rodent pests have been developed and proven effective. For example, the EPTs for managing zokors in the Northwest Loess Plateau, the multiple magnet-triggered traps for managing rat-like hamsters in the North Plain, the dyke-barrier system for managing oriental voles at Dongting Lake and habitat modification for managing rats in the Pearl River Delta. These advances depend heavily on understanding the behaviour of the target species, in particular how they respond to and use their environment. Therefore, ecologically-based rodent management must focus on detailed research of the biology, ecology and behaviour of the target species as well as the surrounding environment, instead of looking for a popular generic recipe applicable for managing all rodent pest species.

Despite this promising progress, rodent control in China still faces many problems. One problem is that the role of government in rodent control has been recently reduced under the new policy of relieving the economic burden on farmers. China used to manage rodent problems in farmland by launching state-level or provincial-level rodent control campaigns, with strict coordination of rodenticide use, baiting methods and public education. Farmers paid part of the cost for rodent control on their own land under the campaigns organised by government. Without the coordination by government, rodent control by farmers is conducted sporadically and not concurrently. As indicated in this chapter, chemical control with a kill rate of less than 90% or with a higher kill rate but only in a small area is not effective. In some instances the problem worsens following application of chemical control. Therefore, government involvement —through training farmers and coordinating the timing of their control actions—needs to occur for there to be effective rodent control in agricultural systems.

A second problem is that farmers have strong reservations about the effectiveness of anticoagulants. Farmers seldom buy anticoagulants in markets because these chemicals kill rodents too slowly. The resistance of rodents to anticoagulants could be another reason for their poor acceptance. This would be likely if they have been used in the same region for many years. Although public education is necessary, it is also important to improve the present anticoagulants to give a shorter kill time, and make them more acceptable to farmers.

A third problem is that population recovery by rodents after chemical control is too fast to achieve sustainable control. Many studies have indicated that the response of rodent populations after chemical control is non-linear (Liang 1982; Liang et al. 1984; Zhang 1996; Huang and Feng 1998; Qi et al. 1998). Killing some individuals may reduce the population numbers initially, but the remaining animals have less competition for food and nesting sites, and less social stress. Therefore, the surviving animals have higher productivity and higher survival rates than untreated populations. Re-invasion is another factor resulting in populations returning quickly to pre-control densities. This is illustrated by the results of a field experiment on Mongolian gerbils (*Meriones unguiculatus*). When 88% of the population was removed, the body mass of pregnant females was reduced from 58 g to

35–50 g (Wang et al. 1998). Dong et al. (1991) reported that, comparing with an untreated area, the litter size and pregnancy rate of Brandt's vole (*Microtus brandti*) increased after 75–83% population was reduced by using warfarin in Inner Mongolia. This compensation in fecundity after chemical control resulted in the population returning quickly to its pre-poisoning density. In the Pearl River Delta, chemical control, even with >90% kill rate, only was effective for less than six months (Huang and Feng 1998). To overcome this problem of population compensation, it is important to follow up chemical control with other control methods such as ecological or physical control.

Fertility control, as a sustainable and environmentally benign control technique (see Chambers et al., Chapter 10), is a promising alternative control method. By using mathematical models, Zhang (1995, 1996) demonstrated that fertility control has an extra effect in keeping rodent populations at a lower level, mostly due to the mating interference by sterilised males or females (Figure 9). Mating interference is largest when there is a mating system involving one male with one female, or one male with multiple females. Other mating systems, such as polygamy, decrease the effect of mating interference. The greater the number of females per male, the lower the level of interference. Experimental studies are urgently needed to test this hypothesis.

Rodent control in China is now facing new challenges. The first challenge is the likely escalation of rodent problems in the coming century. For example, climate change, especially warmer winters and heavy droughts in North China, has been

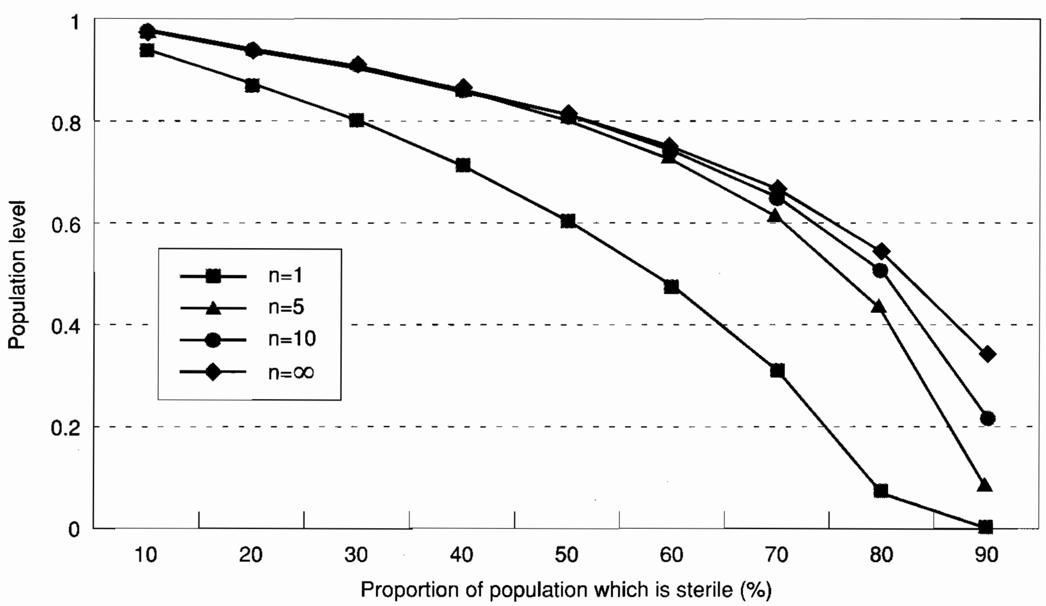

Figure 9.
The effect on the rodent population of mating interference caused by fertility control; *n* is the number of female partners per male (from Zhang 1995).

implicated in causing serious rodent problems. The second challenge comes from the changes in the agricultural system with new technologies being adopted for ploughing, planting and irrigation. Many studies have shown that traditional deep ploughing, canal irrigation, and plantations over a large area are important factors in limiting the carrying capacity of rodent populations (Zhao 1996; Zhang et al. 1997a). In Shanxi Province, it was estimated that 14.9 million Daure ground squirrels were killed from 1985–1987 following canal irrigation of 467,000 ha of arable land (Zhao 1996). In an experiment in Zhang Bei County of Hebei Province, the density of ground squirrels in an arable land area of 20 ha was reduced from 1.05 individuals/ha to 0.3 individual/ha, 10 days after irrigation. In another study, in June of 1964 in Inner Mongolia, the rodent density in ploughed wheat lands, wastelands and banks was 2, 84, and 312 individuals/ha, respectively, which indicated how ploughing affects the rodent population. Unfortunately, with the introduction of new agricultural technology like minimum tillage and drip irrigation or spray irrigation, as well as more diversified and patchy plantations, the negative effect on rodents of traditional agricultural systems is diminishing. The outbreaks of rat-like hamsters and community changes of rodent species in Shunyi District, Beijing, appear to be related to the adoption of these new farming systems. New efforts are needed to deal with these new challenges.

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13. Rodent Pest Management in the Qinghai–Tibet Alpine Meadow Ecosystem

Naichang Fan, Wenyang Zhou, Wanhong Wei, Quanye Wang and Yongjin Jiang

Abstract

The available area of the natural grasslands of the Qinghai–Tibet Plateau is about 1.4 million km^2. As a result of inappropriate reclamation and over-grazing in the past decades, serious degeneration of up to 0.71 million km^2 of the grasslands has occurred. Of this area, 0.37 million km^2 has been damaged by rodents and about 40,000 km^2 of black sandy soil has been formed due to rodent infestation. The plateau pika (*Ochotona curzoniae*) and the plateau zokor (*Myospalax baileyi*) are the two dominant rodent species.

Rodent control is essential for reversing the heavy degeneration of the grassland so that it can be used again for grazing. Beginning in the 1960s, more than ten types of rodenticide have been used for controlling rodents in the Qinghai–Tibet Plateau. In order to reduce the risk of rodenticides to predators and to improve baiting efficiency, a baiting machine was invented which puts baits into the rodents' underground tunnels, based on the invading behaviour of zokors. Both the baiting and killing efficiencies, as well as the safety advantages of using the baiting machine, are greater than the traditional, manual method of ground baiting.

Since the mid-1980s, studies have shifted to developing a sustainable strategy for managing pika and zokor damage by understanding their ecology and interaction with the grazing activities in the region. A demonstration area of 200 ha was set up in a heavily degenerated region with black sandy soil. An integrated management program, which included use of a baiting machine, seeding, fencing, control of weeds and control of grazing intensity, was implemented. The vegetation and the productivity of the grassland were increased shortly after treatment began. An increase of about 648.4 t of dried grasses was observed in the area during the next three years.

Keywords

Alpine meadow, Qinghai–Tibet Plateau, plateau pika (*Ochotona curzoniae*), plateau zokor (*Myospalax baileyi*), integrated pest management

INTRODUCTION

THE AREA of natural grassland in the Qinghai–Tibet Plateau is about 1.4 million km^2, with alpine meadow being the most widespread vegetation type. This area is an important base for animal husbandry. As a result of inappropriate reclamation and overgrazing in past decades, the grasslands have been seriously degenerated. These degenerated grasslands comprise about 0.71 million km^2, of which 0.37 million km^2 is infested with rodents. The main pest rodents are plateau pika (*Ochotona curzoniae*), plateau zokor (*Myospalax baileyi*), *Ochotona daurica*, *Pitymys irene* and *Marmota himalayana*. Plateau pikas and plateau zokors are the dominant rodents and their feeding and burrowing activities damage grasslands. About 40,000 km^2 of black sandy soil has been formed as a result of rodent infestation. In the grasslands of the Qinghai–Tibet Plateau, the average densities of the plateau pika and plateau zokor are more than 4.29 individuals/ha and about 1.07 individuals/ha, respectively. These rodents compete with livestock for food resources. They consume about 0.15 billion t of fresh grass every year, which is equal to the total food intake of 0.15 billion sheep. Rodents also dig and destroy vegetation causing many serious problems such as soil erosion, and reductions in livestock carrying capacity and ecosystem biodiversity.

Zinc phosphate, a rodenticide, was first used for rodent control in the Qinghai–Tibet area in 1958. During the early 1960s, the area of grassland treated with zinc phosphate was more than 333 km^2 in southern Qinghai. From 1964 to 1965, more than 26,667 km^2 in 20 counties was treated using both zinc phosphate and '1080' (fluoroacetate). The area of rodent infestation was reduced from 54,000 km^2 in the 1960s to 38,130 km^2 in 1990. Cumulatively, more than 208,000 km^2 of the infested area was treated with rodenticides during this period.

