Influence of predation on rodent populations

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Predation on populations of small rodents is reviewed. Various types of predators are distinguished; specialists, generalists, residents, and "nomadic" species. Their functional and numerical responses to changes in prey density, and their influence on small rodent numbers, are discussed. The shape of the functional response curve of the predators may be important for the dynamics of the predator-prey system. Generalists with access to alternative prey tend to stabilize rodent numbers, as do migrating specialists, whereas resident specialists may be destabilizing. Field studies on cyclic rodent populations point to the importance of predation during and after the decline phase, and indicate that predation may increase the amplitude and prolong the period of the cycles. Other studies indicate a strong influence of predation on rodent numbers in areas with a diversified prey and predator fauna.

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Описано хищничество на популяциях мелких грызунов. Различаются разные типы хищников:специалисты, всеядные, резиденты и »номадические« виды. Обсуждаются их функциональные реакции и колебания численности в зависимости от плотности жертв и влияние на численность мелких грызунов. Форма кривой функциональных реакций хищников может иметь значение для динамики системы хищник-жертва. У всеядных хищников при возможности выбора жертв наблюдается тенденция к стабилизации численности грызунов, как и у мигрирующих специалистов. В то то же время резидентные специалисты дестабилизируют плотность жертв. Полевые исследования цикличности популяций грызунов показывают большое значение хищничества в течение и после фазы снижения плотности; хищничество может увеличивать амплитуду колебаний численности и удлинять циклы. Другие исследования показали сильное влияние хищничества на плотность грызунов на территории с разнобразной фауной хищников и жертв.

1. Introduction

The importance of predation for the population dynamics of rodents has been a source of controversy. Pearson (1966, 1971) and Pitelka (1973) suggested that predation plays an important role in some rodent cycles, and Maher (1970) suggested that it might be a cause of the population cycle of lemmings in northern Alaska. On the other hand Krebs (1964) concluded that predation could not account for the mortality changes during a lemming cycle in northern Canada. This review aims at summarizing data on the influence of different kinds of predators on the dynamics of small rodent populations, with emphasis on microtines. Since many rodent predators have been studied, we shall not attempt to cover the literature, but only present examples of different types of predation, and the results which have been obtained. Examples have disproportionately often been taken from northern Europe, and other representative studies could equally well have been chosen.

2. Functional types of rodent predators

Several functional types of predators may be distinguished depending on their degree of specialization and mobility. The following classification involves simplification, since some predators are intermediates between the categories described below.

2.1. Degree of specialization

Specialists. Some predators, e.g. weasels and owls, are well adapted for hunting and killing rodents, their main prey (Watson 1957, Erlinge et al. 1974a, b, Erlinge 1975). When rodents are abundant, surplus killing occurs (Hagen 1969, Ryszkowski et al. 1973). The abundance of these predators is closely related to the rodent density (Lockie 1955, Erlinge 1974), especially in arctic and subarctic areas, where small rodent populations fluctuate greatly (Pitelka et al. 1955, Thompson 1955a, Hagen 1969, Linkola and Myllymäki 1969, Maher 1970). Such rodent specialists seem largely dependent on rodent prey for successful breeding. They may change to alternative food, e.g. birds and invertebrates, when rodents become scarce (Southern 1954, Erlinge 1975, Andersson 1976), but usually they have restricted ability, and in northern areas little possibility, of catching other prey than rodents.

Generalists exploit a wide range of food items, and feed on small rodents when they are easily available. When rodents become scarce they change to other food. This change might occur at a higher rodent density than in the specialists. In areas with a diversified prey fauna, generalist numbers may be little influenced by variations in rodent density, and they can raise young on nonrodent prey. Such opportunistic rodent predators are foxes (Englund 1965, Ryszkowski et al. 1973), and some mustelids such as marten *Martes martes* (L.), polecat *Mustela putorius* (L.) and badger *Meles meles* (L.). Some birds such as crow *Corvus corone cornix* (L.) (Loman unpubl.) and gulls (Vermeer 1970) feed on small rodents when they are easily available. In boreal areas, the common buzzard *Buteo buteo* (L.) is a migrating generalist, the diet of which usually contains a high proportion of rodents. It might perhaps qualify as rodent specialist, since some pairs refrain from breeding when rodents are scarce. However, even when rodent density is low, some buzzard pairs raise young, using alternative food such as rabbits (Mebs 1964, Sylvén unpubl.). Other migratory generalists which may prey on rodents are gulls, e.g. *Larus glaucescens* (Naum.) (Pitelka et al. 1955), *L. delawarensis* (Ord.) and *L. californicus* (Lawrence) (Vermeer 1970). In areas with little alternative food, generalist numbers may fluctuate with the abundance of rodents, to which their reproduction and survival is related (e.g., Englund 1970).

