Vole population dynamics: experiments on predation

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Academic dissertation

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by

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II Sundell, J., Norrdahl, K., Korpimäki, E. & Hanski, I. 2000. Functional response of the least weasel, *Mustela nivalis nivalis*. – Oikos 90: 501-508.

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VI Sundell, J. 2002. Population dynamics of microtine rodents: an experimental test of the predation hypothesis. – Submitted manuscript.

These are referred to by their Roman numerals in the text.

Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

	I	II	III	IV	V	VI
Original idea	IH	IH,EK	JS,JE	JS,KN	JS	JS
Experimental design	-	JS,IH,KN	JS,JE,HY	JS,KN	JS	JS
Data gathering	JS,HH,OH, AK,EK,HP,PS	JS	JS,JE,RT,HY	JS,KN	JS	JS
Analyses	JS,OH,IH	JS	JS,JE	JS,KN	JS	JS
Manuscript preparation	JS	JS	JS	JS	JS	JS

In addition to the authors, my supervisor Ilkka Hanski has contributed in various parts of manuscripts **III-VI**. Naturally, many more people have helped as field assistants and by making helpful comments to the manuscripts. Their contributions are acknowledged in the relevant parts of the thesis.

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Contents

Introduction

Great fluctuations in individual numbers can be considered as a characteristic phenomenon for the northern small mammal populations. Such marked population fluctuations have even been reported in many historical writings (Stenseth and Ims 1993a). The mass occurrences of the Norwegian lemming in particular have gained considerable attention in the reports of naturalists, though periodic multiannual fluctuations are common also in other small mammal species in boreal and arctic environments (e.g. Akçakaya 1992).

Since the early 20th century when Charles Elton (1924) published his classic paper on periodic fluctuations of lemmings and voles, and brought the findings of Collett (1911-12) to the attention of a wider audience (Stenseth and Ims 1993a), the periodic oscillations in the numbers of voles, also called population cycles, have been under intensive scientific studies. The phenomenon of periodic multiannual oscillations has been, and still is, one of the most intriguing features in the field of population ecology, which can be seen in number of review articles published in the past years (e.g. Krebs and Myers 1974, Akçakaya 1992, Batzli 1992, Stenseth and Ims 1993b, Norrdahl 1995, Krebs 1996, Stenseth 1999, Lindström et al. 2001, Turchin and Hanski 2001).

Many different hypotheses have been put forward to explain the puzzling phenomenon of vole cycles. Stenseth and Ims (1993b) have categorised these hypotheses into two main categories: intrinsic and extrinsic factor hypotheses. The extrinsic factor hypotheses were further divided into biotic and abiotic factor hypotheses. In addition, various multifactor hypotheses have been proposed as explanations for cycles (Lidicker 1988). Already in 1992, George Batzli (1992) listed altogether 22 different hypotheses to explain the multiannual periodic fluctuations in small mammal populations. Since Batzli's (1992) review article, many new hypotheses have been proposed and old ones have been modified, and a consensus about the causes of vole cycles is still lacking among population ecologists.

Nature of vole cycles in Fennoscandia

The cyclic vole populations in Fennoscandia have a rather regular cycle period of 3-5 years, and a large cycle amplitude. The length of the dominant (average) period and amplitude decrease from north to south (Hansson and Henttonen 1985, 1988, Henttonen et al. 1985, Hanski et al. 1991). Also, the irregularity of the cycles is thought to increase in the same manner towards lower latitudes (Hansson and Henttonen 1988, Hanski et al. 1991, but see **I**). The regularity of the oscillations disappears gradually southwards, such that already in southern Sweden fluctuations are mainly seasonal (Hansson and Henttonen 1985, Hansson and Henttonen 1988). Hansson and Henttonen (1985) discovered that cyclicity correlated well with latitude, maximum thickness of snow cover and length of the period of snow cover. Exceptions to these findings are e.g. some cyclic microtine rodent populations at the lower latitudes of central Europe, in the relatively uniform agricultural and grassland areas, where biodiversity is generally lower than in other habitats at the same latitudes (Ryszkowski et al. 1973, Mackin-Rogalska and Nabaglo 1990).

In Fennoscandia, sympatric microtine rodent species tend to show synchronous fluctuations despite dissimilarities in their diet, with such interspecific synchrony decreasing from north to south (Henttonen et al. 1984, Henttonen and Hansson 1986). Hares, grouse species and insectivorous shrews also show synchronous fluctuations, at least to some extent, with microtine rodents in many parts of Fennoscandia (Lindén 1981, 1988, Kaikusalo 1982, Angelstam et al. 1984, 1985, Hansson 1984, Henttonen 1985, Kaikusalo and Hanski 1985, Korpimäki 1986, Sonerud 1988, Small et al. 1993). Specialised mustelid vole predators exhibit similar kind of cyclicity, though they usually reach peak density following the peak in the vole populations (Lindén 1988, Korpimäki et al. 1991, Oksanen and Oksanen 1992, Oksanen et al. 1992, Korpimäki 1993). Similarly, the numbers of many vole-eating avian predators fluctuate synchronously with voles (Galushin 1974), and their breeding success is largely dependent on the availability of small mammals (e.g. Newton 1979, Mikkola 1983, Korpimäki 1984, Hörnfeldt et al. 1989, see also **I**)

A conspicuous feature in northern vole dynamics is that the decline in population density usually continues through the best breeding season. Such ‘summer declines’ occur despite continuous reproduction under favourable conditions (Hansson and Henttonen 1985). Moreover, many vole populations reproduce during the winter if the density is low and environmental conditions are otherwise favourable. Winter breeding is especially important for the mass occurrences of the Norwegian lemming (*Lemmus lemmus;* Larsson et al. 1973, Hansson 1984, Kaikusalo and Tast 1984, Krebs 1993).

