Mice and rats: the dynamics and bio-economics of agricultural rodents pests

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Mice, rats, and other rodents threaten food production and act as reservoirs for disease throughout the world. In Asia alone, the rice loss every year caused by rodents could feed about 200 million people. Damage to crops in Africa and South America is equally dramatic. Rodent control often comes too late, is inefficient, or is considered too expensive. Using the multimammate mouse (Mastomys natalensis) in Tanzania and the house mouse (Mus domesticus) in southeastern Australia as primary case studies, we demonstrate how ecology and economics can be combined to identify management strategies to make rodent control work more efficiently than it does today. Three more rodent–pest systems – including two from Asia, the rice-field rat (Rattus argentiventer) and Brandt's vole (Microtus brandti), and one from South America, the leaf-eared mouse (Phyllotis darwini) – are presented within the same bio-economic perspective. For all these species, the ability to relate outbreaks to interannual climatic variability creates the potential to assess the economic benefits of forecasting rodent outbreaks.

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Rodents are among the most important global pests (Prakash 1988; Singleton *et al.* 1999), and are often featured in fiction, as in Albert Camus' *The Plague*. The black rat (*Rattus rattus*) played a key role in the plague during the Middle Ages (Scott and Duncan 2001). Farmers in many parts of the world, particularly those in developing countries, tend to view economic losses due to rats and mice as unavoidable (Posamentier 1997; Singleton *et al.* 1999). In fact, the impact of rodents has been greatly underestimated and generally ignored in the general scientific literature, with a small number of exceptions (Elton 1942; Singleton *et al.* 1999).

In a nutshell:

- Mice and rats are major agricultural pests worldwide, spreading disease and competing with humans for food
- Rodent control strategies must consider economics as well as ecology
- Population dynamics must also be taken into account, including intrinsic density-dependent and extrinsic density-independent factors
- This approach will allow us to predict rodent outbreaks and the effects of climatic variability more accurately

Competing with rodents for food

Worldwide, there are about 1700 species of rodents, but only 5–10% are major pest species in agricultural and urban environments, and even fewer cause problems over larger geographic areas. Some of these consume substantial amounts of agricultural produce (Table 1), and in many developing countries, farmers consider rodents the main impediment to higher yields (Makundi *et al.* 1999). Every year, rats in Asia consume food crops that could feed 200 million people for an entire year (Singleton 2003). In Indonesia, rodents are the most important pre-harvest pests in economic terms, causing on average at least 15% annual losses of rice (Geddes 1992). In Africa, the numbers are similar. Damage due to rodents in Tanzania causes an estimated annual yield loss of 5–15% of maize (corn), corresponding to about $45 million, and food which could feed about 2 million people (Leirs 2003; Table 1). In parts of South America, native rodents cause crop damage varying between 5–90% of total production (Rodriquez 1993). Obviously, we need better pest control strategies than we have today.

The design of rodent control strategies has both an ecological dimension, relating to the interaction of the pest population and its resources and enemies (Singleton *et al.* 1999), and an economic dimension, relating to crop damage, which affects yield, and the use of pesticides, which in

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turn affects production costs (Carlson and Wetzenstein 1993). Bio-economic analysis of pest control has been related primarily to invertebrate pests and weeds, whereas vertebrate pests have been largely ignored. Here we show how ecological and economic factors may be incorporated in bio-economic models aimed at improving control strategies of agricultural rodent pests (Figure 1).

Ecology, economy, and bio-economics

Rodents thrive on the rich food supply provided by the agricultural production system. The application of rodent control is often poorly timed or inadequate, so that populations recover quickly, or else control is performed in response to high rodent numbers, after the damage has been done. We need a better understanding of the trade-off between the costs and benefits of control. The outcome of a cost–benefit analysis will depend on, for instance, the value of a crop, the timing, and the cost and effectiveness of control techniques. Unfortunately, ecologists tend to ignore economics, economists typically have a simplistic understanding of ecology, and pest control managers commonly underrate both. A synthesis of these spheres is therefore necessary, and since ecology and economics are so closely interwoven in pest systems, an integrated bio-economic approach is appropriate (Figure 1). We first describe the kind of ecological and economic relations that should form the skeleton of such an approach, and then present the information available for the different example species.

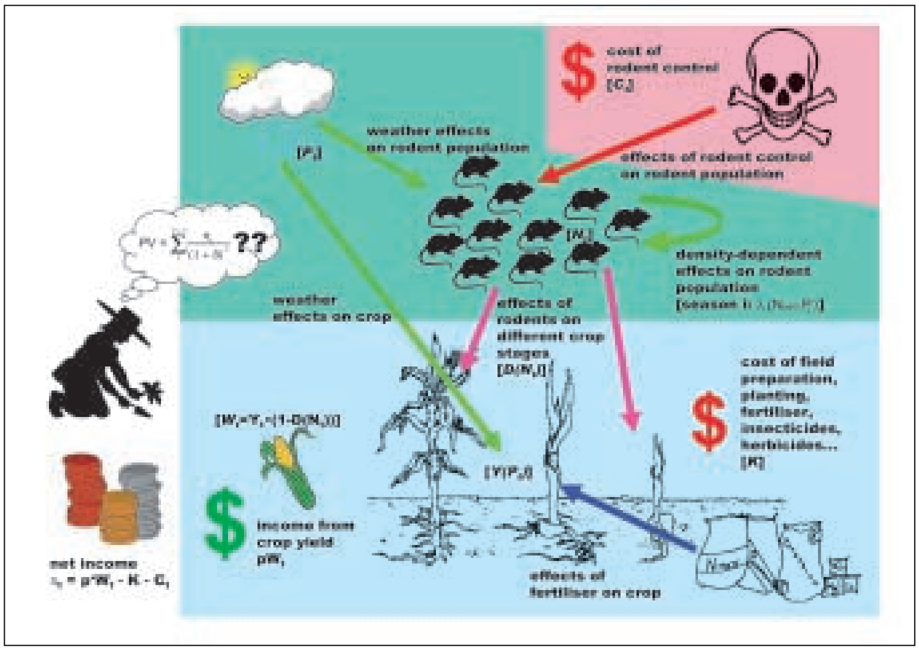


Figure 1. *A synoptic account of the bio-economic interactions in agricultural rodent pest systems. The rodent population is typically influenced by precipitation* (P_t) *and intrinsic factors, which generate a particular density-dependent structure. Farmers' revenue derives from the sale of agricultural products* (W_t) *minus the costs of production* (K). *The link between economics and rodents is both through the damage* [$D(N_t)$] *reducing the potential yield* (Y_t) *and through the cost of controlling the rodent pest* (C_t), *both of which enter the net income* (π_t). *The net income over a number of years, dependent on the planning horizon* T, *is summed as the present value* (PV), *which is to be optimized.*

