

# Predation and Population Cycles of Small Mammals

## *A reassessment of the predation hypothesis*

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The periodicity of mass occurrence of some northern small rodents has been known from at least the mid-sixteenth century, when Archbishop of Uppsala, Sweden, Olaus Magnus, published two reports on the phenomenon. He suggested that lemming abundances peaked at intervals of approximately three years (Stenseth and Ims 1993a). Elton (1942) initiated research on periodic fluctuations in small mammal populations, and since then such fluctuations have been the focus of much research and controversy in animal ecology.

Cyclic fluctuations of population densities of many northern mammals are characterized by a regular period (the interval between successive density peaks) and a highly variable amplitude (the ratio of maximum to minimum population density). In the boreal zone of North America and some parts of Siberia, the cycle period is usually 9–10 (8–11) years, and the cycle amplitude

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### Progress in understanding the role of predation in small mammal population dynamics will come from manipulative experiments

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15–200-fold. Hares and their mammalian and avian predators show some of the most distinct cycles, averaging nine to ten years in length (Keith 1990, Krebs et al. 1992). In arctic tundra and in central and northern Fennoscandia (Finland, Sweden, and Norway), lemmings and voles often show cycles of three to five years, with cyclic amplitude ranging from 20–500-fold (and usually 50–200-fold). These short-term cycles of small mammals can also be found in some more southern agricultural and grassland areas (Hansson and Henttonen 1985). Population oscillations of herbivores with an intermediate period (six to seven years) may be found at the southern perimeter of short-term and long-term cycles (Keith 1990, Lindén 1988).

Although there are differences between North America and Eurasia in the cycle period and in body sizes of fluctuating herbivores and their predators, there also are some over-

all similarities in the cyclic patterns, including regional synchrony in fluctuations of many coexisting species, wide geographical synchrony of cycles, gradual disappearance of cycles southwards, and summer crashes. Regional synchrony of population cycles occurs, for instance, in several species of herbivorous or omnivorous voles and mice, insectivorous shrews, hares, and grouse in Fennoscandia (Hansson and Henttonen 1988, Lindén 1988), and in snowshoe hares (*Lepus americanus*), arctic ground squirrels (*Spermophilus parryii*), willow ptarmigan (*Lagopus lagopus*), and spruce grouse (*Dendragapus canadensis*) in boreal areas of Canada (Boutin et al. 1995, Keith 1990). In eastern Canada, lemming cycles are synchronous in two species of lemmings over thousands of square kilometers (Krebs 1964). In Fennoscandia, short-term vole cycles are synchronous over hundreds of square kilometers (Kalela 1962) but disappear gradually southwards so that in southern Sweden vole populations fluctuate only seasonally with no marked among-year density differences (Hansson and Henttonen 1988). In Canada and Alaska, snowshoe hare cycles are synchronous over large areas (thousands of square kilometers; Chitty 1950). Snowshoe hare fluctuations occur from the northern Yukon in Canada to southern Wisconsin (40°N).

Cyclic declines of herbivore populations usually continue throughout the summer breeding period (Hansson and Henttonen 1985, Krebs and

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Myers 1974). In snowshoe hares, as in voles and lemmings, declines occur in spite of continuous summer breeding, even when environmental conditions appear to be good for reproduction. In both microtine rodent and snowshoe hare cycles, similar changes in reproductive output, age-related survival, and mean body size in the course of the cycle have been documented (Keith 1990, Krebs and Myers 1974).

What interrupts population growth in northern small mammals? There is no clear distinction between small mammal populations that are cyclic and those that fluctuate irregularly (Hansson and Henttonen 1985, Taitt and Krebs 1985); consequently, we are searching for a general hypothesis that will explain cycles as well as less regular fluctuations. We also search for explanations that will apply equally to short-term cycles (such as the three- to four-year cycles of voles) and to long-term cycles (such as the ten-year cycles of snowshoe hares). The simplest single-factor explanation for population cycles is that predation is both necessary and sufficient to limit population growth in small mammals (see box, this page). Previous reviews of population cycles in small mammals have rejected this model (e.g., Chitty 1960, Krebs and Myers 1974, Taitt and Krebs 1985), but in this article we reconsider it in light of recent studies on field populations. We also suggest further experimental work on these issues.

### Testing the effects of predation

In most cases, the community of small mammals and their predators is not the classic theoretical one predator-one prey system, so most theoretical predator-prey models are unlikely to be very useful for understanding how these systems might work. The impacts of predators are both direct and indirect (Lima and Dill 1990). Direct effects occur by means of mortality, and the key question here is whether mortality from predation adds to total mortality or only substitutes for other causes of death. Indirect effects of predators must be invoked if we are to explain changes in reproductive rates and

## Hypotheses on herbivore cycles

Many hypotheses have been developed to explain the existence of short-term and long-term population cycles (see, for example, Akçakaya 1992, Hansson and Henttonen 1988, Haukioja et al. 1983, Krebs and Myers 1974, Norrdahl 1995 for reviews). A recent review by Stenseth and Ims (1993b) divided these hypotheses into three categories: abiotic (weather and sunspots), biotic intrinsic (genotypic or phenotypic physiological or behavioral changes), and biotic extrinsic (food, predation, parasites, and diseases). Because many of these single-factor hypotheses have failed to explain the patterns involved in the cycles, more complicated multifactorial hypotheses have been introduced (Batzli 1992, Lidicker 1988). For example, with respect to abiotic factors, it is difficult to imagine how irregularly varying weather conditions could drive regular short-term and long-term cycles, or that sunspot activity, which fluctuates in approximately ten-year periods, could result in three- to five-year population cycles of voles.