2.2. Degree of mobility

Resident species such as small mustelids respond to low rodent density by increased movements in search of prey, and are forced to make use of other food than rodents (Erlinge 1975). However, they have restricted ability for long range movements. Some other rodent predators e.g. tawny owl *Strix aluco* (L.) (Southern 1970) usually stay in a definite territory even when rodents are scarce, although they have the capacity for long range movements. Their main habitat is deciduous woodland, where they exploit a variety of prey besides small rodents (Southern 1954, Nilsson unpubl.).

"Nomadic" species. Some avian rodent specialists leave the area without breeding if rodents are scarce, e.g. pomarine skua *Stercorarius pomarinus* (Temm.) (Maher 1970). Snowy owls *Nyctea scandiaca* (L.) sometimes make large-scale southward migrations when rodents are scarce (Gross 1947).

Certain species may return to the same area in subsequent years, and breed if rodent density is sufficiently high, e.g. long-tailed skua *S. longicaudus* (Vieill.) (Andersson 1976). It has been suggested that some "nomadic" species, e.g. short-eared owl *Asio flammeus* (Pont.) and pomarine skua (Pitelka et al. 1955) stay and breed in areas where they encounter dense rodent populations (see Galushin 1974). The degree to which previously breeding adults engage in such movements is poorly known. Perhaps, it mainly applies to young individuals breeding for the first time. Nomadic movements and immigration can lead to a rapid predator increase where rodents are common (Pitelka et al. 1955, Lockie 1955, Linkola and Myllymäki 1969, Mysterud 1970, Galushin 1974).

3. Predator responses to changes in rodent density

Two types of predator responses to changes in the density of a given prey category may be distinguished: a functional response causing a change in the predator's diet, and a numerical response, involving a change in the number of predators (Solomon 1949, Holling 1959). Many rodent predators show a functional response to changes in prey density, i.e. the number of rodents taken per unit time by an individual predator increases with increasing rodent density. This seems particularly important for generalists such as the fox and marten (Ryszkowski et al. 1973). In extreme cases the proportion of rodents in a predator's diet may vary almost from 0 to 100%, e.g. in some gulls (Vermeer 1970).

The functional response curve differs in detail between predators, and is usually not known. The shape might profoundly influence the predator-prey dynamics. For a rodent specialist, the curve is likely to rise rapidly as prey density increases (Fig. 1a). For a generalist it will probably rise more slowly, being S-shaped if the predator forms a "search image" for rodents at high densities (Fig. 1b). A preliminary analysis of a simple predator-prey system using the Rosenzweig-MacArthur graphical method (see Maynard Smith 1974) indicates that the two functional response curves in Fig. 1 under certain conditions might lead to entirely different results, one (the "specialist" curve, Fig. 1a) to oscillations, the other (the "generalist" curve) to a stable coexistence of predator and prey. Although the analysis is crude and unrealistic, it indicates that the shape of the functional response curve can be very important for the behaviour of a predator-prey system.

The numerical response is brought about by changes in natality and mortality, and by immigration/emigration. Due to limited capacity of long distance dispersal in carnivores, especially in small mustelids, their numerical response due to such movements probably is much smaller than in birds. However, some species, e.g. arctic fox, sometimes move considerable distances (Pitelka et al. 1955). On the other hand, high reproductive capacity makes possible a rapid increase of small mustelids. In certain situations two litters per year, and a rapid development to sexual maturity occurs in the weasel *Mustela nivalis* (L.) (Deanesly 1944). Many birds produce larger clutches in response to increased density of rodent prey (Klomp 1970).