However, zinc phosphate and 1080 also caused many serious social and environmental problems. Both are acute poisons that have secondary poisoning effects, and are unsafe for non-target species including humans. With the appearance of anticoagulants such as diphacinone, diphacinone-Na, gophacide, difenacoum, bromadiolone and brodifacoum, use of the acute poisons was no longer permitted. A new type of rodenticide, botulin C, was also found to be very effective in killing plateau pika and plateau zokor in the grasslands. The killing rate with botulin C was up to 98%, with less environmental pollution and no secondary poisoning effects on other animals (Shen 1987).

Although anticoagulants and botulin C are effective in reducing pika and zokor damage initially, the populations of these rodents recover rapidly after treatment (Liang 1982). Since the mid-1980s, studies have shifted towards developing a sustainable strategy for managing pika and zokor damage by understanding their ecology and interaction with the grazing activities in this region. In this chapter, the major achievements of these studies are reported and future research priorities are discussed.

Ecological Aspects of the Plateau Pika and Plateau Zokor

Plateau pika

Habitat

Pikas mainly inhabit the plateau steppe, steppe meadow, plateau meadow, alpine meadow and alpine desert steppe at an elevation of 3,100–5,100 m above sea level. They prefer open habitats and avoid dense shrub or thick vegetation (Shi 1983). Table 1 shows that the number of pika burrows decreases with increased vegetation cover and height.

Burrow systems

The burrow systems of the pika comprise two types. One type is the simple or temporary burrow that is shallow and short. It is mainly used in summer and usually has two or three openings, but may only have one opening to the surface. The other type is the complex burrow system which occupies areas of 21–162.14 m^2. The average length of the tunnels is 13 m, with a maximum length of up to 20 m. The average depth of the burrows is 0.33 m, but they may be up to 0.6 m deep. The burrow system has many branches which are connected to each other to form a complex network, sometimes with two layers. There are usually five or six openings, although some have 13 openings. The diameter of the openings is about 8–12 cm. There is one nest in the burrow system, which is located about 0.45 m below the surface (Xiao et al. 1981).

Feeding behaviour and activity rhythms

The plateau pika is a herbivore and responds variably to different plants and plant parts. Enclosure experiments indicate that of 31 plant species in the natural habitat, pikas feed on 23 grass species (mainly belonging to the Gramineae), as well as species belonging to the Cyperaceae and Leguminosae. An adult pika consumes (on average) 77.3 g of fresh grass per day, which is about 50% of its body weight, whereas a 375 kg cow consumes 18 kg of fresh grass per day, which is only 4.8% of its body weight. The food intake of 56 adult plateau pikas equals the food intake of one Tibetan sheep (Pi 1973).

Table 1.
The relationship between the cover and height of ground vegetation and the number of active burrow holes of plateau pika (Shi 1983).

Habitat type[a]	1	2	3	4
No. of plots	9	41	3	8
Vegetation cover (%)	84.22 ± 4.09	96.93 ± 0.84	66.67 ± 8.28	90.63 ± 2.90
Vegetation height (cm)	9.22 ± 2.57	69.29 ± 4.25	2.00 ± 0.00	85.00 ± 6.61
No. of pika holes	24.67 ± 6.74	3.93 ± 1.54	43.33 ± 8.82	0.00 ± 0.00

[a] Key to habitat types: 1 = natural grassland; 2 = original grassland which was cultivated for several years, then abandoned due to deterioration; 3 = grassland which was ploughed but then considered unsuitable for cultivation; 4 = grass sown in deteriorated grassland. Values are Mean ± standard error of the mean.

Feeding comprises 63–78% of the total activity of pikas. When feeding, pikas look around frequently and have a special feeding pattern termed 'pecking'—after feeding for a moment they look around or move a short distance, then feed again. Feeding frequency is 5.7 ± 1.3 pecking bouts per minute (Bian et al. 1994; Fan and Zhang 1996).

The plateau pika is a diurnal animal. Its above-ground activities appear to have two peaks (forenoon and afternoon), and these change according to the different seasons. In October the first activity peak occurs at 09:00 h and the second at 18:00 h, while in July the activity peaks are at 08:00 h and 19:00 h, respectively.

Life span

Based on observations of 401 ear-tagged individuals over three years, the average life span of a plateau pika is 119.9 days, with the longest life span recorded being 957 days (Wang and Dai 1989).

Home range and territory

Plateau pikas live in family groups and show territorial behaviour. Before the reproductive period (March), the average home range is 1,262.5 m^2, while in the breeding season (April) the home range expands to 2,308 m^2. Plateau pikas protect their territories all year. In the breeding season, males and females form pairs to establish new families and new home ranges and protect this territory. During the period of oestrus, the female holds no territory, but the male monopolises the female and drives away other invading males (Wang and Dai 1990).

Reproduction and sex ratio

Each year an adult female can produce 3–5 litters with 1–9 individuals per litter. In the Kuaierma region (37°26' N, 98°42' E), a total of 1,529 plateau pikas were captured from 1964 to 1965. Males made up 46.5% of the total capture and were less abundant than females ($\chi 2 = 7.35$, $p < 0.01$). The average litter size was 4.55 ± 0.95 individuals. In the Duofudun region (35°15' N, 101°43' E), a total of 777 pikas was captured. Males made up 53.16% of the total capture. The average litter size was 4.68 ± 1.29 individuals (Shi et al. 1978).

Plateau zokor

Habitat

The plateau zokor mainly inhabits the alpine meadow, steppe meadow, alpine shrub, farmland, banks and wasteland and is widely distributed in Qinghai, southern Gansu and western Sichuan. Their choice of habitat is characterised by moist soil and degenerated grassland with many weeds.

Burrow system

The plateau zokor constructs a very complicated burrow that consists of one or two main nests, feeding and transportation tunnels, food store holes and blind endings. Feeding tunnels, which are formed during feeding activities, are 60–100 mm deep and 70–120 mm in diameter. The transportation tunnels are about 200 mm deep, and are smooth, large and stable paths from the main nest to the feeding tunnels, with some holes for storing food built nearby. One or two vertical tunnels connect the transportation tunnels to the main nest, which is 0.5–2 m deep, about 150–290 mm in diameter, and often filled with dry and soft grass. The nests of females are commonly deeper than those of males. The holes for food storage and a defecation site are usually near the nest (Fan and Gu 1981).

Feeding habits

Plateau zokors mainly feed on roots, rhizomes and other underground parts of weeds. They also frequently pull parts of plant stems into the burrow as food or nest material. Only the rhizomes and green leaves of Gramineae spp. are consumed. *Potentilla anserina* and *Aiania tenuifolia* are also important food resources for the zokor in *Kobresia humilis* meadows. Zokors store root tubers of *P. anserina* and subterranean stems of *A. tenuifolia* mainly as food over winter (Fan et al. 1988).

Activity rhythms

Although plateau zokors live in the subterranean environment, they exhibit circadian rhythms in the dark burrow systems. Based on a study of 80 marked animals, two peaks of digging and feeding activity occurred in summer and autumn. These were from 15:00 h to 22:00 h (making up 65.3% of the total day's activities) and from 0:00 h to 7:00 h (making up 21.6% of the day's activities). In winter, the activity frequency is low and the daily activities are mainly limited to near the nest at 12:00–22:00 (making up 79.7% of the total day's activities) (Zhou and Dou 1990).

Home range

The home range of zokors changes between seasons. In the reproductive season (spring), the home range of males (499.0 ± 390.9 m^2) is larger than that of the female (21.0 ± 11.8 m^2). In the other seasons, there are no significant differences in the home ranges of males (156.5 ± 45.4 m^2) and females (162.1 ± 153.9 m^2) ($t = 0.332$, $p > 0.05$) (Zhou and Dou 1990).

Reproduction

The plateau zokor has one litter of 1–5 individuals (2.91 ± 1.08) every year. About 38.4% of litters are all males (Zheng 1980). The reproductive period is from March to July with a lactation period of about 50 days (Zhang et al. 1995). A radio-telemetry study indicated that adult males and females never live together, even when females are in oestrus. Mating occurs at the intersection of two tunnels of a male and a female burrow system. An analysis of 20 burrow systems of zokors showed that, in the mating period, the male digs a few long tunnels to intercept the female burrow systems, and usually these tunnels have two branches in order to increase the chance of meeting a female. The situation where two males meet each other has never been observed. A male may mate with several females and a female also may mate with a few males. Therefore the mating system of zokor is probably promiscuous. In the Fengxiakou area of Menyuan County, the sex ratio of the adult male to female is 1:1.67. The mosaic distribution of male and female home ranges increases the chance of meeting with each other (Zhou and Dou 1990).

Invading behaviour

Field studies showed that a burrow system was often occupied rapidly by its neighbours if the host zokor was removed (Fan et al. 1990). This observation indicates that zokors tend to invade any vacant territory. This invading behaviour was further studied in the laboratory, using two large boxes connected by a wooden tunnel. Each box contained one zokor and was filled with damp soil so that the zokor could build its burrow system. After the burrow systems in both boxes were built, one zokor was removed, and the remaining animal's behaviour was monitored. In six experiments, the remaining zokor invaded the other burrow system rapidly, usually within 2–30 hours. In four of the six experiments, the burrow tunnels but not the nests were occupied; in the other two cases, both the tunnels and nests were occupied (Fan et al. 1990).

Based on this observation, a baiting machine, which digs tunnels under the grassland and puts baits in the tunnels, was invented. It was found that zokors used some parts of these artificial tunnels. The longest section used by zokors was 32 m and the shortest section was 0.3 m. Most of the artificial tunnels created by the baiting machine were incorporated into the zokors' natural burrow systems (Fan and Gu 1981; Fan et al. 1990).

Aggressive behaviour

The behaviour patterns of the plateau zokor are classified as follows: sleeping and resting, feeding, carrying food, digging, self–grooming, moving, exploring, approaching, contacting, attacking, escaping and retreating. In the reproductive period, the duration of digging, approaching, contacting, attacking, escaping and retreating increases and mutual tolerance is higher than that in the non–reproductive period. Mutual tolerance between zokors of the same sex is lower than that between males and females (Wei et al. 1996).

Digging behaviour

The zokor is a fossorial animal. Its front claws are very stocky and strong. The digging process is divided into seven steps: excavating, digging up, kicking, pushing, humping up soil, feeding and modifying the tunnel (Wang et al. 1994). By digging, zokors build burrow systems for foraging, hoarding food, reproduction and avoiding predators. One zokor was observed to push 1,023.82 kg of dry soil to the ground surface (30.8% in the grass-greening period, 6.3% in the grass-growing period and 62.9% in the grass-withering period) and form 242.1 mounds per year. The mounds covered about 22.53 m^2 of the grassland (Table 2). In the grass-greening period (April–June) which corresponds to the reproductive period of the zokor, the level of digging is medium. The level of digging is lowest in the grass-growing period (July–August) because the zokor can feed partly on green plants above ground. The level of digging is highest in the grass-withering period (September–November) because dispersal and hoarding activities of the zokor are high (Wang and Fan 1987; Fan and Gu 1981).

Table 2.
The number of and area covered by mounds of the plateau zokor from April to November (Wang et al. 1994).