That populations of herbivorous voles and insectivorous shrews fluctuate synchronously in an area and that populations of the same small mammal species can show cycles of various lengths in different areas, or even be noncyclic in some areas (Hansson and Henttonen 1985), suggest that intrinsic mechanisms alone are not sufficient to generate cycles. If intrinsic processes are necessary for vole cycles, they must operate in conjunction with some biotic extrinsic agents. Biotic intrinsic hypotheses also do not seem to apply to snowshoe hare cycles (Krebs et al. 1992).

Among biotic factors, the food quantity hypothesis has not been supported by supplemental feeding experiments, which have failed to prevent or delay the density decline following a peak density both in cyclic voles and snowshoe hares (e.g., Desy and Batzli 1989, Henttonen et al. 1987, Krebs et al. 1986). Several investigators have not found a close relationship between the quality of food plants and small mammal cycles (e.g., Andersson and Jonasson 1986, Sinclair et al. 1988), but it is still possible that these studies have not analyzed the right chemical compounds (Seldal et al. 1994). There are few field data from parasites and diseases in cyclic herbivore populations, but community-level studies on declining small rodent populations have not found any common pathogens associated with the steep decline phase of many coexisting rodent species (Hansson and Henttonen 1988). Presently, we seem to be left with the hypothesis that herbivore-predator interactions are a necessary driving force in both short-term and long-term small mammal cycles (Hanski et al. 1993, Henttonen et al. 1987, Korpimäki et al. 1991, Krebs et al. 1992). Whether this hypothesis is a sufficient explanation for cycles is an important challenge for the next decade.

growth rates as populations fluctuate. If populations respond to the risk of predation, these indirect effects could be common in small mammals (Hik 1995, Korpimäki et al. 1994, Ylönen 1994).

There are three approaches to test for the direct effects of predation on a small mammal population—the accounting model, the modeling approach, and experimental manipulations.

**The accounting model.** This model is a descriptive approach that determines whether the offtake (prey consumption rate) of predators is equal to the losses of prey. It is based on the mechanistic paradigm of population regulation (Krebs 1995). Plotting predation rates against prey density or productivity to see if the predation mortality is dependent in a direct or delayed fashion on prey density follows the density-depen-

dent paradigm of population regulation (Sinclair 1989). Both mechanistic and density-dependent paradigms assume that predators cause a large fraction of prey losses, if predation is limiting population growth of the prey. The accounting may be done in bioenergetic terms or in numbers of individuals, and in the best cases loss rates may be estimated directly with radio-telemetry (Norrdahl and Korpimäki 1995b, O'Donoghue 1994).

However, there are many problems with the accounting model. Estimating predation offtake is not easy, and accurately estimating prey densities and productivity is even more difficult. This model also assumes that there is no compensatory mortality involved in predation losses. Compensatory mortality occurs when predators kill prey individuals doomed to die in any case, and the remaining individuals in the population are easily able to compensate for predation losses by increasing their productivity (Errington 1963). The prevalence of this "Erringtonian" view on the role of vertebrate predators may explain why the importance of predation in population cycling has been consistently underestimated. If there are other significant sources of mortality in the prey species, predation mortality may not be a large fraction of prey losses, and yet predation could still be a key factor explaining population change (Varley and Gradwell 1960). These problems have been the root cause of much of the controversy over the role of predation in population regulation. Therefore, the accounting model should be used only in preliminary investigations to reveal which predator and prey species dominate the ecosystem. This information is essential for both modeling of predator-prey interactions and manipulating predator densities.

**The modeling approach.** In this approach, models are constructed to predict prey population dynamics, and these predicted dynamics are compared with the prey dynamics observed in the field. These models are usually based on one predator-prey interactions, although in the wild both voles and hares live in

environments with many other prey species and with multiple predators. Therefore, models may give an overly simple picture of natural systems. Multipredator-multiprey situations are harder to model, and even more complications are generated by environmental heterogeneity; for example, prey carrying capacity may vary seasonally and among years, depending on weather conditions. Another problem is the estimation of the model parameter values. Preferably, they should be based on extensive field data (i.e., on the accounting model). Without real knowledge of the parameter values, virtually all kinds of prey population dynamics (stable dynamics, limit cycles, chaos) can be produced by a model (Hanski et al. 1993). However, the key question is what kind of prey dynamics are predicted by parameter values estimated from real field data. Consequently, predator-prey interactions should be modeled only after an accounting model has been developed.

**Experimental manipulations.** In this approach to analyzing the impact of predator numbers on prey dynamics, predator numbers may be reduced by fencing areas or by predator removals. Predator densities may also be increased by introducing individuals into fenced areas, islands, or even unfenced areas. Predator manipulation experiments have many practical problems. Fences are often too small, which may lead to the "fence effect" (Krebs et al. 1973, Ostfeld 1994). Fences and water around islands may prevent the normal dispersal of prey animals. Manipulation and control plots are often established in the best habitats, but the effects of predator density manipulations may be more obvious in marginal habitats. Despite these potential problems, the experimental approach is the only one that is likely to provide unambiguous answers to questions regarding population regulation. Even if the accounting model strongly supports the hypothesis of predator limitation, critics can always claim that these losses are compensatory. Compensatory mortality can be recognized only experimentally, and consequently we are led again to see the

need for manipulative experiments to test these questions.