In cyclic small mammal assemblages in Fennoscandia, the most common and abundant species are the bank vole (*Clethrionomys glareolus*) and the field vole (*Microtus agrestis;* Siivonen and Sulkava 1994). Field voles are common in open habitats, such as fields and forest clear-cuts with plenty of grasses. Field voles are largely folivorous, while the forest-dwelling bank voles are more or less granivorous (Hansson 1983). When the numbers of field voles are low, the bank voles usually move to open habitats (Hansson 1982), otherwise they are competitively excluded by field voles, larger than bank voles. This is in accordance with the rule that the larger species dominate smaller ones in voles (Henttonen et al. 1977, Hansson 1983). In the northern parts of Fennoscandia, other species join the small mammal communities and may replace bank voles and field voles as the most common vole species in many habitats. Species with a northern distribution include the grey-sided vole (*Clethrionomys rufocanus*), the root vole (*Microtus oeconomus*), and the red vole (*Clethrionomys rutilus*). In the northernmost parts and mountain tundra areas of Fennoscandia, the numerically dominant species may be the Norwegian lemming (Siivonen and Sulkava 1994). The water vole (*Arvicola terrestris*), the sibling vole (*Microtus rossiaemeridionalis*) and the wood lemming (*Myopus schisticolor*), as well as different mouse species (Muridae), are only locally and temporally abundant enough to constitute an important part of the rodent communities. The number of rodent species increases from south to north in northern Europe (Henttonen and Hansson 1984), partly due to mixing of southern and northern species in Lapland, but possibly also because the greater amplitude of population oscillations in the north may facilitate the coexistence of competing species (Henttonen and Hansson 1984, Hanski and Henttonen 1996).

Role of predators

Elton (1942) suggested that predation is one of the plausible mechanisms shaping the dynamics of lemmings. Predation as an explanation of vole and lemming cycles did not however gain great popularity, and the intrinsic hypotheses became the main focus of studies especially in North America (Christian 1950, 1978, Chitty 1967), while predators were thought to primarily take the doomed surplus of prey populations, including sick and old individuals, which had already made their contribution to the reproductive output of the population (Errington 1956, 1963). The popular intrinsic hypotheses from the 1950s to the 1970s included the stress hypothesis which stated that rodents in high densities suffer from social stress which lead to increased mortality and suppressed breeding, and consequently decline in population density (e.g. Christian 1950, 1978). Another hypothesis, the so-called Chitty hypothesis, suggested that the population cycles were caused by relative genotypic changes in behaviour and reproduction in vole populations during the cycle (Chitty 1967). Therefore, predation was thought to have only a minor effect on prey populations, and predators were thought, at most, only to deepen and prolong the low phases of the cycle (e.g. Pearson 1966, 1971).

The likely significance of predation in vole cycles was re-evaluated in the late 1970s, when Andersson and Erlinge (1977) published their insightful analysis of different types of predators and of their dissimilar effects on prey populations. The role of predation as a potential factor driving the small mammal cycles has gained increasing attention ever since, and it is nowadays one of the most viable hypotheses to explain vole cycles (Norrdahl 1995, Korpimäki and Krebs 1996, Hanski et al. 2001, Turchin and Hanski 2001; see also following section ‘Viability of predation hypothesis’).

To understand the impact of predators on prey dynamics it is necessary to take into account the differences in certain major categories of predators. Andersson and Erlinge (1977) divided predators into three functional categories: resident generalists, resident specialists and nomadic specialists. This classification is, of course, a simplification, because many predators are in fact intermediate between the categories. In some species, individuals may also change between the categories during their life, and different sexes may have different diet and site tenacity (e.g. Korpimäki 1984). Nonetheless, this classification greatly clarifies the likely differences among predators in their impact on vole populations.

Different predator functional groups have differences in their responses to prey abundance. Nomadic specialists, resident specialists and generalists have different kinds of total responses, which are made up of functional and numerical responses. The numerical response of a predator is a function of natality and mortality, and of emigration and immigration. The nomadic avian predators may react rapidly to changing availability of prey, because of their ability to move long distances (e.g. Galushin 1974, Korpimäki 1985) and to assess the local prey abundance in a short time (Viitala et al. 1995). The numerical response is much slower in resident specialist mammalian predators due to their limited capacity to disperse and limited intrinsic population growth rate (usually one litter per year). Because of their slow numerical response, the numbers of resident specialist predators follow the numbers of their prey with a time lag, which, in theory, tends to have a destabilising effect on predator-prey dynamics (e.g. Maynard Smith 1974). In contrast, numerical response of the resident generalists is expected to be much weaker than in specialists, because the former category may use many other prey species preventing their populations to show deep declines when their main prey, voles, decline. Still recent results have suggested that even the highly mobile avian predators can also react to changing vole density with a time lag (Norrdahl and Korpimäki 2002).

Differences in the functional response of predators also have substantial consequences for predator-prey dynamics. The functional response describes how an individual predator responds to changes in prey density. The exact shape of predators’ functional responses in nature are usually unknown, but specialist predators’ functional response is likely to rise rapidly with increasing prey density (type II functional response, according to Holling 1959). Generalist predators’ functional response is more likely to be S-shaped with low, but accelerating rate of predation at low prey densities (type III, according to Holling 1959). The S-shaped functional response can be generated for example by the generalist predator forming a ‘search image’ for the currently most abundant prey, which leads ‘switches’ between the prey types when their abundances change. Type II functional response, especially if the response is steep, increases tendency towards oscillations, while type III has a stabilising influence on dynamics at low prey density (e. g. May 1973). In contrast to this traditional distinction in the different types of functional responses of generalists and specialists, Oksanen et al. (2001) have suggested that in fact also many generalists exhibit a more like type II functional response.

Specialist predators

Specialist predators can be divided into two functional groups depending on their mobility, resident or nomadic. Nomadic specialists typically have a better ability to move long distances than the resident ones.