Month	Stage of grass growth	No. of zokors	Mounds/zokor	Mound volume (m^3)	Area covered by each mound (m^2)	Dried weight of soil for each zokor (kg)
April	Greening	29	36.00	4.42	2.33	87.60
May	Greening	25	28.98	7.42	2.61	113.77
June	Greening	22	23.96	9.16	2.58	113.40
July	Growing	27	10.06	6.48	0.90	2.94
August	Growing	33	4.03	5.34	0.32	8.68
September	Withering	33	29.97	8.75	3.02	157.80
October	Withering	36	95.04	8.05	9.09	403.31
November	Withering	35	14.04	10.14	1.68	116.32
Total			**242.08**		**22.53**	**1023.82**

Interactions Between Rodent Damage and Grassland Degeneration

The Qinghai–Tibet alpine meadow ecosystem is very vulnerable to disturbances that reduce the coverage and height of the grass vegetation, such as over-grazing by livestock and cultivation. Weeds, as well as rodents, will invade degenerated grassland. Jing et al. (1991) reported that the number of zokor mounds increased with increased grazing intensity ($r = 0.795$, $r_{0.05} = 0.707$, $p < 0.05$) (Table 3).

Table 3.
The density of zokors under different grazing intensities (Jing et al. 1991).

Plot[a]	Grazing intensity (sheep/ha/yr)	Zokor density (mounds/0.25 ha)
1	5.30	462
2	4.43	198
3	3.55	164
4	2.68	4
5	1.80	152
6	6.07	362
7	3.12	270
8	2.12	68

[a] Plots 1 to 5 are in grasslands on the slope of a mountain; plots 6 to 8 are in grassland on the plain.

In Tianjun County of Qinghai in 1959, the area of available grassland was 14,664 km^2, but decreased to 12,901 km^2 by 1984 because of over-grazing and rodent infestation. It is estimated that the livestock carrying capacity was decreased by 1.33 million sheep over this period (2.7 million sheep in 1959 to 1.4 million sheep in 1984) (Table 4). Up to 1991, there was at least 547.6 km^2 of black sandy soil created by rodent activity following grassland degradation, with the area of grassland available for winter and spring use being only 5,873.6 km^2—45.5% of the total area. In theory, this area has a carrying capacity of only 1.03 million sheep, but is actually grazed by 1.30 million sheep (Ma 1991). Therefore, in the first year after management strategies have been implemented (e.g. chemical control and re-seeding or fencing), livestock grazing should be prevented, with only low-level grazing permitted in the second year; this will prevent further degeneration of the grassland through rodent infestation.

A study by Shi (1983) showed that the population densities of the plateau pika and the plateau zokor in abandoned, cultivated grassland was much higher than that in original grassland (Table 5). Cultivation and overgrazing by humans created the suitable habitats for pika and zokor.

In summary, over-grazing by livestock and the inappropriate reclamation of the grasslands for other purposes are the major reasons for grassland degeneration. In the presence of invasion by weeds and rodents, the degenerated grassland will continue to be changed as follows: over-grazing by livestock leads to grassland degeneration which results in rodent infestation and further grassland degeneration. Human activities, especially cultivation and livestock grazing, play an important role in this vicious circle.

Table 4.
Comparison of the area of different grassland types, the yield of fresh grasses and the livestock carrying capacity between 1959 and 1984 (Ma 1991).

Grassland type	Year	Grass yield (kg/ha)	Area of grassland (km^2)	Carrying capacity (sheep/ha)
Steppe	1959	2052.0	2284.67	1.45
	1984	1467.3	2156.20	1.01
Meadow	1959	1731.0	12303.07	1.40
	1984	1278.3	7368.60	0.88
Shrub	1959	3154.5	384.60	2.17
	1984	2049.3	382.53	1.42
Swamp	1959	2980.5	3560.00	1.55
	1984	1951.8	2882.53	0.46
Degenerated grassland[a]	1959	1795.5	105.80	1.15
	1984	586.7	2484.20	0.33

[a] Note that the area of degenerated grassland has increased greatly during this period.

Table 5.
The community composition and population density (individuals/0.25 ha) of small mammals in various grassland types (Shi 1983).

Species	Common name	Artificial grassland	Semi-artificial grassland	Secondary grassland	Wasteland
Microtus oeconomus	Root vole	70.1 (91.3)[a]	54.3 (85.9)	0 (0.0)	0.0 (0.0)
Cricetulus longicaudatus	Lesser long-tailed hamster	1.1 (1.4)	0.6 (1.0)	0.7 (1.1)	7.5 (69.5)
Ochotona cansus	Gansu pika	0.0 (0.0)	5.6 (8.8)	0.2 (0.3)	0.0 (0.0)
Myospalax baileyi	Plateau zokor	5.6 (7.3)	2.7 (4.3)	11.1 (17.8)	0.9 (8.3)
Ochotona curzoniae	Plateau pika	0.0 (0.0)	0.0 (0.0)	50.6 (80.8)	2.4 (22.2)
Total		**76.8 (100.0)**	**63.2 (100.0)**	**62.6 (100.0)**	**10.8 (100.0)**

[a]Figures in brackets represent the percentage of each species in each habitat.

Population Dynamics and Their Prediction

Plateau pika

The total available grassland area of Menyuan, Qilian, Haiyian, Gangcha and Tianjun counties in Qinghai Province is about 36,800 km^2, of which up to 12,000 km^2 (32.7%) is occupied by plateau pikas (Wang et al. 1996) (Table 6).

Table 6.
The population densities and area occupied by plateau pikas and plateau zokors in the useable grassland in some counties of Qinghai Province (Wang et al. 1996).

Species	Density (ha)	Area occupied (km^2)	Percentage (%)
Pika	<20	3 872	10.52
	20–70	5 633	15.31
	>70	2 527	6.87
	Total	**12 032**	**32.70**
Zokor	<20	660	1.79
	20–70	433	1.18
	>70	3 370	9.16
	Total	**4 463**	**12.13**

According to a study by Liu et al. (1980) at the Haibei Alpine Meadow Ecosystem Research Station of the Chinese Academy of Sciences, plateau pikas prefer habitats such as banks, terraces, foothills and gentle slopes in the *K. humilis* meadow and the steppe meadow. The highest population density of the plateau pika was found in wasteland with an average density of 74.64 individuals/ha. The second highest density of plateau pikas (70.36 individuals/ha) was found on the banks and gentle slopes. The average population density in the *Kobresia capillifolia* meadow, which is not their primary habitat, is only 18.99 individuals /ha.

A long-term study has shown that pika populations change significantly between years (Figure 1). The factors causing these fluctuations are not clear, but populations appeared to be oppressed after heavy snows in 1982 and 1988 (Zhou and Wei 1994). In a study conducted from 1985 to 1988, using ear-tagged animals, 57% of the animals that reproduced in the population were those which were born in the first litter of the previous year and 26% were from the second litter of the previous year. Most pikas from the third and fourth litters died before winter. Therefore, the survival rate of the first litter not only decides the population numbers for the present year, but is also an important determinant of the population density of pika in the following year (Wang and Smith 1988). Field observations also indicated that if the reproductive period was extended, the adult females had more litters but the mortality rate of the young pika was higher. Therefore, the population density was lower in the next year (Wang and Smith 1988).

Plateau zokor

In the total area of available grassland in Mengyuan, Qilian, Haiyian, Gangcha and Tianjun counties of Qinghai province, 12.13% was inhabited by zokors. Highest densities of zokors occurred over an area of 3,370 km^2 (Wang et al. 1996) (Table 6).

One long-term study at Haibei station from 1976 to 1992 showed that the zokor population was relatively stable until 1987 when it declined coincident with large scale rodent control (Figure 2) (Zhou and Wei 1994). One explanation for the stable numbers is that the effects of climate and natural enemies are minimal (Wang and Fan 1987).

The population density of zokors in autumn is closely related to the numbers of reproductive females in spring. Density increases after reproduction and is about 1.56 times higher in autumn than in spring. From autumn to the next spring, the population decreases. The population of zokors in spring or autumn can be predicted by using the following regression models (Zhang et al.1991):

$$Y_{Autumn} = 4.864 + 0.9672X_{Spring}$$
$$(r = 0.9823 > r_{0.01} = 0.824, p < 0.01) \quad (1)$$

where Y_{Autumn} is the autumn density of the present year, and X_{Spring} is the spring density in the present year; and

$$Y_{Spring} = 1.426 + 0.7664X_{Autumn}$$
$$(r = 0.8930 > r_{0.01} = 0.824, p < 0.01) \quad (2)$$

where Y_{Spring} is the spring density of the present year, and X_{Autumn} is the autumn density of the previous year.

Damage Assessment and Economic Threshold

According to the definition of Headley (1972), 'economic threshold' is the population density of a pest when the cost for its control equals the minimal value of the product that is lost because of the pest. Therefore, the costs of rodent control should be less than the losses occurring in the absence of control, and the benefits should be maximised. Further, when the cost of pest control in a unit area equals the economic loss due to rodent damage, the pest density is at the economic threshold where rodent control should be undertaken.

Plateau pika

Pikas cause a lot of damage to the grass vegetation, mainly by feeding, gnawing grass roots and burrowing. The damage level to the grassland is closely related to the population density of pikas. The infested area of the grassland escalates with increasing rodent density and high grazing intensity by livestock. Some climatic factors may also influence the level of rodent damage to the grassland (Liang and Xiao 1978; Xiao et al. 1981).

Liu et al. (1980) reported that the population density of the plateau pikas was positively correlated to grassland damage. The relationship between pika density and grass damage can be used to calculate the economic threshold for each habitat using the formula:

$$Y = a + b \log X \quad (3)$$

where Y = % of grass damage and X = pika/ha, and solving for $Y = 0$ (Table 7).

Plateau zokor

Plateau zokors destroy grasslands by feeding and digging. Digging mainly takes place 40–160 mm underground, which destroys most plant root systems (90.7% of the total underground biomass). The original vegetation of grasslands disappears and seriously degenerated grasslands or even large areas of black sandy soil are formed. Field studies indicate that, with increases in zokor density, the total output of grasses decreases while the total output of weeds increases (Fan et al. 1988) (Table 8).

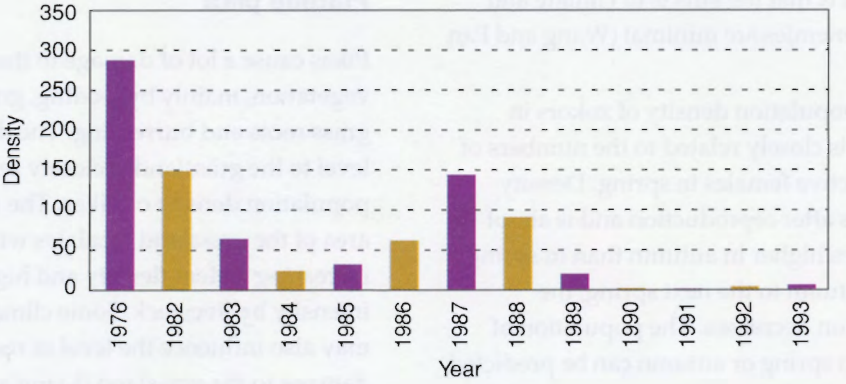

Figure 1.
Population densities of the plateau pika (individuals/hectare) (Zhou and Wei 1994).