## Predation and prey population dynamics

To evaluate the role of predation in prey population dynamics, several important classifications have been suggested in the literature. These include whether predators are specialists or generalists, whether they are resident or migratory, whether they respond in a numerical or functional way to fluctuations in prey abundance, whether their effects on prey are rapid or delayed, how their populations are regulated, and whether they have direct or indirect effects on prey.

**Specialist versus generalist predators.** Generalist predators stabilize prey numbers, whereas specialist predators cause fluctuations in numbers (Andersson and Erlinge 1977). Unfortunately, predators in the real world do not break down into two classes but form a continuum. Moreover, some predators change from being specialists to being generalists in a seasonal and regional fashion. For example, great horned owls (*Bubo virginianus*) in the boreal forest of Yukon, Canada, are snowshoe hare specialists in the winter and generalists in the summer (Rohner 1994). Tengmalm's owls (*Aegolius funereus*; known in North America as boreal owls) are generalist predators of small mammals and birds in central Europe, whereas they are vole specialists in northern Fennoscandia, where there is limited availability of alternative prey (Korpimäki 1986). The terms *specialist* and *generalist* should be used carefully; quantitative models, rather than this simple classification, are needed to evaluate predator effects on prey numbers.

**Resident versus nomadic or migratory predators.** According to theory, resident predators destabilize prey numbers if they are specialists but stabilize prey numbers if they are generalists (Andersson and Erlinge 1977). Nomadic or migratory predators aggregate in areas where their main prey is abundant and leave these areas when prey abundance

declines (Korpimäki and Norrdahl 1989b, 1991). Such predators may dampen prey population cycles if their densities track prey densities without an obvious time lag, whereas they may amplify population cycles if their densities track prey densities with a time lag (Korpimäki 1993). However, in natural systems predators do not follow this simple dichotomy but may be resident during the summer and mobile in the winter. In addition, some predators are resident when environmental conditions are stable but become nomadic in temporally fluctuating food conditions. For instance, Tengmalm's owls are resident in central Europe but nomadic in northern Fennoscandia (Korpimäki 1986). In addition, the mobility of rodent-eating birds of prey usually shows age-class differences: juveniles (less than one year old) are nomadic, whereas adults (more than one year old) are resident on their territories (Korpimäki et al. 1987, Rohner 1994). Therefore, long-term data from marked individuals are needed to classify predators on the basis of their mobility.

**Numerical versus functional responses.** Responses of predators to fluctuations in prey abundance may be either numerical or functional. The numerical response is due to changes in natality, mortality, immigration, and emigration (Andersson and Erlinge 1977, Holling 1966), whereas the functional response of the predator measures the prey capture rate as a function of prey density. The ability to respond numerically to fluctuations in prey populations depends on the mobility, reproductive potential, and generation time of the predator. Numerical responses are typically confounded with aggregative responses of highly mobile species, and these responses are difficult to disentangle. Monitoring density changes of the territorial breeding population is straightforward, but it is difficult to estimate the fraction of nonterritorial "floaters," especially for nocturnal predators, leading to severe bias in estimating numerical responses of predators. Resident avian predators are usually strongly territorial, whereas nomadic birds

of prey are only weakly territorial. The proportion of nonterritorial floaters is probably lower in weakly territorial predators (4% in short-eared owls [*Asio flammeus*], long-eared owls [*Asio otus*], and European kestrels [*Falco tinnunculus*]; Korpimäki and Norrdahl 1991) than in strongly territorial predators (40% in great horned owls; Rohner 1994). Study areas for numerical responses of predators should be extensive and should cover both optimal and sub-optimal habitats to avoid underestimating numerical responses. Breeding dispersal of mammalian predators can extend up to 250 km or more (Ward and Krebs 1986), and of avian predators up to 500–600 km (Korpimäki et al. 1987), when small rodent densities crash.

The functional response is crucial for judging the impact of the predator on the prey species. The availability of preferred and alternative prey, the ability to shift to alternative prey, and interspecific competition for food all affect the functional responses of predators (Andersson and Erlinge 1977). The shape of the functional response curve can determine whether predation mortality has a potential to regulate prey populations (Kuno 1987, Murdoch and Oaten 1975). Functional responses of predators are difficult to estimate and present particular statistical problems in attempting to separate nonlinear and linear responses with noisy field data (e.g., Trexler et al. 1988). Traditional methods to identify the diets of predators, like analyses of pellets and scats, include many possible shortcomings, especially in mammalian predators (Korpimäki and Norrdahl 1991, Reid et al. 1995 and references therein). Therefore, it may be better to use radio tracking of predators to determine the numbers of different prey species killed by predators. Predators seem to consume more prey items per capita at high densities of main prey than at low densities (Adamcik et al. 1978). Therefore, the use of fixed prey consumption rates in the calculations of predation rates in the different phases of the prey population cycle may underestimate the functional response of the predator. In multiple predator–multiple prey systems, many factors in addition to main

prey density will influence consumption rates. Estimating a functional response will be only a start to evaluating these factors.