The bio-economics of rodent control

Rodent ecology: a population modeling approach

The rodent population density N_t at time $_t$ may be seen as a result of past density, environmental factors (hereafter assumed to be precipitation), and control effort. For the species we discuss here, there is a breeding season that can be associated with an annual increase in abundance, and a non-breeding season that can be associated with an annual decline. Ignoring delayed density dependence, a general population model for such a seasonal system is

(1)

$$N_t = \begin{cases} \lambda_b(N_{t-1},P_{t-1},X_{t-1})\, N_{t-1} \text{ during the breeding season} \\ \lambda_{nb}(N_{t-1},P_{t-1},X_{t-1})\, N_{t-1} \text{ during the non breeding season} \end{cases}$$

where λ_b and λ_{nb} are the finite rates of increase over the two seasons, and each is a function of density at time $t-1$ (N_{t-1}), cumulative precipitation over a past period (P_{t-1}), and the amount of control (X_{t-1}) – for example, the quantity of poison applied over the time interval ($t-1$, t).

Agricultural production when pest rodents are present

Ignoring changes in other production factors such as fertilizer and labor effort, the yield per unit area of land (metric tons per ha) in the absence of the rodent pest, $Y_t = Y(P_t)$, increases with precipitation (Ruthenberg 1980). In the presence of pest rodents, this yield will be reduced to some realized yield W_t, given by $W_t = Y_t\,[1-D(N_t)]$, where $D(N_t)$ represents the crop damage as a proportional loss to yield, depending on the abundance of the rodent pest. This relationship may be complex and varies greatly between agricultural systems, but D typically increases with abundance. (Mulungu *et al.* 2003).

Economic evaluations

Apart from the fixed costs associated with crop production, such as field preparation, seed, and, in some systems, variable costs such as fertilizer use, there is a cost C_t associated with controlling rodents – for instance, the cost of the applied poison and the cost per unit effort of spreading the poison.

Table 2. Characteristics of the examined rodent species as agricultural pests, in the area where the respective studies were conducted.

Species	Location	Breeding season	Determinants of	Crop(s)	Plant growth	Period of damage
Mastomys natalensis (Leirs *et al.* 1993, 1996)	Tanzania	March–September	Rainfall effects on maturation and rat survival	Maize	March–July	Mainly at planting (March)
Mus domesticus (Singleton *et al.* 2001)	southeast Australia	September–April (can begin in August and end in June)	Winter–spring precipitation determines availability of good quality food	Wheat	May–December	Planting May–June) and from booting to harvest (October–December)
Rattus argentiventer (Leung *et el.*	west Java	February–April June-August	Monsoon rains–synchrony of cropping	Rice	December–early September	All stages, but mainly at planting (December, May), and generative stage (February–April, June–August)
Microtus brandti (Zhang *et al.* 1999)	Eastern Inner Mongolia	April–September	Precipitation determines grass biomass, which is modified by livestock grazing	Livestock production	Spring–summer	Spring–summer
Phyllotis darwini (Meserve and Le Boulengé 1987)	Chile	September–January	Rainfall which occurs during winter months (May–August) and dtermines plant productivity and rodent recruitment	Maize, potatoes, fruit, and other subsistence crops	Late winter–spring	Late spring–summer

Net current agricultural profit per ha and year is defined as

(2)

$$\pi_t = pW_t - K - C_t = pY(P_t)(1 - D(N_t)) - K - C_t,$$

where K is the sum of the fixed costs of production and p represents the net market price of the crop.

From equations (1) and (2) we see that the direct effect of rodent control on current profit is ambiguous as more control presumably means fewer rodents, and therefore less damage and higher realized yield, but at the same time control costs increase. Likewise, the effect of precipitation on profit is unclear, as more rain means a higher yield while the number of rodents may also increase. These links are further complicated if, for example, damage and realized crop profit one year is contingent upon the state of the system in previous years.

The management problem is to specify the timing and application of X_t, balancing the control costs and crop damage so as to maximize the present value of the net profit per ha,

(3)

$$PV = \sum_{1}^{T+1} \frac{\pi_t}{(1 + \delta)^t} ,$$

where T represents the planning horizon and δ is the rate of discount.

The discount rate and the time horizon can either reflect social (eg an agricultural officer at the village level or a state agency) or individual (a farmer) choices. The social (communal) choice generally implies a lower discount rate and a longer planning horizon than for an individual farmer (Dasgupta and Mäler 1995).

In order to illustrate this bio-economic approach, we have selected two examples for which we have most of the information we need: the multimammate mouse (*Mastomys natalensis*) in small-scale maize fields in Tanzania and the house mouse (*Mus domesticus*) in large-scale wheat fields in Australia. We also review three additional rodent–pest systems from Asia and South America.