Fig. 1. Hypothetical functional response for a specialist (a) and a generalist rodent predator (b). X = rodent density, F(x) = proportion of rodents in the diet. The s-shaped response curve of the generalist might be due e.g. to "search image" formation. c,d: Rosenzweig-MacArthur stability analysis of a simple predator-prey system. Only the shape of the functional response curve differs between the two cases, being given by curve a in case c, and by curve b in d. The dynamic properties may change from oscillations in case *c* to a stable coexistence in case *d*.
The curves in *c* and *d* are based on the following type of equations:
dX/dt = rX(K−X)/K− YaF(X)
dY/dt = −bY + YcF(X)
where X = number of rodents, Y = number of predators, and F(X) = predator functional response. a, b and c are constants. For a discussion of the underlying assumptions, see May (1973).

4. Influence on rodent populations of different types of predators

Results from several field studies point to the importance of predation during and after the decline phase in cyclic populations of small mammals. During the increase and peak phase of the cycle, the impact of predation is usually low. However, the influence on the rodents may vary with the type of predators. The probable influence of some predator categories is described below.

Resident specialists

Weasels are important resident rodent specialists in the northern hemisphere. Since their morphology and hunting technique permits capturing prey in burrows and nests, all rodent age classes and both sexes are subject to predation. Weasels have a high metabolic rate (Scholander et al. 1950, Iversen 1972) due to their long, thin shape (Brown and Lasiewski 1972), and relative to their size they consume much food. Because they have to remain in an area also when rodents become scarce, and because they are efficient hunters, they can probably depress rodent populations to very low numbers (Maher 1967, MacLean et al. 1974). On the other hand, due to limited ability of obtaining alternative prey, especially in northern areas with cyclic rodent populations, they probably suffer high mortality due to starvation
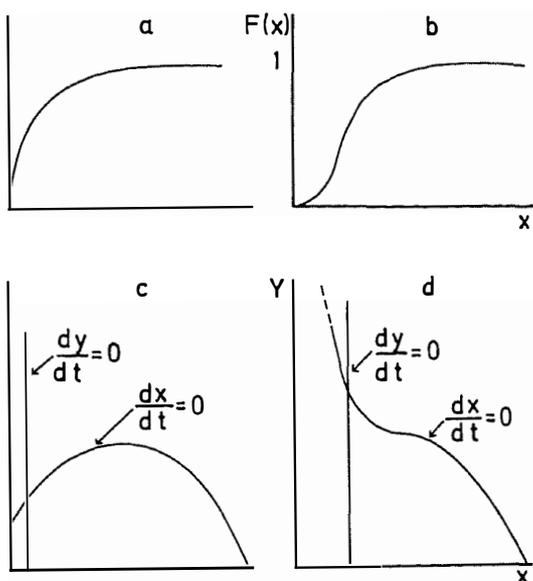
when rodents are scarce, and populations of small mustelids also decrease drastically. When rodents start to recover after a "crash", predation from resident specialists probably is low. Since the population growth usually is slower in predators, they are not able to maintain their numbers relative to the prey population, unless its growth becomes restricted by some other factor than predation.

Partly due to a longer generation time, the increase of resident predators shows a time lag compared with the rodents (Fig. 2). When the prey population for some reason has begun to decrease, the predators may continue increasing in numbers for some time. In areas where little alternative prey is available, the proportion of the rodent population consumed then may increase drastically (Pearson 1966).

Nomadic specialists

When the rodent density decreases after a peak, some avian rodent specialists, e.g. short-eared owls, may disperse from the region (Lockie 1955). Further, such predators often do not breed when rodents are scarce (e.g. Maher 1970, Keith 1973, Andersson 1976). On the other hand, an influx of avian predators has been observed in areas with abundant prey (e.g. Pitelka et al. 1955, Linkola and Myllymäki 1969). The density of nomadic predators therefore might track changes in prey density with a shorter time lag than do populations of resident predators such as weasels.

Most avaian rodent predators are unable to capture rodents in their burrows (but see Maher 1970 for an exception), and mainly catch prey on the ground. This may lead to differential predation on different prey categories. Young juveniles confined to nests are not affected unless the female is captured. Further, since adult males are usually more mobile than females, they probably suffer higher predation (Thompson 1955b, cited in Maher 1970, Møllen 1971). Dispersing and transient individuals without a well-defined home range probably run a higher risk of bird predation (Metzgar 1967).