Total responses (numerical and functional responses pooled) of predators may be more important than functional responses only because many predators show wide numerical responses to changing small mammal densities (e.g., Korpimäki and Norrdahl 1989b, 1991, Rohner 1994). Many theoretical papers have explored how the shape of the functional response could be best determined (Kuno 1987, Murdoch and Oaten 1975), but the numerical response and total response of predators to changing prey densities have usually been ignored.

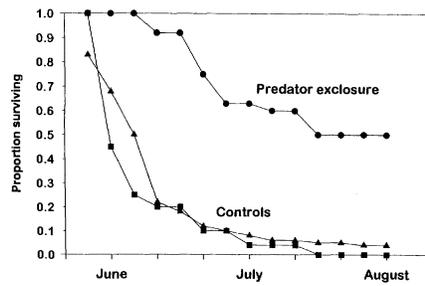
**Rapid versus time-lagged responses.** Time lags are a critical factor determining whether predation promotes prey stability or prey instability. Existing data on time lags are not accurate because they come mainly from studies in which predator densities and diets have been estimated once or twice per year and prey densities twice per year. There is some evidence that responses of resident predators lag well behind changes in vole densities (e.g., Erlinge et al. 1983, Korpimäki et al. 1991), whereas nomadic avian predators respond without time lags to fluctuating vole densities (Korpimäki 1994). Data from prey densities should preferably be collected at the time when predators settle in their breeding territories. In the great horned owl, territorial individuals showed delayed response to the decline of snowshoe hares, whereas nonterritorial floaters soon dispersed from the Yukon study site when hare populations began to decline (Rohner 1995).

**Extrinsic versus intrinsic regulation.** If predator populations are intrinsically self-regulated, for example through territorial behavior, then their ability to regulate prey densities may be compromised. There is some evidence that strong intra- and interspecific territoriality of large resident predators limits their breeding densities (Erlinge et al. 1982), whereas weak territoriality of smaller

nomadic predators allows high breeding densities at peak vole densities (Korpimäki and Norrdahl 1989b, 1991). Because many predators prey on other predators, the amount of intraguild predation may be critical for evaluating the effects of predation on prey numbers (Polis et al. 1989). Among the Fennoscandian predators mainly eating voles, large avian predators shift to alternative prey when the abundance of their main prey crashes. These dietary shifts result in an increase in predation on small mustelids by avian predators, which in turn may reduce densities of small mustelids. Therefore, intraguild predation may considerably lessen the impact of small mustelids on vole populations in the crash phase of the vole cycle (Korpimäki and Norrdahl 1989a).

During the snowshoe hare decline in the boreal forest of Yukon, many predators are killed by other predators (O'Donoghue et al. 1995). Lynx (*Lynx canadensis*) were killed by wolves (*Canis lupus*), wolverines (*Gulo gulo*), and other lynx. Lynx killed red foxes (*Vulpes vulpes*), and great horned owls killed other raptors like goshawks (*Accipiter gentilis*). In the herbivores of the boreal forest, red squirrels (*Tamiasciurus hudsonicus*) and arctic ground squirrels kill snowshoe hare juveniles (O'Donoghue 1994), and on the Canadian tundra arctic ground squirrels kill collared lemmings (*Dicrostonyx groenlandicus*; Boonstra et al. 1990). Intraguild predation produces food-chain linkages that complicate generalizations about stability in food webs.

**Direct versus indirect effects.** Predation has a direct effect on prey survival but may also have indirect effects. Animals may change their foraging behavior under predation risk (Lima and Dill 1990). The mere presence of a mustelid predator (or its scent) may suppress reproduction of voles in the laboratory (Ylönen 1994), although this suppression may also be due to neophobia (Lambin et al. 1995). However, only if these behavioral changes happen in the field can predation risk reduce the reproductive rate of the prey population. If such behavioral changes occur, then the question is whether



**Figure 1.** Survivorship curves for collared lemmings at Pearce Point, Northwest Territory, Canada, in summer 1991. Radio-collared adult lemmings inside the predator exclusion showed much higher survival than those exposed to predators on control areas (data from Reid et al. 1995).

reduced reproductive investment under predation risk is facultative adjustment, or whether it is due to reduced food intake under risky conditions. Laboratory experiments on predation risk are often carried out at unnaturally high densities, and care must be taken to design experiments on predation risk that are realistic.

From these considerations of this section we conclude that progress in understanding the role of predation in small mammal population dynamics will come first from manipulative experiments that include a careful experimental design.