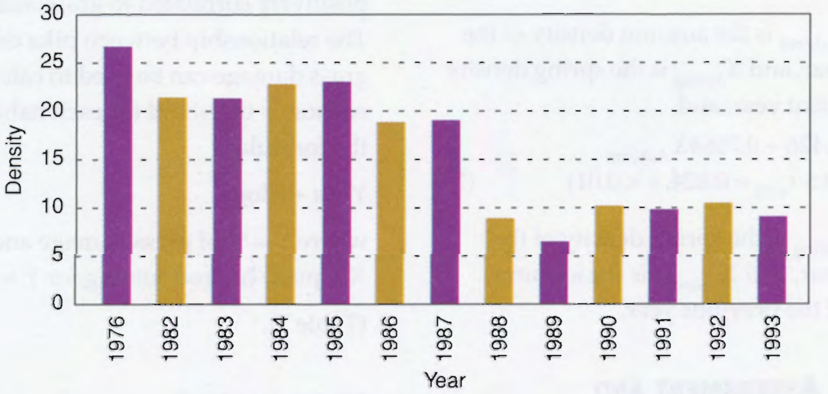

Figure 2.
Population densities of the plateau zokor (individuals/hectare) (Zhou and Wei 1994).

Table 7.
The relationship between the density of pika and the grass damage used to define economic thresholds (Y = percentage of grass damage, X = pika/ha) (Liu et al. 1980).

Habitat	$Y = a + b \log X$	Economic threshold (pika/ha)
All areas	$Y = -115.46 + 120.68 \log X$	9.05
First terrace	$Y = -104.42 + 194.73 \log X$	5.95
Second terrace	$Y = -70.53 + 101.87 \log X$	4.92
Gentle slope	$Y = -63.54 + 88.15 \log X$	5.26
Hills	$Y = -40.13 + 63.12 \log X$	4.32

Table 8.
The relationship between the density of plateau zokor, the damage to grass and the yield of fresh vegetation types (Fan et al. 1988).

Density rank (zokors/ha)	Average density[1] (zokors/ha)	Damage[2] (%)	Area of mound[3] (m^2)	Grass yield[4] (kg/ha)	Sedge yield[5] (kg/ha)	Weed yield[6] (kg/ha)	Total yield[7] (kg/ha)
0	0	0	0	3020	2360	8212	13592
1–10	6.7	13	116	2797	2158	6229	11184
11–20	14.5	18	212	2277	1206	6750	10233
21–40	30.2	45	481	1046	666	5483	7195
41–70	62.9	64	1076	690	75	7180	7945
>70	91.6	84	1489	229	0	4450	4679
Coefficient of correlation		$r2,1 = 0.982$ $p < 0.01$	$r3,1 = 0.999$ $p < 0.01$	$r4,1 = -0.937$ $p < 0.01$	$r5,1 = -0.905$ $p < 0.05$	$r6,1 = -0.634$ $p > 0.05$	$r7,1 = -0.900$ $p < 0.05$

Notes:
(1) Numbers in superscript in the column headings relate to the correlation coefficients at the bottom of the table. (2) Significant levels of correlation: $r_{0.05} = 0.811$; $r_{0.01} = 0.917$.

Zokors not only gnaw grass roots but also push large amounts of poor quality soil to the ground surface, forming mounds of different sizes (Table 2). These mounds cover the original vegetation and the result is degradation of the grassland. The mound volume of the zokor varies with sex, age and seasons. Generally, the mound volume of males is larger than that of females and the mounds of adults are larger than those of the young. The annual losses of grassland due to damage by feeding, hoarding and covering of vegetation by mounds under different zokor densities (Tao et al. 1990) are listed in Table 9.

In the Haibei region of Qinghai Province, *K. humilis* is the dominant plant species in the alpine meadow. In 1987, the optimal grazing intensity was 3.29 sheep/ha. The maximum productivity of the grass was 3,554.4 kg/ha. The price of each sheep was 110 RMB[1]/sheep. So the price of grass (Y_1, RMB/kg) is:

$$Y_1 = 110 \times 3.29/3554.4 = 0.102 \quad (4)$$

The cost of diphacinone-Na baits used to control plateau zokor was 3.105 RMB/ha and the achieved killing rate was 74.4%. In theory, when the killing rate nears 100%, the rodent damage would be reduced to zero and, at this point, the cost of control (Y_2, RMB/ha) using baits is:

$$Y_2 = 3.105/74.4\% = 4.173 \quad (5)$$

The amount of grass (Y_0, kg/ha) which equals the cost of control should be:

$$Y_0 = Y_2/0.102 = 4.173/0.102 = 40.92 \quad (6)$$

The correlation model between the grass losses (Y, kg/ha) and density of zokors (X, zokors/ha) is:

$$Y = 11.2X - 5.61 \quad (7)$$

If $Y = Y_0 = 40.92$, then the economic threshold $X_0 = 4.16$. That is, when the population density of zokors reaches the level of 4.16 zokor/ha, control by baiting should be undertaken if significant economic losses are to be avoided.

Integrated Pest Management (IPM)

An experiment that aimed to find a sustainable solution to rodent damage in the Qinghai–Tibet alpine meadow ecosystem was conducted from 1984 to 1989 in the Haibei region. The study area, located at Panpo, Menyuan County, Qinghai Province, was seriously infested by plateau pikas and plateau zokors. From 1984 to 1986, the above-ground mound density of the plateau zokor was 2,683 mounds/ha, and the active

[1]RMB = renminbi yuan. As of May 1999, 8.14 RMB = US$1.

Table 9.
Vegetation damage for different densities of zokors over one year (Tao et al. 1990).

Density (zokor/ha)	1	3	4	6	7	11	13	14	19	24
Dry grass losses (kg/ha)	14.75	35.55	39.85	50.80	75.75	132.69	152.81	153.66	235.67	266.69

burrow density of plateau pika was 752 holes/ha. The seriously infested area made up 53.35% of the total grassland area. The vegetation types are mainly *K. humilis* meadow, and *Dasiphoia fruticosa* shrub and swamp meadow, and the soil types are plateau meadow soil, swamp soil and plateau shrub meadow soil. A series of measures, including chemical control, sowing, fencing, control of grazing intensity and weed control, were carried out in a demonstration area of 200 ha.

The baiting machine

In spring 1987, 0.075% diphacinone-Na and 0.6% gophacide grain baits were delivered into simulated underground tunnels with the aid of the baiting machine. About 19 g of bait was dropped every 5.5 m in each line. The interval between lines was 10 m. The baiting machine delivered the baits at the speed of about 3.3 ha/hr, about 20 times faster than manual baiting. The killing rates with diphacinone-Na and gophacide baits were 85.1% and 77.3%, respectively, for zokors and 96.9% and 99.8%, respectively, for plateau pikas (Jing et al. 1991) (Table 10), calculated 10 days after baiting and based on the numbers of active burrow holes before and after treatment. The zokor killing rate was significantly higher than that obtained by traditional manual baiting on the ground (Table 10) (Fan et al. 1986; Jing et al. 1987). After half a year, the control efficiency of 0.075% diphacinone-Na grain baits was re-assessed. Of 107 zokor burrow systems checked, only 2 were occupied. The control efficiency for zokors remained high (Jing et al. 1991) and indicated that baiting delivered by the machine was effective for long periods in controlling zokors.

Management by sowing and fencing

Sowing and fencing were implemented after chemical control. Major grass species sown were *Elymus nutas*, *Elymus sibiricus* and *Pucciunelia tenuiflora*. Two years later, the average height of the grass had increased from 99 mm to 860 mm and the average ground coverage increased from 35% to 90%. The grass vegetation formed two layers; an upper layer of sown grasses and a lower layer of weeds. Grasses (Gramineae spp.) became dominant and their yield increased.

Table 10.
Comparison of the efficiency of using the baiting machine and manual baiting methods for the control of plateau zokors and plateau pikas (Jing et al. 1991).

Baiting method	Bait	Killing rate (%)	
		Zokor (active mounds)	Pika (active burrows)
Baiting machine	0.075% diphacinone-Na	85.1	96.9
Baiting machine	0.6% gophacide	77.3	99.8
Manual baiting	0.075% diphacinone-Na	69.3	–

In 1987, grasses, sedges and weeds made up 18.9%, 19.3% and 61.8% of the total above-ground biomass, respectively. In 1988, grasses, sedges and weeds made up 35.9%, 17.7% and 46.4% of the total above-ground biomass, respectively (Jing et al. 1991) (Table 11). The total biomass of the grass in the demonstration area increased by 1.9 times at the end of the first year and by 9.1 times at the end of the second year. After three consecutive years the population densities of the plateau zokors and the plateau pikas were still at low levels (Jing et al. 1991).

Weed control using herbicide

The degenerated grassland is dominated by weed species and is the optimal habitat for zokors. Therefore, weed control using herbicide will help destroy the habitat of zokors, and also has the added benefit allowing greater growth of foraging grasses by reducing competition from weeds. In June 1987, 2,4-dichlorophenoxyacetic acid was used to kill weeds as they began to germinate. A month later, the yield of grasses and sedges had increased and in correlation with the concentration of herbicide applied. At the optimal concentration of the herbicide (0.75 kg/ha), the yield of weeds decreased by 68.8% while the yield of the forage grasses increased by 47%. In autumn, the zokor density was greatly decreased. At the highest herbicide concentration (2.25 kg/ha), the density of zokor mounds decreased from 323 to 0 mounds/ha (Jing et al. 1991) (Table 12).

Economic impact of IPM

By implementing IPM from 1987 to 1989, rodent damage was reduced and the ground vegetation and productivity of the grassland increased greatly in the experimental area. The weight of dry grasses was only 84.7 g/m^2 in 1987 when the IPM experiment commenced, but it increased to 406.52 g/m^2 by 1989. In the experimental area (200 ha), the total yield of dry grasses increased from 80.6 t (which could feed 122 sheep) in 1987 to 728.9 t (which could feed 1,103 sheep) in 1989 (Jing et al. 1991).

The total investment in this IPM, including machine baiting, fencing and sowing was 40,170 RMB, and the income in the three consecutive years of 1987, 1988 and 1989 was 227,710 RMB. Therefore, the ratio of benefit to cost of the IPM in this region was 5.7 (Table 13) (Jing et al. 1991).

Recommendations and Future Research Priorities

In Qinghai Province, the total area of black sandy soils caused by rodents is more than 13,000 km^2. If the IPM strategy demonstrated in the experimental area could be extended successfully to regions of the Qinghai–Tibet alpine meadow ecosystem with heavy rodent infestation, the degenerated grassland could recover. Indeed the grass production would be over 0.103 billion t and this could feed 0.156 billion sheep. However, there are several important pointers for implementing this IPM strategy:

- For highly degenerated grassland with heavy pika and zokor problems, chemical control using baiting machines should be considered first, with weed control and sowing of grasses following immediately. Grazing by livestock should not be permitted in the first year, and limited

Table 11.
Changes in above-ground biomass after sowing or fencing following chemical rodent control (Jing et al. 1991).