In Fennoscandia, a typical true resident vole specialist is the least weasel (*Mustela nivalis nivalis*). It is an effective vole predator because it is capable of entering vole burrows and to eat also the young from the nest (King 1989, but see also **IV**). In winter, the least weasel can hunt voles also under the snow, whereas other predators have difficulties with the thick and hard snow cover (e.g. Lindström and Hörnfeldt 1994). As a highly specialised vole predator, the least weasel can hunt voles when their density is low, and when other more generalised predators have to move for better hunting grounds or to switch to alternative prey species. The stoat (*Mustela erminea*) is bigger than the least weasel, and it has a more generalised diet, but it can be considered as a resident specialist, at least in the northernmost part of Fennoscandia, where the available alternative prey for stoat is more scarce (Erlinge 1975, Erlinge 1981, Korpimäki et al. 1991).

Many avian predators have nomadic habits. They can move long distances to find dense vole populations. Many owl species are specialist vole predators and they tend to disperse widely when the vole populations crash, but some of them stay in their territories despite low density of voles (e.g. Korpimäki 1988). In the latter situations they usually do not breed or they may raise only a few fledglings while preying upon alternative prey.

Birds of prey that have seasonal migration return from their wintering areas to check their old breeding and hunting grounds. If the vole density is low, they may move on to seek for better hunting grounds. The impact of these migratory predators on vole populations is smaller than the impact of non-migratory predators, because the latter will hunt voles also outside the breeding season (Ims and Steen 1990). Non-migratory raptors are also better adapted in hunting voles when the ground is covered by snow. They perch and wait until voles come up on the surface of snow, but they can also hear and take voles under the snow, provided the snow cover is not too hard nor thick.

These two specialist predator types have different effects on vole populations. Resident specialists tend to destabilise predator-prey dynamics, while the nomadic specialists have the opposite effect (e.g. Andersson and Erlinge 1977, but see also Norrdahl and Korpimäki 2002). Generally, the numerical response of resident specialists is relatively slow when the prey density changes. Even if a resident specialist, such as the least weasel, can reproduce remarkably fast [two litters/year and rapid maturation of the young (King 1989, **V)**], it cannot compete in this respect with voles, which can easily ‘escape’ from weasels’ control. Only if some other density-dependent mechanism slows down the reproduction of voles, weasels can catch up with them (Henttonen et al. 1987). Recently, it has been suggested that the density-dependent mechanism that may slow down the growth rate of vole populations is the winter food supply (O. Huitu et al. in prep.). Eventually, when voles become again scarce, weasels suffer high mortality due to starvation and predation. Because weasels are about the size of voles and use the same habitats, they are prone to be predated by other vole-eating predators. Many avian predators use weasels as an alternative prey, when their main prey, voles, is scarce (Korpimäki and Norrdahl 1989a, 1989b). The least weasel is small in size and has no capability to run long distances to seek prey. It has a small elongated body shape that coupled with a high mass-specific metabolic rate and a limited capacity to maintain large energy reserves, imply a very short survival time in the absence of food (Brown and Lasiewski 1972, Gillingham 1984). Collectively these constraints suggest that the numbers of weasels are probably very low when the numbers of voles start to increase again (Andersson and Erlinge 1977).

There is also another possible effect of the resident predators on voles apart from the direct mortality that they cause. According to the breeding suppression hypothesis (Ylönen 1989, Korpimäki et al. 1994 see also Klemola et al. 1998), the simple presence of the predator may affect the reproductive output of the prey. Indeed, breeding females may be more vulnerable to predation than other individuals in the population (Cushing 1984, 1985, Lima and Dill 1990, Magnhagen 1991, Klemola et al. 1997). Females may therefore avoid breeding when predation risk is especially high, because breeding might then lead to higher vulnerability to predation, or females may delay maturation and consequently postpone their breeding because survival of their offspring is likely to be reduced when predation pressure is high (Ylönen and Ronkainen 1994). Delayed maturation and suppressed breeding under predation risk have been observed in laboratory conditions (Ylönen 1989, 1994, Heikkilä et al. 1993, Koskela and Ylönen 1995, Heikkilä 1996, but see also Lambin et al. 1995, Mappes et al. 1998) and has been inferred for the natural populations (Korpimäki et al. 1994, Norrdahl and Korpimäki 1995a). Predator-induced stress has been detected in cyclic hare populations (Hik 1995, Boonstra et al. 1998). Increased predation risk can also lead to decreased activity in voles and consequently lower their food intake, which may cause delay in maturation or reduce reproductive output (Oksanen and Lundberg 1995). In theory, due to such lowered breeding performance of voles under elevated predation risk, weasels can catch up numerically the vole population and potentially cause the crash, deepen and prolong the low phase without other density-dependent mechanisms slowing down the increase of vole populations. In practice, this is however unlikely to happen.

Nomadic avian specialist predators have the ability to respond fast numerically to prey oscillations by moving from one vole population to another depending on their densities. These predators have a stabilising effect on vole dynamics and they have the potential to synchronise vole populations spatially (Korpimäki 1985, Ydenberg 1987, Steen et al. 1990, Korpimäki and Norrdahl 1991a, 1991b, Korpimäki 1994, Steen 1995, Norrdahl and Korpimäki 1996, **I,** but see also Norrdahl and Korpimäki 2002 for another view of the role of avian predators on the stability of dynamics). According to Ydenberg (1987), nomadic avian predators have also the capacity to prolong the low phase of vole dynamics, but modelling work by Ims and Steen (1990) suggests otherwise. In their model, nomadic specialist predators actually shortened the cycle period. The important role of mobile avian predators in synchronising vole populations has also been shown in field experiments (Ims and Andreassen 2000). Heikkilä and his co-workers (1994) hypothesised that the stoat could be the synchronising predator in their study area, in eastern Lapland, at the spatial scale of tens of kilometres.