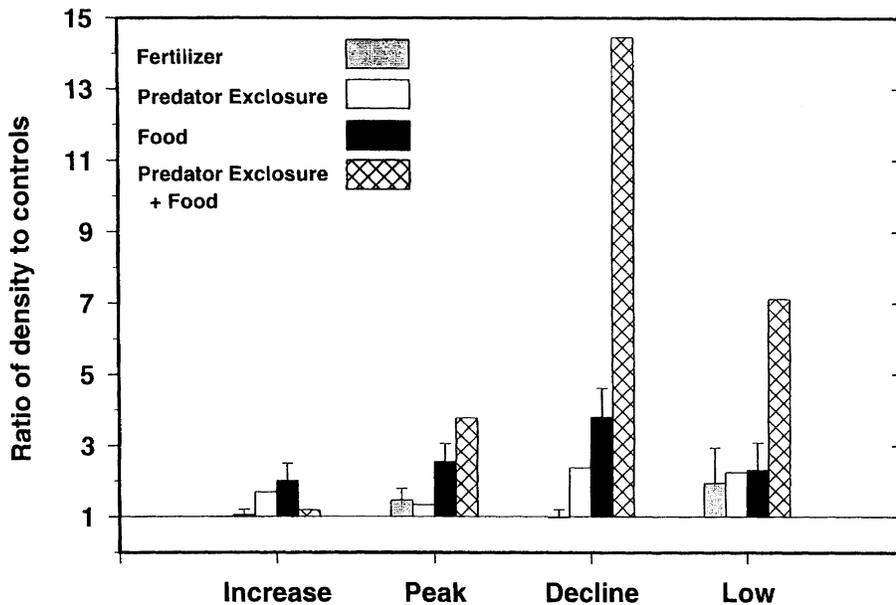
### Predator-prey models

One shortcoming of traditional predator-prey models is the lack of seasonality that is so characteristic at northern latitudes. Hanski et al. (1993) added seasonality (equal six-month summer and winter) to the model of May (1973) and parameterized that model with field data from least weasels (*Mustela nivalis*) and voles (*Microtus* spp.) in western Finland (Korpimäki et al. 1991). The model of Hanski et al. predicted population oscillations of voles that parallel the population cycles observed in long-term data sets in northern Fennoscandia. One weakness of this model was the assumption of sudden changes in parameter values between summer and winter. Hanski and Korpimäki (1995) further developed the model by replacing step functions with smooth functions. This model also produced four- to

five-year population cycles within the observed range of cycle amplitudes observed in voles. The results of these two models are consistent with the hypothesis that vole cycles are driven by delayed density-dependent losses caused by mustelid predators. However, the models tended to predict a cycle period (four to five years) longer than the three-year cycles usually observed in the study area.

There are three existing predator-prey models of the snowshoe hare cycle. Trostel et al. (1987) presented an aggregated predator model of the hare cycle, which showed that the hare cycle could be driven entirely by predation. The crux of this model is the assumption that all of the major hare predators can be combined into one "model predator" that has a specifiable numerical and functional response to changes in hare numbers. This assumption allowed Trostel et al. (1987) to turn a multipredator-multiprey community problem into a classical single predator-single prey system that can be analyzed analytically or with simulation modeling. This aggregation of predators in the model is potentially dangerous, and we do not know if the same conclusions would follow from a more complex model that recognizes the individualistic traits of each predator as well as the possibilities of intraguild predation.

A second model of the lynx-hare cycle (Akçakaya 1992) uses a ratio-dependent predator-prey model, in which the numerical and functional responses are modeled as functions of the ratio of prey-to-predator densities rather than as functions of prey density only (traditional prey-predator models). Parameters of the Akçakaya model give rise to limit cycles when they are changed in the way they are expected to change from south to north, consistent with a latitudinal gradient in cyclicity. This model predicts the cycle period to be around ten years. There are two problems with this model. First, ratio-dependent predation models have been criticized by Abrams (1994) for their biological assumptions. Second, snowshoe hares in North America show no latitudinal gradients in cyclicity. Cycles in snowshoe hares occur across a broad lati-



**Figure 2.** The impact of four treatments on snowshoe hare densities, Kluane Lake, Yukon, 1986–1994, measured by the ratio of population density on manipulated areas to that on control areas at the same time. Manipulations on 1-km<sup>2</sup> blocks were begun during the phase of increase from 1986–1988 and were complete by the peak phase in 1989–1990. The decline occurred in 1991–1993, and the low phase in 1994. The combined treatment of predator exclosure plus food addition had the greatest impact on snowshoe hare numbers (data from Krebs et al. 1995).

tudinal gradient in Canada and Alaska with no evidence of period or amplitude changes from north to south (Keith 1990), although they disappear abruptly at the southern extreme of the snowshoe hare range. Latitudinal gradients in cyclicity from north to south have so far been demonstrated only in Fennoscandia (Hansson and Henttonen 1985).

A third model of the lynx-hare cycle has been presented by Royama (1992). He showed that the snowshoe hare cycle can be described as a second-order process that involves time lags in predator responses and an interaction with winter food supplies, as summarized by Keith (1990). Royama (1992) highlights some problems with his model, particularly with regard to the time lags between predators and prey, but the main use of this model is to show that the interaction model is consistent with the observed data.

### Predator manipulation experiments

One of the first attempts to exclude vole-eating predators from an area was made by Erlinge (1987) in south-

ern Sweden. He constructed a fence (permeable to voles) covering 0.5 ha and followed the population of field voles (*Microtus agrestis*) in this enclosure. Predator exclusion reduced spring decline and mortality rate, resulting in a threefold difference in spring density on the enclosure area compared with the control (Erlinge 1987). Because weasels could enter the fenced area, some mortality also occurred inside the enclosure, and Erlinge (1987) postulated that this weasel effect explained why larger differences were not observed.