Treatments	Above-ground dry biomass (g/m^2)							
	Pre-treatment 1987				Post treatment: 1988			
	Grasses	Sedges	Weeds	Total	Grasses	Sedges	Weeds	Total
Chemical control + semi-fenced	33.02	33.57	107.54	174.13	97.68	48.17	126.02	271.9
Chemical control + sowing + semi-fenced	50.81	33.98	107.53	192.32	389.36	48.16	126.03	563.6
Untreated	11.82	32.61	74.54	118.97	29.26	17.68	253.73	300.7

Table 12.
Grass yields after weed control with different concentrations of herbicide and the effect on numbers of new mounds created by zokors (Jing et al. 1991).

Herbicide concentration (kg/ha)	Above-ground dry weight (kg/ha)			Zokor density (mounds/0.25 ha)	
	Grasses	Sedges	Weeds	Pre-treatment (Apr–May)	Post-treatment (Sep–Oct)
0.0	448	793	1206	483	376
0.375	757	995	980	457	164
0.75	1640	972	377	377	46
1.5	1462	503	401	439	9
2.25	1161	310	331	323	0

Table 13.
Comparison of the costs and benefits of integrated pest management in the experimental area located at Panpo, Menyuan County, Qinghai Province, from 1987 to 1989 (Jing et al. 1991).

Cost (RMB[a]) in 1987						Benefit (RMB)		
Machine baiting		Fencing		Sowing		1987	1988	1989
Motor power	Toxic bait	Iron net	Structure	Seed	Ploughing			
1 296	418	20 000	3 516	12 000	2 940	1 209	117 157	109 344

[a] RMB = renminbi yuan. As of May 1999, 8.14 RMB = US$1.

grazing should be permitted only after the grassland is fully recovered.

- For lightly degenerated grassland with lesser pika and zokor problems, grazing should be stopped immediately and followed by weed control and sowing. Grazing should not permitted again until the grassland is fully recovered.
- For abandoned, non-cultivated grassland, chemical control using the baiting machine followed by weed control and grass sowing must occur to achieve recovery of the grassland.
- In the alpine meadow ecosystem, one polecat can kill 1,554 plateau pikas or 471 plateau zokors each year (Zheng et al. 1983; Wei and Zhou 1997). Therefore, the natural enemies of the pikas and zokors such as weasels, polecats, foxes and eagles should fully protected.

Because the plateau zokor was found recently to have some medical value in healing rheumatism (like tiger bone) (Zhang and Zhang 1997), it is now believed to be of economic importance in this region. Thus, future studies will focus on finding a solution to the conflict between this newly recognised benefit versus the damage caused by zokors through managing their population at a level suitable for good harvest output but causing little damage to the grassland. For pika management, biological control using parasites and/or contraceptive vaccines that potentially have minimal non-target environmental impacts will be considered as research priorities in the future.

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14. Ecologically-Based Population Management of the Rice-Field Rat in Indonesia

Luke K.P. Leung, Grant R. Singleton, Sudarmaji and Rahmini

Abstract

The rice-field rat, *Rattus argentiventer*, occurs throughout most of Southeast Asia and is one of the most economically important pre-harvest pests in rice crops. Based on a capture–recapture study in an irrigated lowland rice agro-ecosystem, populations are limited by the availability of nest sites and food. We recommend the following management strategies: (1) minimise the number of banks to reduce the availability of nest sites; (2) maintain/retain fallow to limit populations; (3) synchronise crops to minimise breeding period; and (4) time the application of mortality control at the early to mid-tillering stage when population density is low, individuals are generally in poor condition and not breeding, and thus populations are least able to compensate for the imposed mortality. Active burrow counts are recommended for assessing population size for management purposes. Live-trapping is recommended for demographic studies. Decision analysis identified strengths in current management practices in West Java, as well as key gaps in our scientific knowledge for developing effective management. Future research priorities are as follows: (1) evaluate the impact of secondary food sources on rat populations; (2) identify cues used by rats to trigger mating; (3) examine the spatial dynamics of crop asynchrony and its effect on the movements of rats; (4) determine age-specific survival for targeting control; (5) develop standardised methods for assessment of yield loss caused by rats; and (6) develop appropriate decision models for use by growers.

Keywords

Rattus argentiventer, rice-field rat, population dynamics, pest management, rice

INTRODUCTION

THE RICE-FIELD rat, *Rattus argentiventer*, is one of the most economically important pre-harvest pests in rice agro-ecosystems in Southeast Asia (Buckle et al. 1985; Geddes 1992; Singleton and Petch 1994). It occurs throughout most of Southeast Asia, including parts of Burma, Cambodia, Vietnam, Thailand, Malaysia, Indonesia and the Philippines (Corbet and Hill 1992). It is the predominant rodent species in most rice agro-ecosystems. Other rodent species (e.g. *Rattus tanezumi*) become dominant only on islands where the rice-field rat is absent (Wood 1994).

The island of Java has long been Indonesia's rice bowl. In 1996, it produced 28 million tonnes, accounting for about 56% of national production. Over half of the rice grown in Java is in irrigated lowland fields (about 3 million ha), a quarter in rainfed lowland fields and the rest in dry, upland fields. The lowland systems produced 96% of rice production in Java in 1996 (Bureau of Statistics, Indonesia).

Rice agro-ecosystems have expanded to increase production. Raffles (1817) estimated that only one-eighth (12%) of Java was cultivated. This had increased to about 18% by 1870, to 50% by 1920 (Booth 1988), and to 64% by 1997. Further expansion is limited by the availability of suitable land (RePPProT 1989). Recent increases in rice production have been achieved mainly through the use of varieties with short growing seasons, increased cropping intensity, and improved water supply. Further increases in rice production may be achieved through reducing pre-harvest losses to rodents (Singleton and Petch 1994). This underpins the purpose of reviewing ecologically-based management of the rice-field rat in this chapter.

Tropical rice agro-ecosystems are one of the most complex and stable agro-ecosystems in the world. Despite its economic significance, the ecology of rice agro-ecosystems is under-studied (Anwar et al. 1984). We conducted a bibliographic search (August 1998) on this topic and found that studies have focused primarily on rice and insect pests.

Rice is the staple food in Asia. By 2025 Asia's production of rice will have to increase by 70% to meet the needs of four billion people (Lampe 1993). Although many methods are used to control rodent pests in Indonesia, pre-harvest damage levels have not been reduced in recent times (see below). Tolerance of rodent damage to rice crops will diminish under the intense pressure to increase production. This chapter aims to provide an ecologically-based approach to integrating rodent control methods. We begin by reviewing the economic significance of the rice-field rat and describing the rice agro-ecosystem of West Java. We then review what is known about the likely key factors that limit the population size of the rice-field rat in rice agro-ecosystems, drawing heavily on the findings of a study by L.K.-P. Leung and Sudarmaji (unpublished data) on the population ecology and habitat use of the rice-field rat in rice fields in West Java. In the final section, we discuss decision-support models for the management of the rice-field rat.

ECONOMIC SIGNIFICANCE

In Indonesia, the rice-field rat has been ranked as the most important pest (non-weed) in Indonesia since 1983 (Table 1). Data collected by the forecasting centres of the Directorate of Food Crop Protection in Indonesia indicate that rats cause pre-harvest losses of around 17% per year to rice crops in Indonesia (Geddes 1992).

Rodent damage to rice crops is a chronic problem in Indonesia, although some years experience higher damage than others (Table 2). In West Java, rodent damage varies greatly among villages and sub-districts, and even among farms within a village—possibly because of the small size of average holdings (<2 ha) and different levels of rodent control effort among growers. Rodent control also lacks coordination. The patchy distribution of rodent damage has a significant impact on individual farmers and villages (Singleton and Petch 1994). On occasions, parts of some provinces suffer total crop loss to rats (Table 3).

IRRIGATED LOWLAND RICE AGRO-ECOSYSTEM

This chapter draws heavily on research conducted in lowland irrigated rice fields of West Java. The main rice producing area in Java is located on the north coast of West Java, and consists of the neighbouring districts of Karawang, Subang and Indramayu. The irrigated area in these districts is 271,000 ha (Kartaatmadja et al. 1997).

Climate

Each year, the Southeast Asian region has distinct dry and wet seasons. In West Java, the dry season is from May to October and the wet from November to April. Around 75% of the annual rainfall occurs in the wet season. In general, two crops of rice are grown each year in the irrigated lowland rice agro-ecosystem: a wet season crop (first crop) from mid-October to February; and a dry season crop (second crop) from April to July/August. The field is fallow over the later part of the dry season when irrigation water is in short supply. Vegetables and a third crop of rice may be grown in some fields where water is still available. A brief fallow may occur between the wet and dry season crops because of a limited supply of labour for land-preparation and transplanting. The timing of crops varies among years because the planting of the first crop is dependent upon the onset of the wet season.

Phenology of rice

The main growth stages of rice, based on a 120-day variety of rice (IR 64) are: tillering (55 days long); reproductive (35 days); milky ripe grain (10 days; abbreviated as milky); and ripening (30 days) (after Reissig et al. 1986). The reproductive and ripening stages are collectively termed the generative stage. There are often different crop stages in a given area, because crops are planted over a period of time depending on the availability of irrigation water and labour for planting. Planting of the first crop (wet season) is usually more synchronised than the second crop.

Table 1.
Ranking of economically important, non-weed pests in rice crops in Indonesia.

Pest	Ranking of decreasing order of economic significance			
	1983–1985	1986–1990	1991–1994	1995–1997
Rice-field rat	1	1	1	1
Brown plant hopper	2	4	2	3
Rice stem-borer	4	2	3	2
Rice leaf folder	3	3	Not ranked	Not ranked

Source: Forecasting Center for Pest and Diseases, Jatisari, West Java.

Table 2.
Incidence of rat damage and damage intensity of rice in Indonesia during the period 1980–1996.

Year	Incidence of rodent damage to rice crops	
	Area damaged (ha)	Damage intensity (%)
1981	198 546	14.5
1982	194 144	17.6
1983	186 989	20.1
1984	186 036	15.9
1985	179 765	17.5
1986	119 602	15.6
1987	80 865	13.6
1988	100 171	15.7
1989	95 175	17.7
1990	76 140	17.2
1991	77 114	18.7
1992	85 512	19.5
1993	No data	No data
1994	86 694	21.9
1995	103 109	20.8
1996	103 109	20.8
Average	**119 819**	**17.8**

Source:
Bureau of Statistics, Government of Indonesia.

Table 3.
Rodent damage and crop loss to rats for lowland rice in 1995.