Generalist predators

The generalist predators are usually bigger in body size than specialists allowing them to hunt a larger range of prey species. Generalists are expected to switch to alternative prey when vole numbers have declined below a certain point. Therefore, the generalist predators act as nomadic specialists and have a stabilising effect on vole dynamics. Generalist predators tend to dampen the population oscillations of their prey (Andersson and Erlinge 1977, Hanski et al. 1991).

Hanski and his co-workers (1991) pointed out that the numbers of generalist predators increase from north to south in Fennoscandia, and they showed, using a mathematical model, that this can explain the observed opposite trend in the amplitude and period of vole oscillations (see also Turchin and Hanski 1997). In southern Sweden, where the vole populations show mainly seasonal fluctuations, the diversity and numbers of generalist predators are high, probably due to more diverse and abundant alternative prey there than in the north. Constantly high predation pressure prevents, according to the predation hypothesis, southern populations to cycle (Erlinge et al. 1984).

The generalist predators are the main force in the alternative prey hypothesis (Angelstam et al. 1984, 1985). According to this hypothesis, generalist predators, which tend to change their diet when the previously most abundant prey decreases below a certain level, cause the decline in the other species that they use as alternative prey. This hypothesis explains why some prey species belonging to different taxonomic groups and having different diet fluctuate synchronously, or with a short time lag, with voles, but this hypothesis does not attempt to explain the ultimate cause(s) of cyclicity.

The predation hypothesis

Observations showing that the numbers of many predators fluctuate synchronously, or with a time lag, with their prey led scientists to ask whether the numbers of predators simply follow the numbers in the prey populations, or whether predators are actually driving the cyclic dynamics of their prey. In many early studies of predators' impact on small rodents (Pearson 1966, 1971, 1985, Maher 1967, Lidicker 1973, MacLean et al. 1974, Fitzgerald 1977, Tapper 1979), predation was thought merely to deepen and prolong the low-density phase of the vole cycle caused by other factors, because the predators were thought to mainly use the 'doomed surplus' of prey population, and hence the losses due to predation were easily compensated by the breeding individuals (Errington 1956, 1963). Following Errington's studies, many papers have been published with contradictory results. Some ecologists still support Errington's ideas about the 'doomed surplus', while others have reported observations of random predation or even disproportionate predation on the breeding stock of the population (Boonstra 1977, Beacham 1979, Halle 1988, Mappes et al. 1993, Norrdahl and Korpimäki 1995a, Koivunen et al. 1996a, 1996b).

Following the full realisation of the existence of different functional groups of predators at the end of the 1970s (Andersson & Erlinge 1977), the impact of predation on small mammal population dynamics has become re-evaluated. New and more informative field observations have provided additional insight to the role of predation in the cyclic vole populations. The most important resident specialist mammalian vole predator, the least weasel, has been observed to have delayed numerical response to its prey (e.g. Korpimäki et al. 1991), which is considered to be essential for cyclic dynamics (May 1973). The main mortality factor in declining vole population has been observed to be predation by small mustelids, and mainly by the least weasel (Norrdahl and Korpimäki 1995b). The diet of the least weasel is now known to be very restricted to small mammals (Korpimäki et al. 1991), a necessary condition for type II functional response of specialist predators. Synchrony in dynamics of sympatric small mammal species that are ecologically quite different (i.e. have different diets) suggests that they share a common predator (Henttonen 1985, Korpimäki 1986).

In addition to these observational studies, further understanding of predation is gained with theoretical models. The basic models of predator-prey interaction were published already in the 1920s (Lotka 1925, Volterra 1926). Since then, these models have been modified and developed by many scientists. Recently, predator-prey models have been used as a tool to investigate vole-predator interactions (Hanski et al. 1991, Akçakaya 1992, Hanski et al. 1993, 2001, Hanski and Korpimäki 1995, Hanski and Henttonen 1996, Turchin and Hanski 1997, 2001, Korpimäki et al. 2002). These models, when parameterised with empirical data, produce similar kinds of dynamics than are observed in nature. The models indicate that predation can give a plausible explanation for the increasing amplitude and period in vole dynamics from south to north (Hanski et al. 1991, Turchin & Hanski 1997), for the increasing relative abundance of *Microtus* towards the end of each cycle, and for increasing diversity of rodents from south to north in northern Europe (Hanski and Henttonen 1996). The models even predict long-term variation in rodent abundance and may explain the apparent disappearance of cyclicity observed in Finnish Lapland in the mid 1980s (Hanski and Henttonen 1996). The large-scale geographical synchrony in Fennoscandia can be explained by predation by nomadic avian predators (Ims and Steen 1990). These observations and modelling studies have produced the current ‘predation hypothesis’, which is not a result of any single study, but can be considered as a result of many research papers published by many authors (e.g. Maher 1967, MacLean et al. 1974, Andersson and Erlinge 1977, Fitzgerald 1977, Hansson 1987, Henttonen 1987, Henttonen et al. 1987, Hansson and Henttonen 1988, Hanski et al. 1991, 1993, Korpimäki et al. 1991, Oksanen and Oksanen 1992, Korpimäki 1993).

In general terms, the predation hypothesis has two components:

1) The multiannual oscillations (= cycles) are due to delayed density-dependent mortality imposed on the small mammal populations by resident specialist predators. The interaction between small mammals and their specialist predators is thus the cause of cyclicity.

2) Generalist mammalian predators and many avian predators have a stabilising effect on small mammal dynamics, which explains the decreasing amplitude and dominant period of small mammal oscillations from north to south in Fennoscandia.

Probably all the authors cited above do not agree with this statement of the hypothesis, and not all of them have considered predation as a main factor in population cycles in their original papers, but nonetheless their work has increased the cumulative evidence supporting the current form of the predation hypothesis. The first part of the hypothesis can also be called the specialist predator hypothesis.