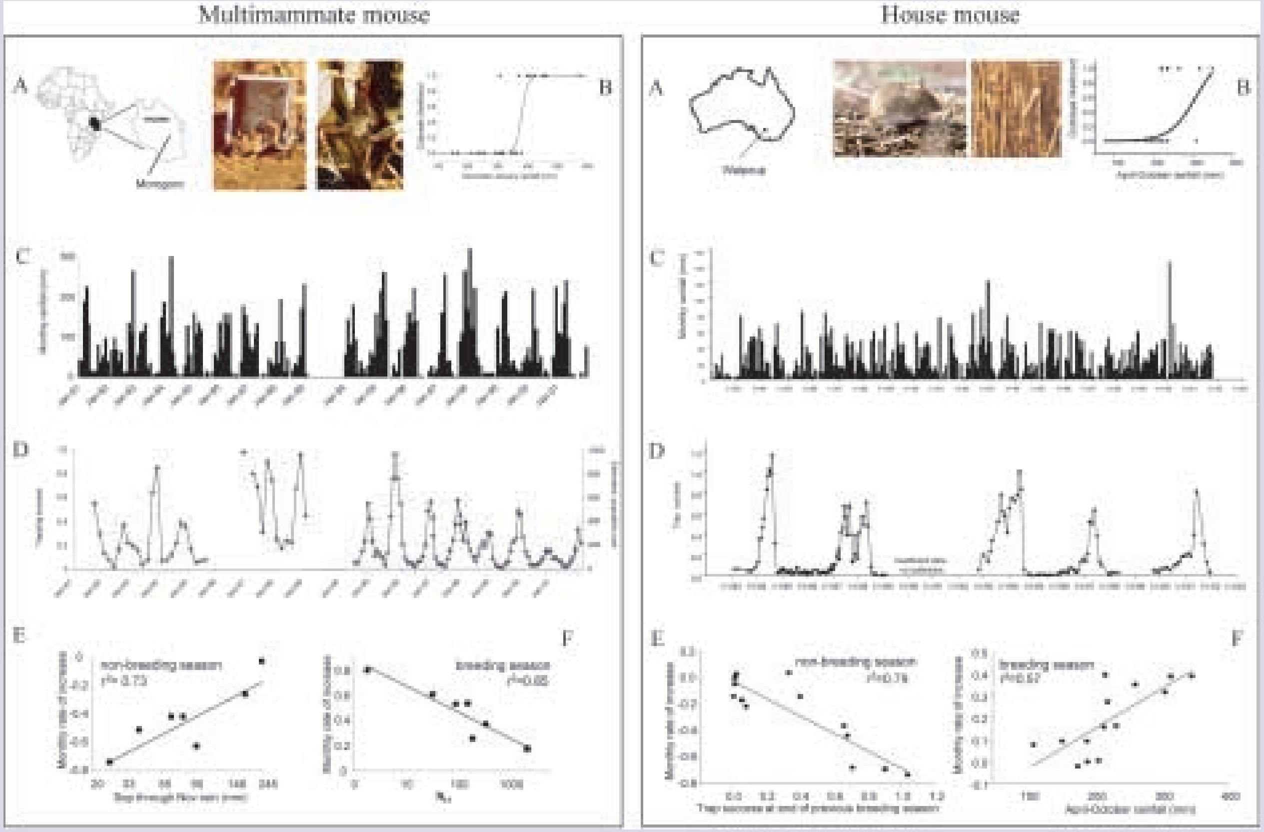


Figure 2. *The two systems used as focal examples are multimammate mice* (Mastomys natalensis*) and house mice* (Mus domesticus*). (Left)* (Mastomys natalensis)*: (A) Multimammate mice in Morogoro, Tanzania, and badly damaged maize. (B) Sigmoidal regression of binary data on outbreaks of multimammate mice during the period 1946–1978, taken from agricultural reports (redrawn from Leirs et al. 1996), against December–January rainfall at Tabora, central Tanzania. The regression equation is outbreak likelihood*

$$= \frac{e\,(-37.68 + (0.099\mathrm{Pt}))}{1 + e\,(-37.68 + (0.099\mathrm{Pt}))}\,,$$

where Pt *represents the rainfall variable. (C) Monthly rainfall over the period January 1981–December 2001. (D) Population dynamics of* M natalensis *at Morogoro, based on trapping success for the period 1981–1989 (from Telford 1989 and Leirs 1995), and closed population capture-recapture estimates from 1994–2001. (E) The rate of increase over the non-breeding season (Nov–May) is positively correlated with cumulative rainfall early in the season (Sept–Nov), but is independent of density. (F) The rate of increase over the breeding season (May–Nov) is negatively correlated with density. (Right)* (Mus domesticus)*: (A) House mice at Walpeup, southeastern Australia, and damage to wheat ears. (B) Sigmoidal regression of binary data on outbreaks of house mice in southern Australia for the period 1981–2001, against April–Oct rainfall (mm). The regression equation is outbreak likelihood*

$$= \frac{1\ .22}{1 + exp\,(-\,(\mathrm{P}_t - 305)/33.2)}$$

where Pt *represents the rainfall variable. Only three years were identified (1983–84, 1986–87, and 1992–93) as leading to periods in which substantial damage occurred and crisis management actions were taken. During the years 1996–97 and 2000–01 mouse density rose to high levels, but damage was negligible and no large-scale control actions were taken by farmers. These years are indicated as open circles. (C) Monthly rainfall from Jan 1982–Oct 2001. (D) Population dynamics of* M domesticus *at Walpeup (data for 1983–2000 redrawn from Singleton* et al. *2001), with abundance expressed as proportional trap success. (E) The rate of increase over the non-breeding season is negatively correlated with density. (F) The rate of increase over the breeding season is independent of density but positively correlated with winter and spring rainfall (cumulative precipitation from April–Oct).*

Multimammate mice in Africa

Distributed throughout Africa, the multimammate mouse (M. *natalensis*) causes more agricultural damage on this continent than any other rodent species. Occasional outbreaks exceed 1000 animals/ha (Leirs 1995), but damage and economic losses are considerable, even in years with low population densities.

Seasonal changes in abundance of these mice are highly dependent on rainfall, and in particular on the timing of the rainy season (Leirs 1995; Leirs *et al.* 1997; Stenseth *et al.* 2001; Table 2; Figure 2). Population increases can be rapid, due to exceptionally high litter sizes of up to 24 young per litter (the mean is 11, compared to an average of 4–6 among other small rodents). Unusually heavy rain early in the wet season improves food supply, which stimulates the early maturation of subadults and out-of-season breeding. This extra generation before the start of the normal breeding season increases the production of young that may result in an outbreak the following year (Leirs *et al.* 1993).

Figure 3. *The result of four nights' catch of house mice in Victoria, southeast Australia in 1917. At the time, grain was stored in stacked bags.*

Crop damage and economic losses during outbreaks can be enormous (Mwanjabe *et al.* 2003). Following the rationale set out above, Skonhoft *et al.* (2003) developed a bio-economic model for managing multimammate mice on maize farms in Tanzania. They concluded that applying control for 2–5 months is optimal economically if control starts early in the rainy season. This strategy provided a higher economic benefit than would be obtained by symptomatic treatment, by applying control continuously throughout the year, or by foregoing control efforts altogether.