Province	Damage area (ha)	Mean damage intensity (%)	Area of total crop loss (ha)
DKI Jakarta	35	10.37	0
Jawa Barat	29 006	16.08	241
Jawa Tengah	11 282	14.32	662
D.I. Yogyakarta	2 138	11.28	0
Jawa Timur	4 493	22.18	485
D.I. Aceh	5 755	17.90	0
Sumatera Utara	878	16.00	10
Sumatera Barat	1 073	20.20	25
Riau	700	20.50	12
Jambi	597	24.10	105
Sumatera Selatan	2 380	22.50	217
Bengkulu	949	12.70	0
Lampung	1 473	18.60	70
Bali	212	25.40	0
NTB	550	15.90	0
NTT	45	5.30	0
Kalimantan Barat	1 476	32.40	337
Kalimantan Tengah	2 781	23.70	446
Kalimantan Selatan	140	20.20	0
Kalimantan Timur	1 385	23.10	19
Sulawesi Utara	612	28.80	110
Sulawesi Tengah	9 815	14.60	158
Sulawesi Selatan	23 362	32.40	2 179
Sulawesi Tenggara	1 972	24.80	149

Source: Bureau of Statistics, Government of Indonesia.

Sympatric species

As well as domestic species, seven other vertebrate species are commonly found in the lowland irrigated rice agro-ecosystem in West Java: the house shrew (*Suncus murinus*), the large bandicoot rat (*Bandicota indica*), a skink—*Mabuia multifasciata*, a frog —*Rana crytrala*, and two snakes — *Ptyas korros*, and *Coluber radiatus*. Based on our trapping data, the large bandicoot rat occurs at relatively low densities compared to the rice-field rat.

Avian predators are rare in the lowland rice agro-ecosystem in Java. Other predators are sighted occasionally such as the Javan mongoose (*Herpestes javanicus*), the fishing cat (*Felis viverrina*), the small Indian civet (*Viverricula malaccensis*), and many unidentified species of snakes also occur (L.K.-P. Leung, personal observation).

The native house rat (*Rattus rattus diardii*) is a commensal species and is occasionally found in the rice fields. The Polynesian rat (*Rattus exulans*) and the rice mouse (*Mus caroli*) occur in other rice agro-ecosystems.

Food

Very little is known of the diet of the rice-field rat. Stomach content analysis reveals that they consume crabs, snails, insects, rice and other plant material, which commonly occur in the rice ago-ecosystem (Rahmini, unpublished data). Rice at the ripening stage is the most important food; fragments of rice grains were found in 100% of stomachs examined ($n = 50$) and constituted more than 50% of the stomach content by volume (L.K-P. Leung, unpublished data).

Goot (1951) observed that rats in captivity survived for only four or five days when fed exclusively on weeds, rice plants at the tillering stage, crabs, snails, or insects; whereas rats survived for several months when fed on starch food such as rice grains, maize, soya beans, peanuts, and sweet potatoes. Murakami (1990) found that captive rats survived for more than two weeks when fed exclusively on rice plants at the ripening stage. In contrast, survival was poor when they were fed rice plants at the tillering and reproductive stages. The results of these experiments need to be interpreted cautiously because rats in the field have a choice of food. Nevertheless, these two studies indicate that rice at the ripening stage is the most nutritious food for the rice-field rat in a rice agro-ecosystem.

In mixed-crop systems in West Java, relative damage to crops by the rice-field rat indicates it prefers rice to maize, peanut, and, soya bean (S. Suriapermana, personal communication). For this group of crops, litter size is highest in rats living in rice (Goot 1951).

Habitat

The original habitat of the rice-field rat is grassland, where its breeding is seasonal (Harrison 1951, 1955). In West Java, the irrigated lowland rice agro-ecosystem consists of a continuous tract of rice fields and a network of roads, streams, irrigation channels and drainage lines. 'Islands' of villages (*kampongs*) are scattered across the landscape. Sugarcane, peanuts and other crops are grown on 'islands' of elevated ground. Populations of the rice-field rat are present in villages and elevated croplands only when rice crops are not at the ripening stage (Goot 1951).

Earth banks along margins of paddies are an important habitat for the rice-field rat in this ecosystem because when the paddies are flooded, burrows in earth banks are the primary source of shelter. Banks are important also for breeding females because young are born and reared almost exclusively in burrows (L.K.-P. Leung and Sudarmaji, unpublished data). Rat burrows are found in the substrate of paddy fields only after harvest when the fields are drained and not waterlogged. After harvest, rats also construct nests underneath piles of rice straw left in the fields.

Breeding

Lam (1980, 1983) conducted detailed and extensive studies of the reproduction of the rice-field rat in Malaysia and has shown that a single breeding season occurs where one crop is grown per year, and that two breeding seasons occur if two crops are grown per year. He also has shown that the breeding seasons correspond closely with the reproductive and ripening stages of the rice crop, and suggests that nutritional factors, particularly the presence of rice at the reproductive stage, trigger reproduction in the rice-field rat. Tristiani et al. (1998) obtained similar findings in populations of the rice-field rat in West Java.

L.K.-P. Leung and Sudarmaji (unpublished data) have determined from autopsy of females that mating begins just prior to maximum tillering. At this stage, the testes are at their largest in nearly all males, indicating peak breeding condition. The first litters of young are born during the booting stage. Post-partum mating occurs (Lam 1983) and a second litter can be born during the ripening stage and a third shortly after harvest (L.K.-P. Leung and Sudarmaji, unpublished data).

The onset of mating at the maximum tiller number stage allows females to make full use of the ripening crop for meeting the high energy demands of raising young. The ability of the rice-field rat to synchronise reproduction with the phenology of the rice crop is possibly the key to its success in the rice agro-ecosystem. This ability was possibly selected in its original grassland habitat. Thus the rice-field rat may be evolutionarily pre-adapted to invade rice agro-ecosystem because of the similar phenology of rice and other species of the Graminaceae.

Female rice-field rats can conceive at the age of 45 days (Lam 1983), and can potentially produce up to three litters per cropping season. The first litter of the season generally does not breed because of the rapid decline in quality of the food supply within two weeks of harvest. However, the availability of high quality food only needs to be extended by 3–4 weeks for these females to breed and successfully rear young. Asynchronous crops will therefore extend the breeding season of rats and allow the first litters of the cropping season to breed and successfully raise young. Therefore the number of breeding females would increase exponentially. This contention is supported by studies of the breeding status of different age classes of female rats collected in an asynchronous cropping area in West Java in 1996: from a sample of 410 adult females caught immediately post-harvest, 56% of those pregnant were less than two months of age (Rahmini, unpublished data).

Asynchronous cropping is typical of fast-growing varieties of rice. Traditional varieties in Southeast Asia are photosensitive and mature at a particular time of the year, even when crops are planted over a period of weeks (Grist 1975). Synchronous maturation was possibly selected as a defensive mechanism against rodents or other pests.

Monitoring pest populations

Accurate assessment of rodent population density assists the grower to properly schedule control efforts. Also, reliable estimation of population density is a prerequisite for research into factors determining distribution and abundance of the pest. Management decisions are only as accurate as the sampling methods employed.

The reliability of a relative abundance index is based on its linear relationship with the population size (Caughley 1977). Two relative indices (active burrow counts and catch index) have been developed and calibrated against directly enumerated population sizes of the rice-field rat in lowland rice agro-ecosystem (L.K.-P. Leung and Sudarmaji, unpublished data). We are aware of only two other studies that have achieved this (Parer and Wood 1986; Moller et al. 1997).

L.K.-P. Leung and Sudarmaji (unpublished data) recommend active burrow counts for assessing population size of the rice-field rat for management purposes because this method is simple and reliable, and is not affected by the growth stage of rice crops. The catch index, although less accurate than active burrow counts, is recommended for population studies because animals caught in live traps can be measured to estimate other demographic characteristics such as sex ratio, survival and age structure.

Likely Key Factors Limiting Population Size

In West Java, there appear to be three principal factors limiting the population size of the rice-field rat. However, there is a dearth of long-term studies and an absence of manipulative studies, so these conclusions are preliminary.

Farm management practices

Agricultural ecosystems undergo major fluctuations in biomass and disturbance. In West Java, the major disturbances occur during land preparation and at harvest. For example, land preparation for each rice crop involves concurrent, widespread cultivation of fields and substantial reformation of banks. These actions have major impacts on the distribution and abundance of the rice-field rat. Added to this is the rapid switching of rice crops from sub-optimal to optimal rat habitats associated with the growing and ripening phases of the crop.

Farm management practices by growers therefore have major impacts on rat populations. They influence the temporal and spatial availability to rats of shelter, nesting sites, and the quality and quantity of food. They also impose direct mortality on rats through physical actions such as hunting, trapping, fumigating etc.(see Singleton et al., Chapter 8).

Availability of nest sites

In the irrigated lowland rice agro-ecosystem, the availability of nest sites is a key limiting factor for populations of the rice-field rat (L.K.-P. Leung and Sudarmaji, unpublished data). The abundance of rats is lower in the middle than along the margin of crops, where nest sites are available in adjacent banks.

In West Java, earth banks of primary and secondary irrigation channels form a major network in lowland rice fields. These are prime nesting sites for rats and as a consequence large populations of rats are associated with these structures (L.K.-P. Leung and Sudarmaji, unpublished data).

Rat burrows are occasionally found in bunds (small banks) in paddies. Farmers, however, usually construct bunds to a dimension that is too small for rats to build a burrow system.

Food supply

Population size and body condition decline during the dry season fallow and both are at their minimum shortly after fallow, around the early to mid-tillering stage. This is possibly due to diminished availability of food during the later part of the dry season fallow when both the abundance of invertebrates (Wolda 1978) and plant growth are reduced.

After fallow, the rice-field rat persists in low numbers in rice fields during the tillering stage of the first crop. Goot (1951) observed that a small number of rats remained in the field when their burrows were not disturbed by land preparation. Population growth is closely associated with the ripening of the crop when quality food is abundant. The process of population growth at the local level consists of breeding and subsequent recruitment of juveniles into the population as well as immigration of rats attracted to the ripening crops (Lam et al. 1990; L.K.-P. Leung and Sudarmaji, unpublished data). Maximum densities of population are reached shortly after harvest. Direct enumeration of rats from fumigating burrows and disturbing straw piles indicates that densities range from 120 to 240 rats per hectare (L.K.-P. Leung and Sudarmaji, unpublished data). Similar densities have been obtained by counting all rats caught in large areas during an eradication campaign (Table 4).

Table 4.
Total counts of rats present in irrigated lowland rice fields in West Java after harvest of the dry season crops, August–September, 1998.

Site	Area (ha)	Number of rats	Number of rats per ha
Pabuaran	230	51 000	222
Patokbeust	130	17 157	131
Binong	516	64 844	125
Pagaden	911	30 644	34

Source: S. Suriapermana, unpublished data.

Ecologically-based Population Management Practices for the Rice-field Rat

Population ecologists often remark that their studies and theories 'provide insight' into pest management. To be useful, however, these ideas must be part of a decision-theory framework. The challenge is to combine the current scientific knowledge on the biology and management of the rodent species we wish to control with the social, economic and political factors that influence the adoption of management actions by farmers. The simple restrictions that cultural and religious beliefs place on some management actions for agricultural pests (see Norton and Heong 1988) emphasises the importance of determining how farmers are likely to perceive and react to a rodent pest problem and to recommended management actions. Frameworks for developing a 'decision analysis/systems analysis' approach to vertebrate pest management have been developed (Norton and Pech 1988; Braysher 1993) and have been applied to rodent pest problems in agricultural systems (Brown et al. 1998).