In Fennoscandian predator-prey communities involving the microtine rodents, the keystone species are thought to be the least weasel, a vole specialist, and its main prey species, the field vole (Henttonen 1987). In the northern parts of Fennoscandia, the stoat becomes an important member of the specialist predator guild, and the root vole, the grey-sided vole and the Norwegian lemming join the prey assemblage as numerically important small rodent species. It is worth noting that lemmings, when living in areas of low productivity, are thought to be usually more limited by food than predators (Turchin et al. 2000). Generally, *Microtus* voles are probably more important than other species of small mammals in the vole-mustelid interaction, because they are common and they can reach much higher breeding densities than e.g. *Clethrionomys* species. *Microtus* females have overlapping home ranges, and the young born early in the breeding season tend to stay and breed close to their mother (Myllymäki 1977, Pusenius and Viitala 1993), which allows the build-up of high local densities. Field voles are also larger and clumsier than *Clethrionomys* species, which is thought to make them more vulnerable to weasel predation (Henttonen 1987, Hanski and Henttonen 1996, but see **III**). Among *Clethrionomys* species, the grey-sided vole is an exception. It is biologically more like *Microtus* species, because it can breed in higher densities (Viitala 1977) and it is larger and clumsier than other *Clethrionomys* species. It is also mainly folivorous like *Microtus* species (Hanski and Henttonen 1996). A high density of voles is thought to be essential for successful breeding by weasels. Female weasels have rather small territories (0.2-2 ha; Nyholm 1959, Erlinge 1974, King 1975) when they have young, and their energy requirement is relatively high. Erlinge (1974) estimated that at least 10 reproducing voles/ha are necessary for the breeding female of the common weasel (*Mustela nivalis vulgaris*), and Tapper (1979) did not found breeding below the density of 14 voles/ha (see also **V**).

Outline of the thesis

The aim of this thesis is to study the effects of predation on vole population dynamics. To know more precisely what should be explained, I first described as necessary background the population dynamics of voles at the scale of entire Finland with the help of data on their avian predators (**I**). These vole-eating predators have a strong numerical response to the density of voles (Newton 1979, Mikkola 1983), which response is a product of natality, mortality, immigration and emigration. In the first part of the thesis I have used the breeding performance of avian vole-eating predators as a proxy to study vole dynamics and to detect possible changes in vole dynamics during the recent years.

The least weasel is thought to be the most important predator to shape the northern vole cycles (e.g. Hanski et al. 2001), therefore I have especially focused in studies of the functional (**II**, **III**, **IV**) and numerical responses (**V**) of this species. The functional response is generated by changes in the predation rate of the predator, which is also influenced by the prey selection of the predator. I have studied these aspects of the functional response of the least weasel experimentally in semi-natural conditions with single prey species but dissimilar prey densities (**II**), and with mixed prey species community (**III**) but constant prey density. In the latter experiment, prey preference was studied also in the laboratory. In paper **IV**, I studied prey selection and potential body size-dependent predation within species in a laboratory experiment and with field data gathered during three vole cycles, and proposed an alternative explanation for the Chitty effect. The Chitty effect describes the commonly observed phenomenon of the changing body size of voles in the course of the cycle (Chitty 1952, Boonstra and Krebs 1979).

The contribution that paper **V** makes towards a better understanding of the weasel's numerical response is to provide data on reproduction of weasels in captivity. This kind of information, like any data on reproduction, is largely lacking for weasels, and what data there are concerns the larger, ecologically rather different subspecies of weasels, the common weasel. I manipulated the amount and the quality of food in the onset of the breeding season to test earlier assumptions about the weasel's reproductive biology.

In the final paper (**VI**), which reports the main experiment of this thesis, I tested the predation hypothesis in a field experiment in which weasel's numbers were manipulated on large islands. The numbers of weasels, as a specialist predator, tend to follow the numbers of voles with a time lag (e.g. Korpimäki et al. 1991). In this experiment, I manipulated weasel numbers by adding weasels to experimental populations at a point in time when vole numbers are increasing but weasels are still few in the natural populations. The aim of the experiment was to eliminate the time lag in weasel's numerical response and thereby to prevent voles from increasing and keep their density at a low stable level (Fig. 1).