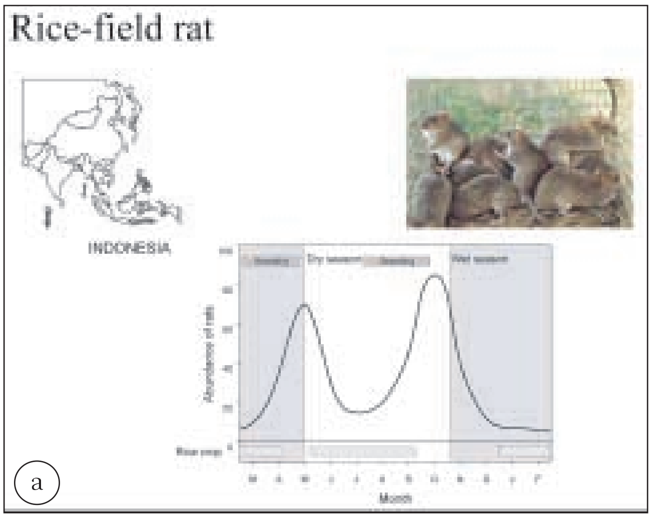
Economically, the best strategy involves applying control methods for 2 months just before the planting. This matches the traditional method for controlling mice around the planting season to some extent, but not the strategy of the responsible government bodies, who release funds for pest control only when rodent densities are high. For example, in early 1998 the Tanzanian Ministry of Agriculture spent about $80 000 (excluding labor costs) on rodent control, treating about 38 000 ha with zinc phosphide when damage levels had already reached over 40% (Mwanjabe 1998).

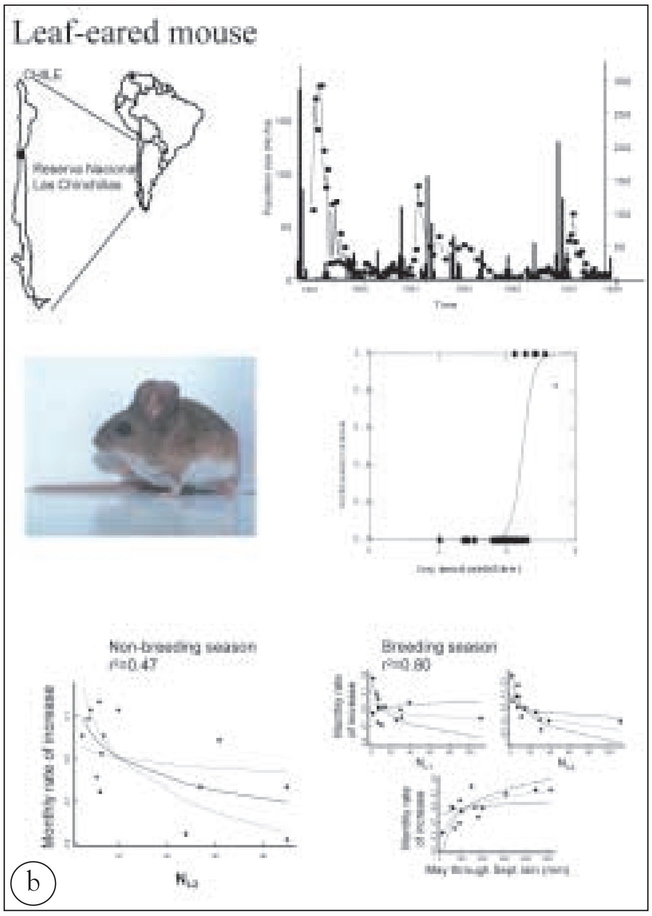
The house mouse in Australia

The house mouse (M. *domesticus*) is a pest species with a worldwide distribution. In southeastern Australia, it is the main rodent pest causing pre- and post-harvest losses, with irregular outbreaks in excess of 800 mice/ha causing damage to crops, stored produce, livestock, and infrastructure (Figure 3). During a major outbreak, losses exceed $40 million, which can reduce national agricultural production by 3–4% (Singleton 1997). In non-outbreak years, however, densities are typically less than 50 mice/ha, resulting in negligible economic loss (Singleton *et al.* 2001).

In Australia, the house mouse shows seasonal changes in abundance (Table 2), but in contrast to the multimammate mouse, rainfall correlates with the rate of increase during the breeding season, while the density at the end of breeding affects the decline over the non-breeding season (Figure 2). In addition, an extended breeding season and the condition of mice at the commencement of the breeding season are important factors leading to an outbreak (Singleton *et al.* 2001). These factors are influenced by rainfall, as is the rate of increase which can be modeled as a function of crop yield or the strongly correlated cumulative rainfall from autumn to spring (April to October) (Pech *et al.* 1999). The substantial between-year variability in rainfall characteristics of southeastern Australia is the primary cause of the irruptive dynamics of house mice. Assuming the model given in Figure 2b is used to initiate rodent control, the cost of mouse damage is minimized when the threshold April–October rainfall for predicting a plague is 270 mm (Davis *et al.* 2003).

Currently, control measures take the form of aerial applications of a rodenticide (zinc phosphide) over large areas (100 000 to 500 000 ha) once an outbreak and damage have already occurred (Brown *et al.* 2002). The expected benefits of early intervention to mitigate the impact of mouse outbreaks have been clearly demonstrated (Redhead and Singleton 1988). The costs and benefits of various management practices have been estimated in an economic model and incorporated into an information transfer and decision support system for managing mouse populations (Brown *et al.* 2001).