Desy and Batzli (1989) used 0.13-ha enclosures to carry out a factorial experiment on the prairie vole (*Microtus ochrogaster*) with manipulations of predation and food supply. They observed a two- to threefold effect on density for both factors over the summer period, and the combined treatment effects were additive. The studies were limited to the growing season, so that longer time effects were not studied. Meserve et al. (1993) were able to exclude predators for more than two years on four plots (0.56-ha each) in central Chile and to measure the effects on populations of a large

caviomorph rodent, the degu (*Octodon degus*). They recorded a two- to threefold increase in density and increased survival rates on the predator enclosure plots.

The collared lemming at Pearce Point in arctic Canada persisted at low density for six years. By fencing an 11-ha area, Reid et al. (1995) tested the hypothesis that predation by generalist predators (red fox) and specialist predators (rough-legged hawk; *Buteo lagopus*) was sufficient to keep lemming densities low. Excluding predators improved survivorship of adult lemmings (Figure 1), but population densities did not increase dramatically because new recruits moved outside the fenced area and were killed by predators as they dispersed. This lemming population seems to be locked into a predator pit by intensive seasonal predation.

Snowshoe hare population cycles in North America seem to be caused by an interaction between food supplies and predation (Keith 1990, Krebs et al. 1992, 1995). To test this model, Krebs and his coworkers built electric fences around two 1-km<sup>2</sup> blocks of boreal forest in the Yukon to exclude mammalian predators. Inside one fenced area they provided commercial rabbit chow as supplemental food. Both predation reduction and food addition increased hare numbers in the range of two- to threefold, but the interactive effect of these two factors was much stronger, approximately 11-fold in the decline and low phase of the cycle (Figure 2). They also tried in these experiments to increase food supplies naturally by fertilizing two blocks of forest. Fertilization had little impact on hare numbers, even though plant growth responded dramatically to the addition of limiting nutrients (mainly nitrogen; John and Turkington 1995). Supplemental food addition by means of adding commercial rabbit chow produced a much larger effect, presumably because of the high quality of this artificial food. The key process in this system seems to be predation, and the food effects are mediated through changes in hare behavior responding to predation risk (Hik 1995).

Islands are convenient for preda-

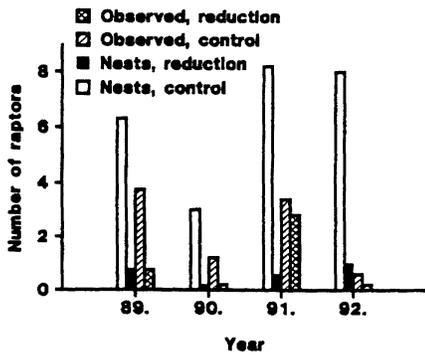


Figure 3. Nest numbers of European kestrels, Tengmalm's owls, and other raptors, and pooled numbers of all vole-eating raptors observed hunting in avian predator reduction and in control areas in western Finland, June 1989–1992. The number of both reduction and control areas (3-km<sup>2</sup> each) was five during 1990–1992 (four in 1989), and the bars give mean per area. The difference in the mean number of raptor territories between reduction and control areas was significant in all years, whereas the difference in the mean number of hunting raptors observed in censuses was significant only in 1989 and 1990 (data from Norrdahl and Korpimäki 1995a).

tor removal studies, but few workers have had the facilities to reduce predator numbers on large islands. Tamarin and colleagues (Tamarin 1978, Tamarin et al. 1987) reported a stable population of beach vole (*Microtus breweri*) on a small Massachusetts island that had no mammalian predators. Tamarin suggested that the stability of the vole population reflected the fact that there was no dispersal sink on the island and that the key action of predation is to remove dispersing voles. Lidicker (1973, 1988) found a similar stability in an island population of California vole (*Microtus californicus*) and suggested a multifactor explanation for stability that involves eight factors, including predation.

Marcström et al. (1989) reduced numbers of red fox and pine marten (*Martes martes*) on two large Swedish islands (23.5 km<sup>2</sup> and 18 km<sup>2</sup>) in the Gulf of Bothnia. They removed predators for five years on one island and then reversed the treatment and removed predators for four years from the second island. Mountain hares (*Lepus timidus*) increased two- to threefold in density when these predators were controlled, and col-

lapsed back again when predator control was relaxed. Marcström et al. (1989) concluded that predation by foxes and marten limited mountain hare numbers on these islands.

Norrdahl and Korpimäki (1995a) studied the effects of removal of breeding nomadic avian predators (mainly European kestrels and Tengmalm's owls) on two *Microtus* voles (*M. agrestis* and *M. epiroticus*) and the bank vole (*Clethrionomys glareolus*) in western Finland. They removed potential breeding sites of raptors from five unfenced farmland areas; control farmland areas had nest boxes in addition to natural cavities and stick-nests. In each of the four years of the study, removal of nest sites resulted in lower breeding densities of raptors in manipulated areas than in control areas. In densities of hunting raptors, however, the difference between reduction and control areas was significant only in 1989–1990 (Figure 3). Raptors may hunt far from their nests, and in 1991–1992 they might have aggregated to manipulation areas. Removal of breeding raptors caused short-term changes in the main prey (*Microtus*) dynamics. No long-term differences in vole densities between manipulated and control areas were found, possibly because weasel densities tend to increase in raptor reduction areas, and increased weasel predation on voles might compensate for decreased avian predation losses.