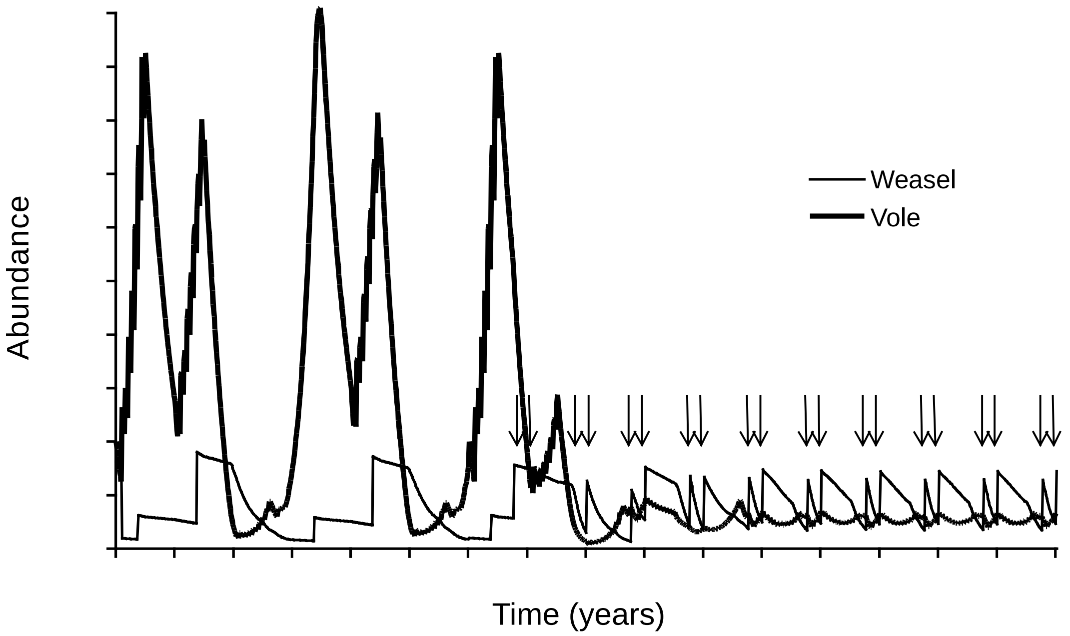

Fig. 1. The idea of the experiment in study **VI** shown as a sample prediction of a stage-structured vole-weasel model (I. Hanski, personal communication). Five weasels are released/km^2 in January and at the end of March (arrows). The thick line represents the vole population density and the thin line the weasel population density.

Material and methods

In this thesis, I have used observational data in papers **I**, **IV**, **V** and to a lesser extent in paper **VI**. Avian predator ringing data and vole trapping data covering most of Finland were analysed in paper **I**, while data for paper **IV** came from the Lapua-Kauhava region (63º N, 23º E) in western Finland. The breeding colony of weasels (**V**) was maintained in the Lammi Biological Station (61º N, 25º E). Experiments were run in the laboratory (**III**, **IV**, **V**) in the Lammi Biological Station and the Konnevesi Research Station (62º N, 26º E), and in semi-natural enclosures (**II**, **III**) in Lapua in western Finland, and in the Konnevesi in central Finland. The large-scale field experiment (**VI**) was done in large islands in Lake Saimaa, Lake Pielinen and Lake Päijänne in central and eastern Finland (Fig. 2).

In the first paper (**I**), the main data used for studying spatial dynamics of voles consisted the number of nestlings of vole-eating avian predators ringed by Finnish amateur and professional ornithologists. These data have been collated by the Finnish Ringing Centre, University of Helsinki, from 1973 to 2000. The avian predator species chosen for this study were Tengmalm's owl, the Ural owl (*Strix uralensis*), the long-eared owl (*Asio otus*), and the rough-legged buzzard (*Buteo lagopus*), all of which are highly dependent on vole density in their breeding performance. The reference trapping data on voles come from various sources and areas in Finland. The data were analysed for cycle length, spatial synchrony, and for possible recent changes in the cyclicity patterns.

The basic designs in the enclosure experiments of papers **II** and **III** were similar. Both studies were conducted in enclosures that prevented voles and weasels from leaving the study area. The sizes of the enclosures were 0.5 and 0.25 ha in Lapua and Konnevesi, respectively. Both enclosures were constructed in old field habitats, but they differed in that enclosures in Lapua were covered with a net to prevent the entry of avian predators while enclosures in Konnevesi were not so covered. In study **II**, sibling voles were released and maintained in the enclosures at different densities. After a few days, one weasel was released in each enclosure.

Fig. 2. Map of the study areas.

The performance of both voles (mortality rate and space use) and weasels (predation rate, activity, hunting success and space use) were observed with the help of radiotelemetry. Experiment **III** was similar to the experiment **II**, with the exception that now the vole density was the same in every enclosure, while the proportions of bank voles and field voles were varied. Activity, predation rate and prey preference of weasels were recorded. In both experiments (**II**, **III**), the vole densities were kept constant during the experiment by replacing dead voles. In addition, prey choice of the least weasel was studied in the laboratory using vole beddings as a prey odour source (**III**). The beddings from vole cages of two species were placed in the end of the arms of Y-shaped tube system. In the experiment, the weasel was allowed to choose between the beddings of the two vole species.

The laboratory experiment in paper **IV** tested the minimum size of holes through which weasels and two species of voles, field voles and sibling voles, can enter. Field data from the Lapua-Kauhava region (Fig. 2) on predation pressure (snow-tracking data) and on vole abundances and weight variation (snap-trapping data) collected during the three vole cycles were used to provide additional support for the ideas arising from the laboratory experiment.

For the needs of the main experiment (**VI**), a large breeding colony of weasels was established at the Lammi Biological Station (**V**; Fig. 2). As a by-product, it provided helpful knowledge on weasels' reproductive biology. With possibility to control environmental factors, further information was obtained on the effects of food availability and quality on weasel reproduction at onset of breeding season.

The main experiment of this thesis (**VI**) was designed to test the predation hypothesis, and it involved manipulation of weasel numbers in three large (5-10 km^2) islands, while three adjacent comparable islands were used as controls (Fig. 2). Vole-eating avian predator ringing data (from the Finnish Ringing Centre) and tracking data on weasel and stoat abundances (from the Finnish Game and Fisheries Institute's Wildlife Triangle Programme) from the areas surrounding the study islands were used as background information on vole population dynamics. The experiment started with monitoring of vole population dynamics in study areas to detect the best time for the start of weasel release (i.e. the early increase phase of the vole cycle). The initial vole population monitoring was done with the small quadrat method (Myllymäki et al. 1971). Later on, when weasel additions had started, live-trapping was used to record the effect of weasel additions to field vole population dynamics. Avian predators were monitored by seeking displaying raptors and owls and their fledglings in the study areas. The abundance of mammalian predators was recorded with snow-tracking and tracking tunnels (King and Edgar 1977). Finally, the grouse abundance was studied by annual censuses with the line transect method, following the census rules of the Wildlife Triangle Programme of the Finnish Game and Fisheries Research Institute (Lindén et al. 1996).