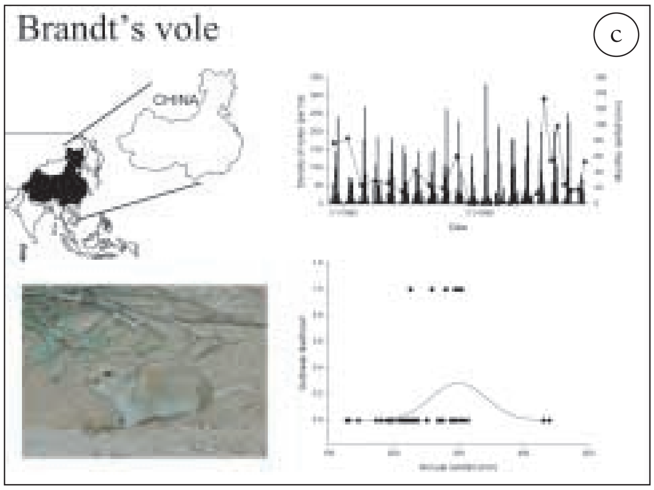


Figure 4. *Agricultural rodent systems with irregular population dynamics in Indonesia, Chile, and China. (A) The seasonal structure and its resulting dynamics are illustrated for the rice-field rat (Rattus argentiventer) in Southeast Asia (Java, Indonesia) (Sudarmaji, Singleton et al. unpublished). (B) The leaf-eared mouse (Phyllotis darwini) in South America, presented with data from central Chile (Lima et al. 2002). A sigmoidal regression is given of binary data on outbreaks, against annual rainfall Pt. The regression equation is . During the non-breeding season, there is delayed density-dependence in the monthly rate of increase. During the breeding season, there is a direct and delayed negative effect of density on the rate of increase over the breeding season, but a positive effect of rainfall from May–Sept. (C) The Brandt's vole (Microtus brandti) in Asia, presented with data from Inner Mongolia, where most outbreaks occur in years of average precipitation (Li and Liu 1999).*

■ Broadening the view: three examples

Indonesia: rice-field rat

The rice-field rat (*Rattus argentiventer*) is a pre-harvest pest species throughout most of lowland Southeast Asia (Table 1). In Indonesia, the economic losses are substantial every year, but may increase drastically during outbreak years (up to 1000 rats/ha). In contrast to the African multimammate mouse and the Australian house mouse examples, grain in this region is grown two or three times a year, during both the dry (irrigated) and wet seasons.

Rice-field rat populations exhibit typical seasonal changes in abundance (Figure 4), and outbreaks appear to be related to specific rainfall patterns that extend the breeding season (Table 2). Since breeding is linked to the generative stage of the rice crop (Lam 1983; Leung *et al.* 1999), asynchronous planting extends the breeding season because rats may disperse and colonize new crops as they ripen. In the Vietnam's Mekong Delta, the main limiting factor to rice-field rat populations appears to be seasonal flooding of the rice fields. In Indonesia, the harvesting of rice and intensive land preparation for the next season's crop are important limiting factors.

The efficacy of control has been limited, not only by the cost of rodenticide, but also because farmers tend to apply control actions independently of each other on their own small (0.5–1.5 ha) fields, leading to rapid reinvasion of treated crops by the rats. Unified control at a community level is clearly required. The community trap-barrier system (CTBS) (Singleton *et al.* 1999) is a new approach, developed from a solid understanding of the rats' breeding ecology, habitat use, and annual seasonal dynamics (Leung *et al.* 1999). It requires small patches of crop to be planted 3 weeks earlier than the main crop. The early maturing crop attracts rats from surrounding fields up to 200 m away and lures them into traps along a plastic fence. On an experimental scale, the benefit:cost ratio of the CTBS varies from 24:1 when rat densities are high to a small net cost when rat densities are very low. Farmers in west Java who have tested the CTBS havetypically increased production by 10–25% in seasons when rice yields are around 4.0–4.5 metric tons/ha (Singleton *et al.* 2003).

Given that in some seasons there is a net cost to farmers if they use the CTBS, it would be advantageous to be able to forecast seasons of high rat numbers. Obviously, a bio-economic modeling approach, similar to the one used for both the multimammate mouse and the house mouse, would be beneficial.

Chile: leaf-eared mouse

The leaf-eared mouse (*Phyllotis darwini*) is one of the rodent species that causes the most damage on subsistence farms in western South America (Fuentes and Campusano 1985; Table 1). In outbreak years, population size may reach up to 200 animals/ha.

Breeding of the leaf-eared mouse is highly seasonal (Figure 4; Table 2). The outbreaks are correlated with years of unusually high rainfall, which may be related to the occurrence of El Niño disturbances (Jaksic 2001). The population dynamics of this species are also influenced by direct and delayed density dependence, the latter primarily due to predation by barn owls. During rainy years, competition for food is relaxed and the mutual feedback loops between mice and barn owls may dominate (Lima *et al.* 2002).

Spreading lethal poisons after the outbreaks have already developed is common practice.

Inner Mongolia: Brandt's vole

The distribution of Brandt's vole (**Microtus brandti**) includes grasslands in middle-eastern Inner Mongolia, eastern Mongolia, and parts of southern Russia (Figure 4). This system differs from the previous examples, in that Brandt's voles do not damage crops, but compete indirectly with people for food. In years of very high densities (> 400 voles/ha), these rodents damage pastures, compete with livestock, contribute to desertification through the disturbance of soil and removal of vegetative cover (Zhong *et al.* 1999), and can increase the likelihood of human contact with *Yersinia pestis*, the causative agent of bubonic plague.

In Inner Mongolia, the annual decline of Brandt's vole populations during the non-breeding season is density dependent. The higher the abundance of voles in autumn, the greater the over-winter density decline (Zhang *et al.* 2003). During the breeding season, the rate of increase depends on the height and cover of the vegetation. Populations decline where grass is short and sparse, probably due to a lack of food, but also because tall, dense grass impedes social interactions and reduces the ability of the voles to detect predators. Intermediate grass levels, which lead to outbreaks, tend to occur in years with average levels of precipitation (Zhang *et al.* 2003). Thus, given the constant impact of livestock grazing, there is a convex-up relationship between the likelihood of an outbreak and precipitation (Figure 4).

Control of Brandt's voles currently depends on the use of non-specific lethal baits. The voles' specialized habitat requirements suggest that an economically beneficial strategy should include management of the grazing pressure by livestock as well as direct control of the voles. The optimal strategy for maintaining livestock production may therefore include trading off a reduction in the number of livestock against the cost of rodent control.