The geographical synchrony of small rodent cycles could be due to similarity in climatic factors (Sinclair et al. 1993), or due to nomadic predators reducing the patches of high prey density close to the average density of a larger area (Korpimäki and Norrdahl 1989b, Ydenberg 1987). In the five raptor reduction and five control areas, hunting raptors aggregated at high prey density areas in the early breeding season (April) and after their breeding season (August), but not during the late breeding season (June) when they were required to feed their young in the nest (Norrdahl and Korpimäki 1995a, in press). The reduction of breeding raptors increased variation in small rodent density among areas but not within areas (Figure 4). The difference in variation between rap-

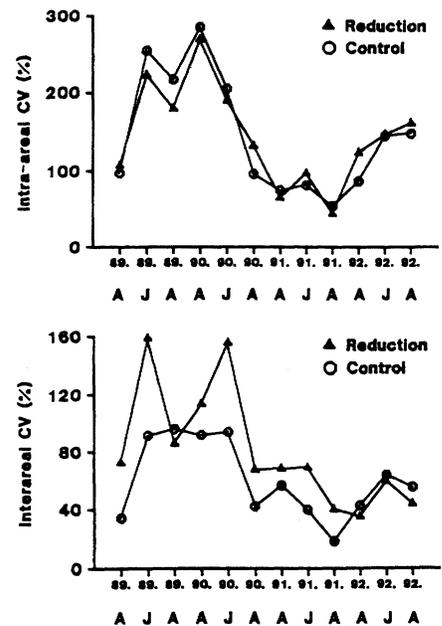
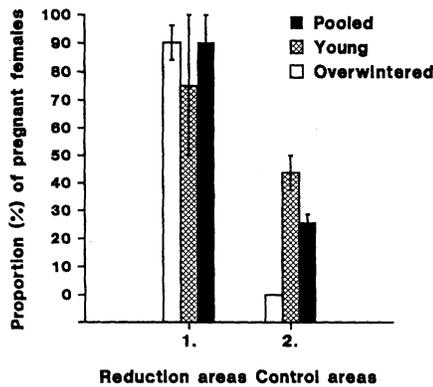


Figure 4. Coefficient of variation (CV, %) of small rodent density within 3-km<sup>2</sup> raptor reduction and control areas (interareal CV) and among these areas (intra-areal CV) in April (A), June (J), and August (A) 1989–1992 in western Finland. Comparisons were made between five reduction–control area pairs in 1990–1992, and between four such pairs in 1989. In 1989–1990, when the number of hunting raptors was higher in control than reduction areas (Figure 3), the interareal variation in small rodent density was also higher in the reduction areas than in the control areas. In 1991–1992, when there was no marked difference in the number of hunting raptors (Figure 3), there was also no obvious difference in the interareal variation in rodent density (data from Norrdahl and Korpimäki 1995a, in press).

tor reduction and control areas was largest in the late breeding season of birds of prey (June), and decreased rapidly after the breeding season (August). These results support the hypothesis that geographical synchrony of small rodent cycles may be caused by nomadic predators aggregating at high prey density areas. Predation and climatic factors apparently are complementary, rather than exclusive, and contribute to the synchrony in herbivore cycles.

The reproductive investment of voles was studied by Korpimäki et al. (1994) in western Finland. In the crash phase of the three-year vole cycle, they removed weasels from



**Figure 5.** Proportion of pregnant females among overwintered and young bank voles trapped in four weasel reduction areas and four comparable control areas (2–4-km<sup>2</sup> each) in June to August 1989 and June to August 1992 in western Finland. The bars give the mean ( $\pm$  standard error) per area (data from Korpimäki et al. 1994).

four unfenced areas in late April and May and studied the reproduction of voles in four weasel reduction and four control areas. Reduction of small mustelids increased the proportion of pregnant bank vole females (Figure 5), but there was no obvious effect of reduction on the proportion of pregnant *Microtus* vole females. Korpimäki and co-workers concluded that predation risk apparently reduced the reproductive investment of free-living bank vole females. Accordingly, the presence of small mustelids (or their scent) may slow the reproductive rate of some species of voles. Because antipredatory behaviors occurred on a large scale, their results provide additional evidence that small mustelid predators may drive crashes in short-term vole cycles. This experiment was the first to show that density manipulation of a terrestrial vertebrate predator in unfenced areas may affect the reproductive investment of vertebrate prey.

## Conclusions

Our understanding of the role of predation in small mammal cycles is increasing rapidly, but there are still large differences of opinion about its effects. We can reduce these differences of opinion by careful studies of predator–prey systems. In this

**Table 1.** Predictions of the predator hypothesis for small mammal fluctuations.

Prediction	Experimental test
Losses due to predation will be density-dependent or delayed density-dependent.	Measure predation mortality in natural populations. Radio-telemetry can often be used to facilitate these measurements.
Delayed density-dependence will lead to fluctuations in prey numbers.	Cyclic prey populations must have predation rates that show delayed density-dependence.
Direct density-dependence will not lead to fluctuations in prey populations.	Noncyclic prey populations should have predation rates that are directly dependent on prey density.
Reduction or increase of predators will change prey population fluctuations.	Prey populations on unfenced areas, within fences, or on islands with few or no predators will not show cyclic dynamics.  Introduction of specialist predators to noncyclic prey populations will induce population cycles.
Manipulated risk of predation will alter the indirect effects of predators on prey dynamics.	Techniques to increase perceived risk will produce large effects on reproduction and growth of prey individuals.  Predator removal will increase reproduction and growth of prey individuals.
Predation mortality is additive rather than compensatory.	Total mortality rate will change proportionately as predation mortality is reduced.