Main results and discussion

Avian predators and large-scale spatial dynamics of voles (I)

Study **I** shows that specialised vole-eating avian predators are highly dependent on vole density for their breeding success. Changes in breeding success are reflected in the number of nestling ringed in any particular area and time and were then used as an indirect measure of vole abundance. The results confirmed the previously documented latitudinal gradient in cycle length based on spatially and temporally more limited vole trapping data (Hansson and Henttonen 1985, 1988). The cycle length increases from southwest to east and to north in Finland. In previous studies, southern Finland has been classified as a semi-cyclic area, where cycles are more irregular than in the north (Hansson and Henttonen 1988, Hanski et al. 1991). In contrast, our results suggest that cyclicity has been more regular in southern Finland than northern Finland in 1973-2000, with the caveat that the present data are relatively scarce for northern Finland. A recent change in cycle length is only evident in northeastern Finnish Lapland, where the cycle length has increased from 4 years in 1973-1986 to 5 years in 1987-2000. However, these analyses cannot detect any very recent changes in cyclicity, such that may have happened in the last five years as indicated by some vole time series (e.g. Henttonen 2001).

Spatial synchrony among vole populations decreased with increasing pairwise distance, but results in **I** nonetheless supported the existence of a very large-scale synchrony, up to several hundred kilometres. The scale in spatial synchrony found here is clearly greater than previously documented in studies of vole populations in Scotland, southern Norway and Japan (Steen et al. 1996, Lambin et al. 1998, Bjørnstad et al. 1999a, MacKinnon et al. 2001). With the present data, it is not possible to detect synchrony at scales smaller than the 50 x 50 km^2 study square. It might well be that vole populations are not in good synchrony at smaller scales in landscape mosaics of open and forest habitats. In the present analysis such possible small-scale asynchrony becomes averaged, and is probably of minor importance for avian predators, which can hunt over large areas. On the other hand, it is clearly not possible to detect large scale synchrony if the study area is small (e.g. Lambin et al. 1998). In general, the possible mechanisms to explain synchronous fluctuations in vole populations are thought to be dispersal of voles themselves, synchronising predation by mobile predators of voles, and spatially correlated climatic factors (Bjørnstad et al. 1999b). Dispersal of voles is likely to synchronise populations at small scales, while highly mobile avian predators and climatic perturbations can operate at much larger scales. Thought is not possible to find out the cause of spatial synchrony by just studying the spatial extent of autocorrelation, such results may suggest that some explanations for the observed patterns are more feasible than some others. Lambin et al. (1998) and MacKinnon et al. (2001) suggested that either the dispersal of voles or the predation by the weasel might cause the observed small-scale synchrony in Scottish field vole populations. Vole populations in Norway were proposed to be synchronised by vole dispersal (Steen et al. 1996) or by avian predators (Ims and Andreassen 2000). In Hokkaido, Japan, the synchronising agent in the populations of grey-sided vole is thought to be predation, while dispersal might be the key process in the populations of Japanese wood mouse (*Apodemus speciosus*; Bjørnstad et al. 1999a). Dispersal of voles can hardly explain the large-scale synchrony documented in **I**, but both avian predators and spatially correlated climatic factors can do it.

Functional response of the mammalian specialist predator, the least weasel (II, III, IV)

I found that the least weasel has a type II functional response typical for specialist predators (**II**; Andersson and Erlinge 1977). The predation rate increased with increasing prey density, and non-breeding weasels tended to kill more voles than they needed just for metabolism. This phenomenon, called surplus killing, is typical for small mustelids (Oksanen 1983). The functional response obtained in this experiment was less steep than previously inferred from field data but using a crude indirect method to construct the functional response (Turchin and Hanski 1997). The functional response was not due to increased activity nor change in space use by the weasel but the better hunting success at higher prey densities. At the same time, the results indicated a higher survival for an individual vole at higher densities, consistent with the type II functional response.

In the following experiment (**III**), weasels were allowed to hunt two vole species in constant density. This experiment clearly showed that although least weasels are specialist predators of small mammals, they are generalists with respect to different species of small mammals, generally killing vole species according to their relative abundances, or even showing predator switching to hunt disproportionately more the more abundant species. Results also suggested that male weasels are more efficient predators than females.

The field vole is thought to be the most important prey species for weasels, and the field vole-least weasel interaction the driving force of cyclic vole dynamics (Henttonen 1987, Hanski and Henttonen 1996). Our results do not necessarily disagree with this argument, even though we found an indication for preference for bank voles by the least weasel. However, our experiment was conducted in a low density situation, whereas what really matters may be the greater degree of spatial aggregation of field voles in comparison with bank voles, especially important for breeding female weasels with small territories during nursing and exceptionally great food requirement. On the other hand, we do not believe that field voles are easier to catch by weasels, even if they are not as agile as bank voles. Outside the breeding season of both voles and weasels, and especially in low and moderate vole densities, the spatial aggregation of field voles is probably not very pronounced, because field voles are then scarce, and/or those (small) aggregations are so sparsely distributed that most weasels cannot find them. I suggest that in the experiment in **III** the higher predation rate on bank vole reflected higher vulnerability of bank voles than field voles, due to the smaller size and less aggressive behaviour of bank voles. Another important factor increasing the vulnerability of bank voles in the experiment was the type of habitat used in our experiment. Because typical habitat for bank voles is forest, and bank voles tend to escape weasels by climbing up trees, the used habitat with only some willow bushes might have prevented bank voles from using their most efficient escaping tactic (Jedrzejewska and Jedrzejewski 1990). Still, the habitat used in the experiment, the old field, is by no means unnatural for bank voles, which are commonly found in meadows and old fields, sometimes in high densities, and especially when field voles are scarce (Hansson 1982). In the laboratory study, no 'intrinsic' preference of weasels for bank voles such as suggested by Pekkarinen and Heikkilä (1997) was found while using only the odours of the species as cues to the weasel.