In northern areas, seasonal immigration of avian rodent specialists may lead to a considerable increase in the predator pressure during summer. On the other hand, this may be counteracted by a variety of alternative prey becoming available to the resident predators, e.g. due to the simultaneous influx of small migratory birds.

Generalists

Foxes, which may take large quantities of rodents (Ryszkowski et al. 1973) can dig up burrows, and therefore may also take less mobile prey categories. Digging is probably even more commonly used by the badger, a resident generalist, but rodents constitute a small part of its diet (Skoog 1970, Göransson unpubl.). Further, it hibernates for up to six months of the year in northern regions. In areas with a diversified fauna, generalist

predators can meet a decrease in rodent density by shifting to alternative prey. Generalist populations ought therefore to be more stable. Coupled to "search image" formation or some other process causing a sigmoidal functional response (Fig. 1b), this might counteract fluctuations in rodent density. Due to a broad food basis, generalist species can be more numerous than specialists in areas with a diversified fauna, or else the generalist predators due to their large body size consume greater amounts of food.

Thus, the total impact by large generalists (such as foxes) on a dense rodent population is greater than by specialists (such as stoats *Mustela erminea* (L.)) (Erlinge unpubl.) at least during the increase phase.

5. Some examples of predation on small mammal populations

Integrated studies, which consider the combined influence of all important predators, are rare. Usually, either avian or mammalian predators were selected for study, and their combined effect was indirectly assessed, if at all. Below, some of the most detailed studies on the influence of predators on rodent populations are summarized.

Lemmus trimucronatus in northern Alaska

Pitelka et al. (1955) and Maher (1970) examined the influence of the major avian predator, pomarine skua, on the population of the brown lemming on the coastal tundra, also considering other predators. Maher concluded that predators might depress a spring population of 25 per acre (62 ha^{-1}), but not of 35 per acre or above. Avian predators truncated peak lemming populations, but could not reduce the lemmings to the low point of the cycle. High predation on reproducing females during the early summer seemed important, and a model of relations between skuas and lemmings (Collier 1972) indicated the marked influence on the lemming density of variations in the number of pomarine skuas.

Thompson (1955a) suggested that continued predation by weasels during winter, when rodents were their only food, reduced the lemmings to very low numbers. MacLean et al. (1974) recorded heavy winter predation by weasels (in 35% of lemming winter nests), and concluded that weasels and birds reduced the lemmings to a very low level in the following summer. Maher (1967) described a lemming population on Banks Island being almost exterminated by stoat predation in winter. Predation is thus an important component of the lemming mortality in some years.

Microtus californicus at Berkeley, California

Pearson (1966, 1971) studied predation by carnivores in a cyclic population of *Microtus californicus*. Predator impact varied greatly, being high at the end of the population crash, and low at the increase phase, partly due to
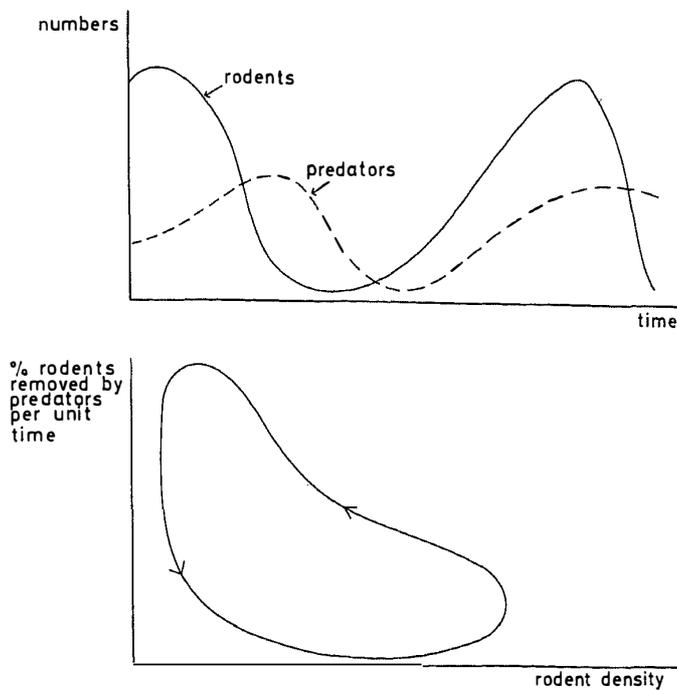
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Fig. 2. Variations in numbers of rodents (solid line) and predators (broken line) during a small rodent cycle (above) and impact of predators at various phases of a rodent cycle (below; both modified after Pearson 1966).