We have applied our knowledge of the ecology of the rice-field rat, reviewed in this chapter, to develop an ecologically-based appraisal of the appropriateness of different management actions (Table 5). This appraisal was developed through consultation with scientists and agricultural extension staff. In some cases the scientific knowledge was too weak to critically evaluate the likely efficacy or economics of a particular management practice. Therefore, the decision-analysis presented in Table 5 includes a number of 'best guesses' and simply provides a working model. Among the 15 practices examined, seven practices are not supported by any scientific evidence and will need to be critically tested by field trials.

Based on this decision analysis approach, we recommend an integration of four management strategies for appraisal in replicated field trials prior to their implementation.

- First, the number of banks in rice fields should be kept to the minimum to limit the availability of nest sites. The flooding of rice fields serves to deter not only rats but also weeds and other pests. Banks are the only nesting sites in irrigated rice fields, and cannot all be eliminated because they are used as roads and for managing water levels for irrigation. Better planning and technology may reduce the number of banks. On the experimental farm of the International Rice Research Institute (IRRI), the number of banks was minimised by converting open drain lines to underground pipes, and rodent damage was reduced as a consequence (Mark Bell, IRRI, personal communication). Also, concreting the surface of banks will prevent rats from building burrows. However, both underground pipes and concreting are costly and are rarely appropriate for developing countries.

- Second, planting of crops and harvesting should be synchronised over a large area so as to shorten the period that ripening rice is available to rats and hence reduce their breeding season. In West Java the main constraints to synchronised planting are water and labour supply. However, it appears that water supply schedules can be modified to reduce asynchrony of planting of crops (S. Suriapermana, personal communication).

- Third, fallow over the dry season should be maintained to reduce rat population size. This also reduces numbers of some insect pests (Grist 1975). In some regions in Southeast Asia there is pressure to boost crop production by growing three crops per year. This is already being practiced in the Mekong Delta in Vietnam, and rodent damage appears to have increased as a consequence (Singleton and Petch 1994). In 1998, massive rodent control campaigns were necessary for protecting a third rice crop trialled in parts of Java and Bali (S. Suriapermana, personal communication).

- Fourth, if mortality control is used, it is best applied at the early to mid-tillering stage after the dry season fallow when populations densities are low and animals are weak. If rat densities are significantly reduced over a large area at this time, populations would have little immediate capacity to compensate for their reduction in numbers. This timing of action is

Table 5.

Decision analysis of practices for managing populations of the rice-field rat in West Java, Indonesia. Eight parameters were considered. The table also includes scientific basis and priority given to each practice. No analysis was conducted for empty matrix cells. The analysis took place during a workshop at the International Rice Research Institute in 1998. (Timing: lp = land preparation; sb = seed bed; tp = transplanting; b = booting; m = milky; r = ripening; h = harvest; f = fallow. Suitability of practices: ✓ = yes; X =no; ? = unknown; N/A = not applicable.)

Management practice	Timing	Feasible	Economic	Socially acceptable	Environmentally friendly	Sustainable	Scale of adoption	Ecosystem focus	Scientific basis	Priority
Routine										
Field sanitation	lp to b	✓	✓	✓	✓	✓	village	✓	?	high
Synchronous seeding and planting	sb,tp	✓	✓	✓	✓	✓	village	✓	for	high
TBS[a] by farmer group	crop	✓	✓	?	✓	✓	village	✓	for	high
Reduce bund size within rice fields	lp	✓	✓	✓	✓	✓	village	✓	for	high
Encourage natural enemies of rats	all	?	?	✓	✓	?	district	✓	?	high
Plastic barrier for nurseries	sb	✓	✓	✓	?	✓	village	N/A	for	high
Fumigation	lp,b,m,r	✓	✓	✓	X	✓	village	?	against	moderate
Digging burrows	lp,sb,r	✓	?	✓	X	X	village	X	?	moderate
Hunting at night	lp,sb	✓	X	✓	✓	X	village		?	low
Trapping with net	>h	✓	X	✓	✓	?	village		?	low
Apply if high densities are forecast										
Do not plant rice as the third crop		✓	✓	✓	✓	✓	farmer	N/A	for	high
Remove rice straw after harvest	f	✓	✓	✓	X	X	village	✓	for	high
Monitor abundance of rats in field	lp to m	✓	✓	✓	✓	✓	village	?	for	?[b]
Apply rodenticide	f, tp	✓	?	✓	X	X	village	?	?	moderate
Pump water down burrow entrance	>dry f	✓	?	✓	✓	?	village	X	?	moderate

[a]Trap–barrier system
[b]Need economic threshold data.

consistent with the recommended use of chemical rodenticides. After the rice crop reaches the booting stage, rodenticides become less efficacious because the baits are less attractive to rats (Buckle et al. 1979).

How Our Ecological Knowledge Can Influence Current Management Practices

The previous section highlighted management strategies that need to be implemented or maintained (e.g. fallow) for successful rat management. Our ecological knowledge of rodent populations can also be used to modify existing actions so that they are more efficient and effective.

In West Java, much energy and effort is applied each year in digging and fumigating rat burrows. This is the most common form of pre-harvest control of rodents in rice fields because it requires little capital compared to rodenticides. However, these actions generally are conducted during the ripening stage of the crop—about five weeks too late for maximal effect. In many parts of Java, 'gropyokan' is a tradition, with people joining together just after the harvest to kill rats by digging and fumigating burrows in rice fields. Mortality control at this stage is not an efficient use of resources and labour because many of the rats they kill would have died anyway during the fallow period. Indeed, removing high numbers of rats early in the fallow period may result in better survival of remaining rats than if no control was implemented because of reduced competition for food and shelter. If more rats were to survive through until the commencement of the next breeding season, then post-harvest control activities may be counter-productive.

In West Java, the one exception to applying mortality control at early to mid-tillering would be when the fallow period is short and rat densities are high. In this situation there is a high risk of significant rat damage when the next rice crop is transplanted.

Where To From Here?

An important output from a decision analysis process is clear identification of the key gaps in our scientific knowledge for developing effective management of a particular rodent pest. Table 6 summarises the gaps in our knowledge of the ecology and biology of the rice-field rat and the priority for obtaining this information to strengthen our management of the species. Our major shortcomings include a lack of understanding of factors that influence age-specific survival and inter-year fluctuations in the amplitude of populations, and knowing little of where rats live and what they survive upon during the fallow periods.

Our understanding of the ecology of the rice-field rat in West Java has enabled identification of optimal timing, location and scale of actions and whether they are consistent with goals of sustainable agriculture, minimal environmental impact and humaneness. Through knowledge of the socioeconomic status of the farming communities in the region we have assessed also the likely impact and practicalities of the recommended management actions. An important next step is to closely liaise with growers to determine which management actions they are willing to adopt, what modifications they would require before an action would be adopted, and to ascertain whether there are other actions they would like to include in an integrated management program. Once the management practices have been modified and approved by the growers we will need to assess the impact of integrating these management actions on populations of the rice-field rat. This would require a village-level study involving close cooperation with growers and a replicated, controlled, experimental design. The assessment of the success of the study will not be measured by the number of rats caught or killed, but by the reduction in damage caused by the rice-field rat, compared to the cost of implementing the management practices. For this approach to be successful and to be sustained by farmers, the management actions need to be reviewed at least annually in consultation with growers.

In summary, an ecological approach has provided the tools and building blocks for developing an integrated management approach. Developing field projects to evaluate the approach in close liaison with growers at the village or district level provides the necessary furnishings and quality control for developing an effective and operational management approach.

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15. Population Ecology and Management of Rodent Pests in the Mekong River Delta, Vietnam

Peter R. Brown, Nguyen Quy Hung, Nguyen Manh Hung and Monica van Wensveen

Abstract

Rodent pests are a growing problem in rice agro-ecosystems of Vietnam. However, little is known about which rodent species are responsible for losses to crop production, let alone how best to manage their impact. A survey of rat species in nine provinces in the Mekong River Delta found that the dominant rodent species found in rice ecosystems were the rice-field rat, *Rattus argentiventer* (60%) and the lesser rice field rat, *Rattus losea* (15%). Ten other species accounted for the remaining 25% of the population, and were unlikely to cause significant damage to pre-harvest rice. The breeding patterns of the two main rodent species and the relative population dynamics of rodents in different habitats were obtained from live-trapping studies (capture–mark–release) in a range of representative habitats based in and around the rice growing regions of Long An, Kien Giang and Tra Vinh provinces. Traps were set in rice crops (one and two rice crops per year), channel banks, melaleuca forest, undisturbed grassland, and coconut and banana plantations. Supplementary kill trapping was conducted to determine the breeding status (percentage of adult females breeding, litter size and embryo development) of the rats and to confirm their taxonomy.

Our focus on the ecology of the key rodent pest species has helped to define a range of potential management practices that are considered to be environmentally sustainable, economically feasible and socially acceptable. These practices are divided into routine actions that can be conducted all the time and preventative actions if high rat numbers are forecast.

Keywords

Species composition, habitat use, breeding, rice crops, ecology, *Rattus argentiventer*, *Rattus losea*

Introduction

RATS ARE THE number one pre-harvest pest of rice in many countries in Southeast Asia (Geddes 1992; Singleton and Petch 1994). In Vietnam, rodents are one of the three most important problems faced by the agricultural sector (Huynh 1987) and the level and intensity of damage has increased since about 1992 (Table 1). In the Mekong River Delta, there were 10,125 ha of damaged rice recorded in Long An, Dong Thap and Kien Giang provinces in the 1991/92 winter–spring season. In the winter–spring season of 1992/93, the area damaged increased to 44,000 ha over ten provinces. Crop losses were estimated at 300,000–400,000 tonnes of rough rice. Damage was recorded in Long An Province to over 10,000 ha with 10–30% losses, and 4,000 ha with 50–100% losses; in Ha Tien (Kien Giang Province), 800 ha were damaged with 80% losses. In 1996, the area damaged by rats increased to 130,000 ha over most provinces of the Mekong Delta. Rats also cause damage to other crops such as corn and potato in the suburbs of Ho Chi Minh City, in coastal regions (Binh Thuan Province) and in highland regions (Dong Nai Province). The factors that have lead to increased losses include more intensive farming and a general increase from two to three crops planted per year (Singleton and Petch 1994).

The factors that lead to increases in rat numbers and the importance of various habitats for breeding and shelter have not been addressed in Vietnam. The principal pest species is thought to be *Rattus argentiventer*, however little is known about the taxonomy or the population ecology of the species of rodents which inhabit rice ecosystems in Vietnam. In contrast, rodent species that are hosts for human plague in Vietnam have been studied extensively (Gratz 1988; Suntsov et al. 1997). Population studies of *R. argentiventer* have been conducted in Malaysia (Wood 1971; Lam 1980, 1983; Buckle 1990), Indonesia (Murakami et al. 1990; Leung et al., Chapter 14) and the Philippines (Fall 1977), but these results may not be appropriate for the Mekong River Delta which experiences annual floods. Furthermore, the mosaic pattern of habitats that exist in the Mekong Delta may be favourable or unfavourable for rats.