■ Conclusions

The agricultural systems we have covered in this paper vary from modern, capital-intensive, large-scale monocultures to traditional, small, fragmented fields and free-range livestock ranges. Four of the five examples show irruptive populations dynamics triggered by interannual variation in precipitation. All the species in question belong to five genera from two families and show typical seasonal fluctuations in rodent numbers, but different timing of density-dependent and density-independent mechanisms. Such general and comparative insight is of key importance when designing appropriate pest control strategies. Indeed, these data suggest that current governmental funding for rodent pest control should be devoted instead to research, especially in developing countries. Not doing so may prove costly in terms of both lost income and food supplies.

Since the annual density-dependent process is of first order (Stenseth 1999) in the African multimammate mouse and the Australian house mouse systems, it is primarily a population dampening process. The positive effect of precipitation, on the other hand, generates outbreak conditions in both species. Despite several similarities, we found important differences in the seasonal, density-dependent and density-independent structures in the five case studies. The multimammate mouse and the rice-field rat show irregular outbreaks but are both chronic pests in other years as well. By contrast, house mice are an "all-or-none" pest, with costly damage in some years but hardly any in others. On the other hand, delayed density dependence may easily generate inherently unstable dynamics. The existence of delayed density dependence may imply some trophic interaction such as predation.

A bio-economic model incorporating such basic ecological principles provides a valuable framework for pest management systems – one which properly takes into account both ecology and economics. Farmers need to make decisions every year about whether or not they will invest in rodent control and, if so, to what extent. The ability to predict outbreaks of rodent populations is therefore likely to be critical. In most cases, outbreaks are dependent on stochastic environmental events such as rainfall, so that timely forecasts, by their nature, will not be certain; some outbreaks may not be predicted, while predicted outbreaks may not occur. Since both errors incur an economic loss due to lower crop yield and unnecessary control expenses, respectively, the practical application of forecasts is rather complex (Davis *et al*. 2003).

In this review we have largely ignored complexities related to habitat structure and patchiness. From the rice-field rat example, it is obvious that the ecological models should incorporate dispersal between crop fields whenever agricultural and pest control activities on neighboring fields are not synchronized. What farmers should do in such systems will be largely dependent on what their neighbors do. A game-theory approach (Carlson and Wetzenstein 1993) may be appropriate, in combination with bio-economic modeling. Demonstrating the economic rewards to farmers who cooperate within such a unified framework is, of course, a mixed economic and institutional challenge.

Precipitation and seasonality are important determinants of the dynamics of all five pest systems. This links the worldwide problem of agricultural rodent pests to another current global problem: climate change (Stenseth *et al*. 2002). Climate change is likely to change the length of the breeding season and increase the variance and/or change the mean precipitation. The reviewed systems show that high numbers of small rodents can compete with people if the appropriate conditions are provided. In fact, climatic change combined with changes in agricultural technique might put us at a competitive disadvantage to mice and rats.

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References

Brown PR and Singleton GR. 2001. Mouser (Version 1.0) CD Rom, CSIRO, Australia.

Brown PR, Chambers LK, and Singleton GR. 2002. Pre-sowing control of house mice (*Mus domesticus*) using zinc phosphide: efficacy and potential non-target effects. *Wildlife Res* **29**: 27–37.

Carlson and Wetzenstein. 1993. Pesticides and pest management. In: Carlson G, Zilberman D, and Miranowski J (Eds). Agricultural and environment resource economics. New York: Oxford University Press. p 268–317.

Caughley J, Monamy V, and Heiden K. 1994. Impact of the 1993 mouse plague. GRDC Occasional Paper Series No 7. Camberra, Australia: CRDC.

Dasgupta PS and Mäler KG. 1995. Poverty institutions and the environmental resource base. In: Behrman J and Srinivasan T (Eds). Handbook of development economics. Vol II. Amsterdam: Elsevier. p 2371–63.

Davis SA, Leirs H, Pech RP, *et al*. 2003. On the economic benefit of predicting rodent outbreaks in agricultural systems. *Crop Prot*. In review.

Elton C. 1942. Voles, mice and lemmings. Hertfordshire, UK: Wheldon & Wesley. Reprinted 1965.

Fiedler L. 1988. Rodent problems in Europe. In: Prakash I (Ed). Rodent pest management. Boca Raton, FL: CRC Press. p 5–66.

Fuentes ER and Campusano C. 1985. Pest outbreaks and rainfall in the semi-arid region of Chile. *J Arid Environ* **8**: 67–72.

Geddes MW. 1992. The relative importance of pre-harvest crop pests in Indonesia. *B Nat Res Inst Kent UK* **47**: 70 p.

Jaksic FM. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* **24**: 241–50.

Lam YM. 1983. Reproduction in the rice field rat, *Rattus argentiventer*. *Malay Nat J* **36**: 249–82.

Leirs H. 1995. Population ecology of Mastomys natalensis (Smith 1834) multimammate rats: possible implications for rodent control in Africa. *Agricultural Editions, scientific publications of the Belgian Administration for Development Cooperation, Brussels, Belgium*. **35**: 273.

Leirs H. 2003. Management of rodents in crops: the Pied Piper and his orchestra. In: Singleton GR, Hinds LA, Krebs CJ, and Spratt DM (Eds). Rats, mice and people: rodent biology and management. Canberra, Australia: ACIAR. p 183–90.

Leirs H, Stenseth NC, Nichols JD, *et al*. 1997. Seasonality and non-linear density-dependence in the dynamics of African *Mastomys* rats. *Nature* **389**: 176–80.

Leirs H, Verhagen R, and Verheyen W. 1993. Productivity of different generations in a population of *Mastomys natalensis* rats in Tanzania. *Oikos* **68**: 53–60.

Leirs H, Verhagen R, Verheyen W, *et al*. 1996. Forecasting rodent outbreaks in Africa: an ecological basis for *Mastomys* control in Tanzania. *J Appl Ecol* **33**: 937–43.

Leung L K-P, Singleton GR, Sudarmaji, and Rahmini. 1999. Ecologically-based population management of the rice-field rat in Indonesia. In: Singleton GR, Hinds LA, Leirs H, and Zhang Z (Eds). Ecologically-based management of rodent pests. ACIAR: Canberra. p 305–18.