article, we have highlighted five major areas, whose careful study will help us to achieve this goal:

- We need more comprehensive field data relevant to the six central classifications that are made to evaluate the role of predation—specialist versus generalist, resident versus migratory, numerical versus functional responses, rapid versus time-lagged responses, predator self-regulation, and predation risk effects. We have found large gaps in our current knowledge, especially of predator long-distance movements induced by population cycles of small mammals. What is the scale of dispersal, and how can nomadic predators rapidly find areas of food abundance? European kestrels may use the ultraviolet visibility of vole urine and feces (Viitala et al. 1995), but the cues used by other predators remain to be examined. Satellite radio-tracking with small transmitters should help to solve this enigma.

- More effort should be devoted to measuring the time lags between population fluctuations of prey and predator densities, because such lags are critical to our understanding of the stabilizing or destabilizing effects of predation.
- Territoriality, inter- and intraspecific competition, and intraguild predation among predators are poorly understood. Yet these factors can limit the densities of predators in the peak phase of the population cycle and thus also limit predation mortality in small mammal populations.
- The indirect effects of predation are currently controversial and present particular difficulties in evaluation for field populations. Unless predation risk can be measured independently, or its level manipulated in the field, arguments that invoke predation risk as an explanation for changes in reproductive and growth rates of small mammals in the course of the population cycle may be circular, because they

may be based on spurious correlations between factors in declining populations. Crowded laboratory studies tell us little about the predation risk effects in nature. The fact that small mammals usually live in multipredator environments has also been overlooked in studies on predation risk. Different hazards induced by various predators may, at least in theory, either compensate for one another or increase predation mortality via predator facilitation in a complex field situation. (Predator facilitation involves behavior changes in prey animals that decrease the chances of mortality from one predator but make them more vulnerable to a second predator; Charnov et al. 1976.)

● There is a need for multipredator–multiprey models, but their construction may not be easy task. We also need comprehensive field data from the modeled system to make reliable basic assumptions and to use correct parameter values in the model simulations.

What have we learned by manipulating predator populations on two continents and in reviewing the literature? We list the main predictions of the predator hypothesis for small mammal cycles in Table 1 and suggest some critical experimental tests of these predictions. Four issues should be emphasized in testing these predictions. First, in predator manipulation studies the densities of all main predators should be manipulated. If only part of the predator assemblage is included in the manipulation, the remaining predators may have the potential to increase their predation rate, resulting in only minimal treatment effects on prey dynamics. Partial removal of predators may also relax competition and intraguild predation among predators. A better strategy might be to augment predator densities by introducing new predator individuals or species, but vertebrate predators are mobile and easily leave unfenced experimental areas when prey densities decrease to a critical level.

Second, we propose large unfenced predator manipulations on mainland sites. In a majority of fencing experiments, enclosures have been too small (0.1–0.5 ha) in rela-

tion to the home range size of small mammals and especially of their predators. It is difficult to extrapolate the results of small enclosures to field situations, which have unlimited movement possibilities for predators. In addition, it may be impossible to fence voles without preventing their movements in and out of the enclosure and allowing access of least weasels to the enclosures. Care should also be taken when applying the results from manipulation experiments on islands to mainland conditions because prey and predator communities on islands may be less diverse and animals have restricted dispersal possibilities on even large islands.

Third, there is often a lack of sufficient replication in predation manipulation studies (Crawley 1992). Few studies include many replicates, but replicates are necessary if treatment and control areas, rather than animals living on these areas, are to be used as independent observation units in statistical tests.

Fourth, the scale of experiments appears to be small in most studies. Many authors have stressed the importance of scale (e.g., Korpimäki et al. 1994, Lima and Dill 1990), but few have been able to work at the proper scale. The apparent problem of small scale was revealed even in the study of Norrdahl and Korpimäki (1995a), although they used 3-km<sup>2</sup> manipulation areas (Norrdahl and Korpimäki 1995c).

The predator manipulation studies we suggest are time consuming and expensive, and we wonder whether any research council will finance these long-term studies. However, only these kinds of manipulation experiments can serve as a comprehensive test of the predation hypothesis. We would like to underline possible shortcomings of natural “manipulation” experiments that researchers have used to show the effects of predators on prey population cycles, such as a disease-reduced red fox density in Sweden during the late 1970s and 1980s. This “natural” reduction experiment revealed fox predation as a potentially important factor in limiting hare and grouse numbers (Lindström et al. 1994), but the evidence is based on correlative data. In addition, when

fox densities were reduced due to the disease, pine marten densities increased, apparently because of the decreased competition from foxes (Lindström 1989). This increase may also have dampened the effects of predators on prey populations.

Can the predation hypothesis explain both short-term vole cycles and long-term snowshoe hare cycles? The answer is a tentative yes, because this hypothesis has considerable empirical, theoretical, and experimental support. But the answer is tentative, because replicated predator manipulation studies in large unfenced areas are still badly needed, and its predictions need to be tested rigorously. The importance of predation as a regulating factor in small mammal populations in relation to other factors such as food or social behavior needs further experimental research. At the present stage we feel confident in rejecting the “Erringtonian” view of the role of predators in population cycles of small mammals.

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