Table 1.
Area damaged by rats (ha) in the Mekong River Delta and other parts of Vietnam, 1992–1997 (adapted from Hung et al. 1998).

Year	Mekong River Delta	Other areas	Total area damaged in Vietnam
1992	18 640	–	18 640
1993	107 481	–	107 481
1994	134 616	–	134 616
1995	74 408	18 849	93 257
1996	130 777	130 723	261 500
1997	129 512	245 488	375 000

This chapter aims to provide an ecologically-based approach to the management of rodent pests in the Mekong River Delta of Vietnam. With a good understanding of the species composition, biology and behaviour of pest species it should be possible to devise management actions that are sustainable (environmentally and culturally) and could be combined with integrated pest management programs that are in place for insects, weeds and plant diseases (Singleton 1997). To provide some initial insight into the ecology of rodent pests in rice agro-ecosystems in the Mekong River Delta, data were collected from 1994 to 1998 on (i) the composition of rat species and (ii) the population dynamics, habitat use and breeding of the main rodent species, the rice-field rat (*R. argentiventer*) and the lesser rice-field rat (*Rattus losea*). Because none of this work has been published, we will begin by considering the methods adopted. We will then present the results of this study and suggest some preliminary management recommendations. As the data are limited, further studies are necessary to refine these strategies. Also highlighted are areas where critical information is lacking and further research is required.

METHODS

Study sites

The provinces of Long An, Kien Giang and Tra Vinh are situated in the Mekong River Delta of Southern Vietnam (Figure 1).

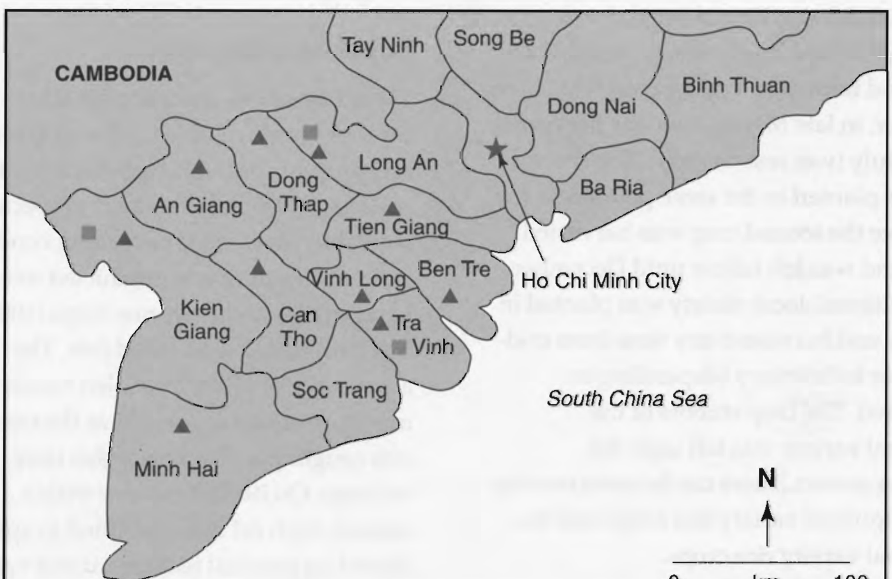

Figure 1.
Provinces of the Mekong River Delta of southern Vietnam. Shown are locations where the composition of rat species was determined (▲) and where the population dynamics of rats were assessed (■).

The annual rainfall in the region is 2,000–2,500 mm, which falls predominantly in the wet season (April to November). The topography is generally flat and some areas are regularly flooded during October and November, when the river systems overflow. The average temperatures range from 22–32°C in the dry season and 25–30°C in the wet season. There is an extensive network of channels and canals running through the delta delivering water for irrigation of rice crops. The width of the channels ranges in size from 1 m (tertiary channel), 2–5 m (secondary channel) and >5 m (primary channel).

The main rice crops grown at each study site were improved variety rice crops (90 day duration such as IR-54404, OM-1490 and OM-1037) and traditional, local variety rice (160–180 days duration). The first crop of improved variety rice was sown when flood waters subsided in December and was harvested in March (dry season crop), then the second improved variety crop was sown soon after, in late March, and was harvested in early July (wet season crop). The second crop was planted in the same paddies as the first. Once the second crop was harvested, the ground was left fallow until December. The traditional, local variety was planted in mid-July and harvested any time from mid-December to February (depending on conditions). The crop stubble of the traditional variety was left until the following season. There can be some overlap of the improved variety rice crops and the traditional variety rice crops.

Rat species composition

The composition of rat species from nine provinces was determined from six sampling occasions from November 1995 to July 1997. Fifty rats were collected at each sampling occasion (except in March 1996 when 100 rats were caught) from rice fields and from a 100 m length of a channel bank. Rats were collected by live-capture wire traps (200 × 100 × 100 mm) and from digging burrows until the required number of rats were obtained. It is not known whether this sampling procedure may cause bias towards some species. There have been no published studies that consider this bias for rodents in Southeast Asia. On subsequent visits to the sites, rats were collected from the same general area or within approximately 100 m of the area used previously. Rats were identified to species following van Peenen et al. (1969), Lekagul and McNeely (1977) and Tien (1985a,b) using external features and skeletal dimensions. Data are presented as percentages.

Population dynamics

Table 2 describes the trapping schedules for capture–mark–release studies and for breeding studies. At Long An, the rats collected were not identified to species, nor were they assessed for breeding condition.

Live-trapping was conducted using hand-made, single-capture traps (100 × 100 × 200 mm) baited with dried fish. The abundance of rats was pooled for each month, and was expressed as the number of rats caught per 100 trap-nights (trap success). On its first capture within a trap session, each rat was identified to species (based on external features, using van Peenen et al. 1969, Lekagul and McNeely 1977, and Tien 1985a,b; it was not possible to identify some animals because of taxonomical problems) and was marked using a numbered brass ear tag (Hauptner, Germany). Each rat was sexed and assessed for breeding condition, weighed (± 1 g), and tail length (if intact), hind foot length, ear length and head-body length were measured (± 1 mm). Each rat was released at the point of capture.

The minimum weight for an adult female classification was based on the lowest weight at which a rat was pregnant (determined by palpation) or lactating. Any rat lighter than this was considered juvenile or sub-adult. Palpation generally detects embryos from the second trimester, and so will underestimate breeding performance.

Breeding

At Kien Giang, kill samples were taken of rats from various habitats from captures in trap–barrier systems (see Singleton et al. 1998 and Chapter 8 for description), from live-capture traps, digging burrows and catching by hand with nets. Females were dissected to determine the condition of the uterus, number of embryos, size of embryos (± 1 mm) and number of uterine scars. Rats were considered pregnant if the uterus contained visible embryos.

Results and Discussion

Species composition

Twelve species of rodents were recorded from nine provinces (Table 3). Overall, the most common species was *R. argentiventer* (61%) followed by *R. losea* (15%) and *Rattus koratensis* (7.2%). *R. losea* was the most common species in Kien Giang. The *Mus* genus was likely to include *M. caroli* and *M. musculus*.

Table 2.
Summary of trapping conducted at Long An, Kien Giang and Tra Vinh provinces for capture–mark–release and breeding studies.

Study site	Trapping regime schedule (No. traps per trap line)	Duration	Habitats and number of trap lines
	Capture–Mark–Release		
Long An	50 traps, 1 night per week	Aug 94–Dec 96	Improved variety rice (1) Grassland (1) Cassava field (1) Melaleuca forest (1)
Kien Giang	35 traps, 2 nights per 2 weeks	Oct 97–May 98	Traditional variety rice (3) Improved variety rice (3) Melaleuca forest (3) Grassland (3) Secondary channel (3)
Tra Vinh	35 traps, 3 nights per 4 weeks	May 97–May 98	Improved variety rice (5) Primary channel bank (1) Banana plantation (1) Coconut plantation (1)
	Breeding		
Kien Giang	50 rats each month	Aug 97–May 98	Various

According to Sung (1999), there are 64 species of rodents belonging to 27 genera and 7 families in Vietnam. The species identified by Sung (1999) are generally similar to those that were found in our samples. In the agricultural fields of the Mekong River Delta, Sung (1999) lists *R. argentiventer* and *M. caroli* as common species with *Rattus flavipectus, Rattus exulans, Rattus nitidus, Mus musculus, R. koratensis, R. losea* and *Bandicota indica* found primarily around settlements. Other species of rodents identified by Sung from the zoographical zone of the Mekong River Delta were *Bandicota bengalensis, Rattus germaini* and *Rattus norvegicus*, but *Rattus rattus* was not listed. We did not capture *Mus cervicolor* which was a species identified by Sung (1999) as being present in the Mekong River Delta. Rodent species can be morphometrically similar but genetically distinct species (e.g. *Mastomys* spp., Granjon et al. 1997). Because of the diversity of species present, it can be easy to misidentify animals, particularly juveniles. Therefore, more work needs to be done to understand the taxonomy of these species in the Mekong River Delta.

Population dynamics at Long An

The highest abundance of rats occurred in September, when the local variety of rice was in the vegetative growth stage (Figure 2). The lowest abundance of rats occurred in June—when the second improved variety crop was at the maximum tillering stage, and in November and December—at the end of the flooding period. The proportion of rats caught in improved variety rice crop habitats compared to other habitats was similar throughout the year. There were no data on breeding from Long An, so we cannot determine whether increases in rat numbers were due to immigration or reproduction.

Population dynamics at Kien Giang

Eight species of rodents were identified from 449 captures. The capture rates of *R. argentiventer* (43.7%) and *R. losea* (45.2%) were similar. The next highest capture rate was *R. flavipectus* (5.1%). Seven captures were not identified to species (1.6%), with the six other species accounting for 4.4% of captures.

Both *R. argentiventer* and *R. losea* were more abundant in the improved rice variety habitat than in other habitats (Figure 3). The relative proportion of each species was similar within these habitats, except *R. losea* was more abundant in improved variety rice in May 1998.

Breeding of adult female *R. argentiventer* and *R. losea* was intermittent, although both species tended to be in breeding condition in similar proportions over time (Figure 3) (November: $\chi^2_1 = 0.11, P > 0.05$; February: $\chi^2_1 = 1.03, P > 0.05$; March: $\chi^2_1 = 0.16, P > 0.05$; May: $\chi^2_1 = 0.14, P > 0.05$). No breeding was evident in October 1997, December 1997 (very little trapping occurred because of flooding) or April 1998. The only breeding that occurred in January 1998 was in the melaleuca forest ($n = 1$). Breeding did not occur in the vegetative growth stage of the improved variety rice crop, but tended to occur in the latter two-thirds of crop growth from late tillering to harvest (a period of two months). Therefore breeding appeared to be linked to the presence of high quality food.