Li ZL and Liu TC. 1999. Population cycle of Brandt's vole (*Microtus brandti*) and rodent community succession in Xilingele-Meng. *Zool Res* **20**: 284–87.

Lima M, Stenseth NC, and Jaksic FM. 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semiarid Chile. *Ecol Let* **5**: 273–84.

Lund M. 1988. Rodent problems in Europe. In: Prakash I (Ed). Rodent pest management. Boca Raton, FL: CRC Press. p 29–33.

Makundi RH, Oguge NO, and Mwanjabe PS. 1999. Rodent pest management in East Africa – an ecological approach. In: Singleton GR, Hinds LA, Leirs H, and Zhang Z (Eds). Ecologically-based management of rodent pests. Canberra, Australia: ACIAR. p 460–76.

Marsh R. 1988. Rodent problems on the North American continent. In: Prakash I (Ed). Rodent pest management. Boca Raton, FL: CRC Press. p 2–11.

Meserve PL and Le Boulengé E. 1987. Population dynamics and ecology of small mammals in the northern Chilean semiarid region. *Fieldiana Zoology New Series* **39**: 413–31.

Mulungu LS, Makundi RH, Leirs H, *et al*. 2003. The rodent density-damage function in maize fields at an early growth stage. In: Singleton GR, Hinds LA, Krebs CJ, and Spratt DM (Eds). Rats, mice and people: rodent biology and management. Canberra, Australia: ACIAR. p 301–03.

Mwanjabe PS. 1998. Final report of rodent control operations for the period of December–June 1998. Internal report. Tanzania: Ministry of Agriculture and Cooperatives, Plant Protection Division.

Mwanjabe PS, Sirima FB, and Lusingu J. 2002. Crop losses due to outbreaks of *Mastomys natalensis* (Smith 1834) Muridae, Rodentia, in the Lindi Region of Tanzania. *Int Biodeterior* **49**: 133–37.

Pech R, Hood G, Singleton G, *et al*. 1999. Models for predicting plagues of house mice (*Mus domesticus*) in Australia. In: Singleton GR, Hinds LA, Leirs H, and Zhang Z (Eds). Ecologically-based management of rodent pests. Canberra, Australia: ACIAR. p 81–112.

Posamentier H. 1997. Communication in national rodent management programmes. *Belg J Zool* **127**: 171–80S.

Prakash I (Ed). 1988. Rodent pest management. Boca Raton, FL: CRC Press.

Redhead TD and Singleton GR. 1988. The PICA strategy for the prevention of losses caused by plagues of *Mus domesticus* in rural Australia. *EPPO Bull* **18**: 237–48.

Rodríguez JE. 1993. Roedores plaga: un problema permanente en América Latina y el Caribe. Santiago, Chile: FAO, Oficina Regional para América Latina y el Caribe.

Ruthenberg H. 1980. Farming systems in the tropics. Oxford: Clarendon Press.

Scott S and Duncan CJ. 2001. Biology of plagues. Cambridge: Cambridge University Press.

Singleton GR. 1997. Integrated management of rodents: a southeast Asian and Australian perspective. *Belg J Zool* **127**: 157–69S.

Singleton GR, Hinds LA, Leirs H, and Zhang Z. 1999a. Ecologically-based rodent management. Canberra, Australia: ACIAR.

Singleton GR, Sudarmaji, Tan TQ, *et al*. 1999b. Physical control of rats in developing countries. In: Singleton GR, Hinds LA, Leirs H, and Zhang Z. (Eds). Ecologically-based management of rodent pests. Canberra, Australia. p 178–98.

Singleton G, Krebs C, Davis S, *et al*. 2001. Reproductive changes in fluctuating house mouse populations in Southeastern Australia. *Proc R Soc Ser B - Bio* **268**: 1741–49.

Singleton GR. 2003. Impacts of rodents on rice production in Asia. IRRI Discussion Paper Series No 45. Los Baños, Philippines: International Rice Research Institute.

Singleton GR, Sudarmaji, and Brown PR. 2003. Comparison of different sizes of physical barriers for controlling the impact of the rice field rat, *Rattus argentiventer*, in rice crops in Indonesia. *Crop Prot* **22**: 7–13.

Skonhoft A, Stenseth NC, Leirs H, *et al*. 2003. The bioeconomics of controlling an African rodent pest species. *Environ Devel Econ*.

Stenseth NC. 1999. Population cycles in voles and lemmings: density-dependence and phase dependence in a stochastic world. *Oikos* **87**: 427–60.

Stenseth NC, Leirs H, Mercelis S, and Mwanjabe P. 2001. Comparing strategies of controlling African pest rodents: an empirically based theoretical study. *J Appl Ecol* **38**: 1020–31.

Stenseth NC, Mysterud A, Ottersen G, *et al*. 2002. Ecological effects of climate fluctuations. *Science* **297**: 1292–96.

Telford SR, Jr. 1989. Population biology of the multimammate rat, Praomys *(Mastomys) natalensis*, at Morogoro, Tanzania, 1981–1985. *B Fla State Mus* **34**: 249–88.

Whisson D. 1996. The effect of two agricultural techniques on populations of the canefield rat (*Rattus sordidus*) in sugarcane crops of north Queensland. *Wildlife Res* **23**: 589–604.

White J, Wilson J, and Horskins K. 1997. The role of adjacent habitats in rodent damage levels in Australian macadamia orchard systems. *Crop Protection* **16**: 727–32.

Zhang Z, Anguo C, Zhendong N, and Xiuqing H. 1999. Rodent pest management in agricultural ecosystems in China. In: Singleton GR, Hinds LA, Leirs H, and Zhang Z. (Eds). Ecologically-based management of rodent pests. Canberra, Australia: ACIAR. p 261–84.

Zhang Z, Pech R, Davis S, *et al*. 2003. Extrinsic and intrinsic factors determine the eruptive dynamics of Brandt's voles (*Microtus brandti*) in Inner Mongolia, China. *Oikos* **100**: 299–310.

Zhong W, Wang M, and Wan X. 1999. Ecological management of Brandt's vole (*Microtus brandti*) in Inner Mongolia, China. In: Singleton GR, Hinds LA, Leirs H, and Zhang Z (Eds). Ecologically-based management of rodent pests. Canberra, Australia: ACIAR. p 199–214.