the lag in population growth between predator and prey (Fig. 2). The predators did not prevent the rodent population from increasing, and did not seem to initiate the crash, but apparently further suppressed the population after the decline, and delayed its recovery. Pearson therefore suggested that these predators (including feral cats) enlarged the amplitude of the rodent cycle, and increased the interval between successive population peaks.

Rodent predation in a Polish forest/field area

Ryszkowski et al. (1971) found that the density of forest rodents was markedly depressed during the non-reproductive period every year, but increased in autumn to about 30–40 individuals per ha. Predation pressure was high, especially when the field vole population was low, and was calculated to about 70% of losses in the rodent populations. The common vole *Microtus arvalis* (Pall.) inhabiting field areas was subject to highest predation at low population density (estimated at 47% of the numbers present; Ryszkowski et al. (1973)). When the voles increased and reached mass occurrence, predation was low (9%) in spite of a strong functional response (from about 30 to 80% rodents in the diet) and some numerical response (increased numbers of cats and buzzards) among the predators.

Predation on Microtus agrestis in south Swedish habitats

Predation on small rodent populations (primarily *Microtus agrestis* (L.)) is being examined in the Revinge area, southern Sweden, by the Wildlife Research Group

at Lund University. There is a seasonal variation in *Microtus* numbers, with a moderately high vole density in autumn (50–100 voles per ha) and a decrease to low density at the beginning of the reproductive period in spring (normally 5–10 voles ha^{-1}), but there is no several-year cycle (Hansson unpubl.).

Together with rabbits (*Oryctolagus cuniculus* L.) the small rodents are primary food for many vertebrate predators in the area, including fox *Vulpes vulpes* L., feral cat *Felis domesticus* L., badger, polecat, stoat *Mustela erminea*, weasel, common buzzard, rough-legged buzzard *Buteo lagopus* L., kestrel *Falco tinnunculus* L., long-eared owl *Asia otus* L., tawny owl, and hooded crow. Data on numbers of predators, their food consumption, and the proportion of *Microtus* in their diet form a basis for estimating the impact. Fig. 3 shows preliminary estimates for two months in autumn. The number of *Microtus* at the beginning of the period (October) was estimated at 100000 voles as a maximum, a density of 50–100 ind. ha^{-1} (Hansson pers. comm.). The total number taken by predators during October and November was estimated at about 45000 voles, nearly half the original number. Predation continues throughout autumn and winter although with reduced intensity. Our data indicate that predation is responsible for the reduction in vole numbers during autumn and winter (non-reproductive period).

Common buzzard and feral cat were the most important predators in autumn. Both can be characterized as partially migrating generalists, i.e. some of the buzzards are visitors in the area from autumn to spring (Sylvén unpubl.), and the cats act as migrating predators, switching from domestic subsistence to predation on small rodents in the field at certain times (Liberg unpubl.). The predators next in importance (fox,
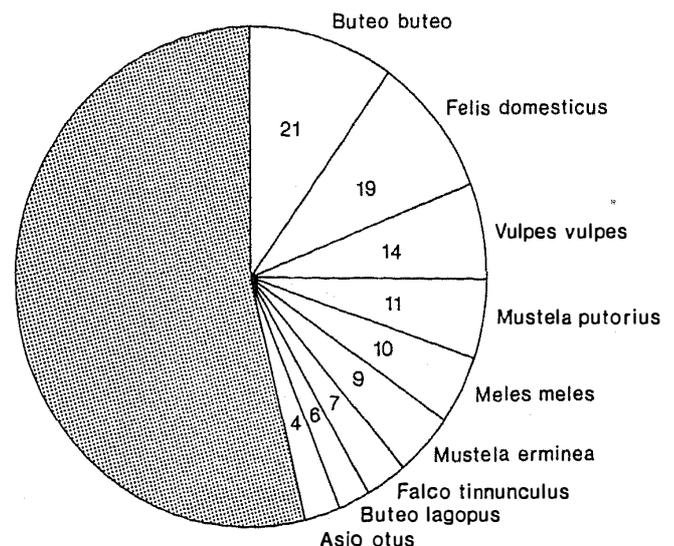

Fig. 3. Estimated impact of predators (% individuals removed) on a *Microtus* population during a two month period (October–November 1976). Dotted area denotes the unexploited part of the population. The figures show the proportion of the total impact due to the various predators.

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polecat, badger) are all stationary generalists. The impact of small rodent specialists (stoat, kestrel, long-eared owl) was lower. This was due to their small size and corresponding low food consumption.

Predation in the Snowshoe hare cycle

The "ten-year cycle" in snowshoe hare is clearly of interest in relation to small rodent population dynamics, since interactions between the hare population and external factors might be similar to those in cyclic small rodents, although involving a longelonger time scale.

The model presented by Keith (1973) after 12 yr of study ascribes an important role to predators during the early low phase of the cycle. At this stage, a high rate of predation depresses hare population density and extends the period of decline (i.e. a similar conclusion as reached by Pearson (1966) for *M. californicus*). However, predators do not seem able to stop the population growth during the increase phase, which is caused by hare-vegetation interactions.

6. Discussion

6.1. Importance of predation

Although opinions differ on the influence of predators on rodent populations, a more general picture is gradually emerging of what is taking place in many predator-rodent systems.

Normally, resident predators seem to be unable to stop the increase of a rodent population. This is usually brought about by increased mortality due to other causes and by decreased reproduction (Krebs 1964, Krebs and Myers 1974). However, there is evidence that predation may reduce the prey population to lower levels than would otherwise occur, and increase the interval between successive peaks (Thompson 1955a, Pearson 1966, Keith 1973, Lidicker 1973, Ryszkowski et al. 1973).

Whether or not predators have a stabilizing effect on rodent populations depends on several factors, such as degree of specialization, mobility, reproductive potential, generation time, and also on the presence of alternative prey. Substantial time lags caused e.g. by the longer generation time in predators than in rodents might have a destabilizing effect, enhancing oscillations (e.g. Maynard Smith 1974). Resident specialists, which keep hunting the few remaining rodents after a decline will probably also have a destabilizing effect (Pearson 1966). However, mobile specialists like birds of prey may leave when rodents become scarce, searching for areas where prey is more common. They may therefore have an opposite influence, truncating peak rodent populations (Maher 1970, Galushin 1974, Collier 1972). Generalist predators with alternative prey may have a stabilizing influence, since they include a considerable proportion of rodents in their diet only when rodents are common, switching to other prey during periods of rodent scarcity.

6.2. Conclusion for modelling predator-rodent interactions

The amount of detail required in a predation model obviously depends on the importance of predation as compared to other rodent mortality factors. If predation plays a minor role, it may be sufficient to model only one important predator, e.g. a resident specialist such as a small mustelid, as this sustains predation during the early part of cyclic lows of the prey population. In northern areas, a migrating or nomadic type of predator might merit consideration. In environments with a diverse fauna, a generalist predator, which survives on other prey when rodents are rare, may be important. For either of these predator types, the rate of predation depends on, among other things, energy requirements, functional response curve, availability of alternative prey, amount of surplus killing, litter size, generation time, and degree of mobility, which may influence the numerical response via immigration or emigration. Obviously, a realistic representation of all these aspects would lead to a very complicated model.

In some systems it may be necessary to treat avian and mammalian rodent predators separately due to their highly different mobilities. At least a crude representation of the availability of alternative prey seems desirable, since it may strongly influence the predator population when rodents are scarce.

Since a predator's energy requirements for maintenance and reproduction will probably greatly influence the number of prey taken per day, it should be given a fairly accurate representation. Surplus killing may also need to be considered. For reasons discussed above, accurate knowledge of the shape of the functional response curve seems essential.

Other features which might profoundly influence the population dynamics of the prey are predator litter size, and magnitude of the time lag of the predator's numerical response to changes in prey density (Maynard Smith 1974). Simple models based on differential equations usually assume that prey ingested are instantaneously converted into new predators. Since such models neglect delay e.g. due to development time, they may be too crude for predator-rodent interactions, which may require use of difference equations (see Maynard Smith 1974).

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