Table 1. Major agricultural rodent pest problems for food crops in selected regions, their importance as food competitors with people, and methods of control being applied in Africa, Asia, Australia and South America.

Rodents species	Region	Major crop(s)	Estimated damage	Pest status	Main control	Notes
Africa						
Mastomys spp	Sub-Saharan Africa outside central rainforest block	All cereals, groundnut, tubers	Tanzania: 5–15% of harvest annually; outbreaks >80% Nigeria: maize 42%; rice at seedling stage 11% during an outbreak; sorghum 10–90% Senegal: rice >80% during an outbreak Kenya 2.3–75% (mean 11.5%)	Very high	Ad hoc rodenticide	See overview in Fiedler (1988)
Arvicanthis spp	Sub-Saharan Africa Africa south to Zambia	All cereals, groudnut, tubers, vegetables	Same as Mastomys; in areas where both occur, it is difficult to distinguish damage by different species	Very high		
Meriones shawi	Northern Africa	Cereals, vegetables	Morocco: 40–70% losses during outbreaks; Tunisia: 10–50%	Very high during outbreaks		
Tatera spp	Eastern Africa	Cereals, tubers		Low		
Taterillus spp	West Africa, Sahel	Groundnut	Senegal: 10%	Low, high during outbreaks		
Rattus rattus	Madagascar, locally in Africa	Maize, rice				
Thryonomys sp		Rice	Nigeria: rice average 5%	Moderate	Hunting, traps	
Rhabdomys pumilio	Eastern and *southern Africa*	Cereals		Moderate		
Cricetomys gambianus	Sub-Saharan Africa	Cereals, root crops, fruits vegetables cacao		Moderate but locally high	Traps	
Mole rats *(Heterocephalus)* spp, Tachyorctes spp, *Cryptomys spp)*	Eastern and southern Africa	Root crops, enset, Vegetables		Very high	Traps	
Squirrels (*Xerus* spp)	Semi-arid sub-Saharan Africa	Maize, coconut, groundnut	Kenya: 9.7% of planted maize, 5.4% of maize cobs	High		
Porcupines	Sub-Saharan Africa	Maize, coconut groundnut		High		

Continued

Table 1. ***Continued***

Rodents species	Region	Major crop(s)	Estimated damage	Pest status	Main control	Notes
Asia						
Rattus argentiventer *R losea*	Southeast Asia	Rice	Indonesia: 10–20% Malaysia: 2–5% Vietnam: >10% to >500,000 ha Thailand: 6% lowland, 7% upland	Very high	Rodenticide, physical control, fumigation, bounty system	Impacts on rice production see Singleton (2003); grasslands and non-rice cereals in China see Zhong *et al.* (1999) and Zhang *et al.* (1999)
Rattus rattus, *R tanezumi, other Rattus* spp	Southeast Asia	Rice, sorghum, tuber crops	Laos: upland crops 10–15%; up to 100% in outbreak years Cambodia: patchy, no data Philippines: (patchy) 1–10%; up to 40% at district level	High High Moderate	Rodenticide, physical control	
Bandicota bengalensis *B indica, Mus* spp	South Asia	All cereals and tuber crops	India, Bangladesh: 5–10%, some years >50% at district level	Very high	Rodenticide, physical control	
Microtus brandti, *Meriones unguiculatus,* *Mysopalax baileyi*	China	Grasslands	Inner Mongolia: 15–44% Quinghai-Tibet: 370 000 km^2 badly affected	Very high	Rodenticide	
Cricetulus spp, *Microtus* spp *Rattus* spp, *Myospalax fontanieri*	China	All cereals, vegetables,	15 million metric tons (5–10%)	Very high	Rodenticide, physical control	
Australia						
Mus domesticus		All cereals	Outbreaks: 5–30% of harvest at regional level; non-outbreak <2%	Very high	*Ad hoc* rodenticide	Impacts on cereal crops see Caughley *et al.* (1994); impacts on sugar crops (1996); impacts on macademia nuts see White *et al.*
Rattus sordidus		Sugarcane	US$1–2 million annually (2–5%)	Moderate	Rodenticide habitat modification	
Rattus rattus		Macadamia nuts	Up to US$1–2 million annually (30%)	Moderate	Rodenticide	

Table 1. ***Continued***

Rodents species	Region	Major crop(s)	Estimated damage	Pest status	Main control	Notes
South America						
Holochilus spp	Argentina, Brazil, Uruguay Venezuela	Rice, sugarcane, maize	Outbreaks: 20%	High	Rodenticide	See Rodriguez (1993)
Akodon spp	Bolivia, Peru	Cereals, rice, maize, peanuts	Outbreaks: 10–90%	Very high	Rodenticide	
Calomys spp	Argentina, Bolivia	Cereals, maize	Outbreaks: 10–90%	High	Rodenticide	
Oligoryzomys spp, *Phyllotis*	Argentina, Chile, Peru	Fruits, maize, sugarcane	Outbreaks: 12–20%	High	Rodenticide	
Sigmodon spp	Colombia, Venezuela, Peru	Rice, sugarcane, cereals				
Zygodontomys spp	Venezuela, Colombia	Sugarcane, rice				
Europe						
Apodemus spp	Northwest Europe	Cereals, non-cereals		Moderate		See Lund (1998)
Microtus agrestis	Northwest Europe	Forestry, orchards		Low		
Microtus arvalis	Northwest Europe	Horticulture, pastures, cereals during outbreaks		Moderate, high		
Arvicola terrestris	Northwest Europe	Tubers, vegetables, orchards		Moderate		
North America						
Microtus spp	Eastern US	Orchards, vegetables,		High	Rodenticide	See Marsh (1988)
Geomys sp, *Thomomys* sp		Alfalfa, rangelands		High	Rodenticide	
Spermophilus spp	Western US	Forage crops		High	Rodenticide	

Less detailed data is provided for Europe and North America to give a global overview. Other species may be much more important locally as pest species. Regional variation in crop choice and climate may affect a species' relevance as a pest. Damage figures are rarely available and methods of assessment are unstandardized. In most cases, more than one species in a genus are involved in pest problems, but not all species in a genus are necessarily pests. See [supplementary information on Frontiers website] for references and further details.