Weasels can show, like other vole-eating predators, a preference for some particular functional category or size class within the prey species or population (Koivunen et al. 1996a, 1996b). For example, breeding female voles are thought to be more vulnerable to weasel predation than other functional groups in the population (Cushing 1985, Klemola et al. 1997), and avian predators tend to select male voles as prey (e.g. Mappes et al. 1993). Similarly, predators can hunt more some size classes of prey, not because they prefer certain size classes as such, but because certain size classes happen to be easier to catch. Because the least weasel is the world's smallest carnivore, capable of entering the vole burrows and tunnels, it has been suggested that there is no refuge sites for voles from weasel predation (Simms 1979). Nonetheless, we found that voles weighing approximately 20 g can go through smaller holes than even the smallest female least weasel, indicating that the small-sized voles might have refuge sites from weasel predation.

In paper **IV**, we relate the findings about the minimum hole sizes through which voles and weasels can enter to one important phenomenon about vole cycles, the Chitty effect (*sensu* Boonstra and Krebs 1979). The Chitty effect describes the change of average body vole size of voles during the cycle. According to the Chitty effect, voles are larger in the peak phase than in the increase and decline phase (Chitty 1952). The existence of the Chitty effect has been used as a counter argument against the predation hypothesis. In paper **IV**, we demonstrate the occurrence of the Chitty effect in vole populations in the study area in western Finland. We also report how the mean size of voles decreases with the increased predation risk by the least weasel. Predation by the least weasel is known to be the main mortality factor in declining vole populations (Norrdahl and Korpimäki 1995b), and that only one vole out of one hundred voles may survive through the decline phase (Korpimäki et al. 1994), indicating very strong selection pressures on voles during that phase. Based on our own results and the results of other related studies, we hypothesise that the Chitty effect may be a result of body size-dependent predation by the least weasel, and also that increased predation on large vole individuals can be a general explanation of vole size variation also other systems where the least weasel is not the main predator of voles. The explanation is not based so much on the size of the predators, but on the fact that small-sized individuals have more refuge sites than larger individuals. In other words, what really matters is the size distribution of voles and the size distribution of tunnels and burrows they can use as refuges.

There are further observations that support the above hypothesis. In areas that lack a common and effective predator, voles and lemmings are typically observed to be larger in body size than in comparable areas with predators. Yoccoz and Mesnager (1998) explained high survival rates and large body sizes in non-cyclic alpine bank vole populations by the absence or scarcity of weasels. Similarly, Martinsson et al. (1993) observed that bank voles tend to be larger in predator-free island, and Wilson et al. (1999) found larger collared lemmings (*Dicrostonyx groenlandicus*) in their predator exclosures than in areas exposed to predators. Other supporting observations were made by Harper and Batzli (1996); they observed that *Microtus* voles increased burrowing when there were predators around compared to a predator-free situation.

Admittedly, the evidence put forward in paper **IV** to support the body-size dependent predation as a possible explanation of the Chitty effect is indirect and the proposed causality cannot be verified at the moment. Another explanation of the Chitty effect, also caused by predation and not mutually exclusive with the hypothesis of size-selective predation, is reduced foraging activity or foraging in marginal habitats in the presence of predators, which might lead to suppressed growth and consequently smaller body size and obligatory delay in maturation (Oksanen and Lundberg 1995, Norrdahl and Korpimäki 2000). However, more data on the degree of possible size-selective predation by the least weasel, and on the size distribution of holes/burrows/cavities that voles can use as refuge sites would required to critically test the hypothesis put forward in paper **IV**.

If the hypothesis of size-selective predation is correct, it would have interesting implications for the role of delayed breeding in voles and for the evolution of size dimorphism in weasels. For example, the observed critical size of 20 g (**IV**) is approximately the size of voles when they attain sexual maturity (Fig. 3). Maturation and body size in voles are usually linked, because individuals grow more rapidly during maturation than those individuals that stay in the non-breeding state as sub-adults (e.g. Myllymäki 1977). In cyclic populations, a fraction of young voles mature during the summer in which they were born. The proportion of non-breeders is greater in the peak and in the decline phases than in the increase phase (e.g. Kalela 1957, Krebs and Myers 1974). The idea of delayed breeding or breeding suppression as a response to predation risk has been much debated during the past decade (e.g. Ylönen 1989, 1994, Magnhagen 1991, Lambin et al. 1995, Heikkilä 1996, Mappes et al. 1998, more about breeding suppression hypothesis in section 'Specialist predators'). In most of these studies, breeding itself is thought to be risky under increased predation risk. Another explanation proposed for the delay in maturation might be that actually a similar proportion of voles mature independent of the phase of the cycle, but predation is biased towards mature and therefore larger individuals (especially large pregnant females), which would be observed as a smaller proportion of mature individuals when predation pressure is high. It is also possible that the presence of predators induces suppression of maturation, thereby causing a delay in reproduction if small individuals have better chances of survival than larger ones under high predation pressure. Earlier mentioned (see section ‘Specialist predators’) reduced foraging under increased predation risk, and consequent obligatory suppression in maturation and small size, are yet another predation related explanation to account for the small proportion of mature voles in the peak and decline phases (Oksanen and Lundberg 1995, Norrdahl and Korpimäki 2000).

For weasels, the hypothesis of minimum passable hole size leads to an explanation of body size dimorphism in weasels. When their main food, voles, is scarce, there are two possible strategies available for weasels: either to be small enough to effectively hunt the remaining small voles in their burrows, or to be large enough to be able to utilise prey individuals or species that are too dangerous to attack for small weasels. If this is the case, there is an advantage of being either small, like female weasels, or being large, like male weasels. In this perspective, there is no advantage of being a medium-sized weasel.

The existence of refuge sites for voles can contribute to the persistence of voles through the cyclic lows. According to the general theory, the presence of a refuge for prey increases the stability of predator-prey dynamics when a fixed number of prey have a refuge, though this effect is not necessarily strong enough to stabilise otherwise oscillatory dynamics (e.g. Crawley 1992).

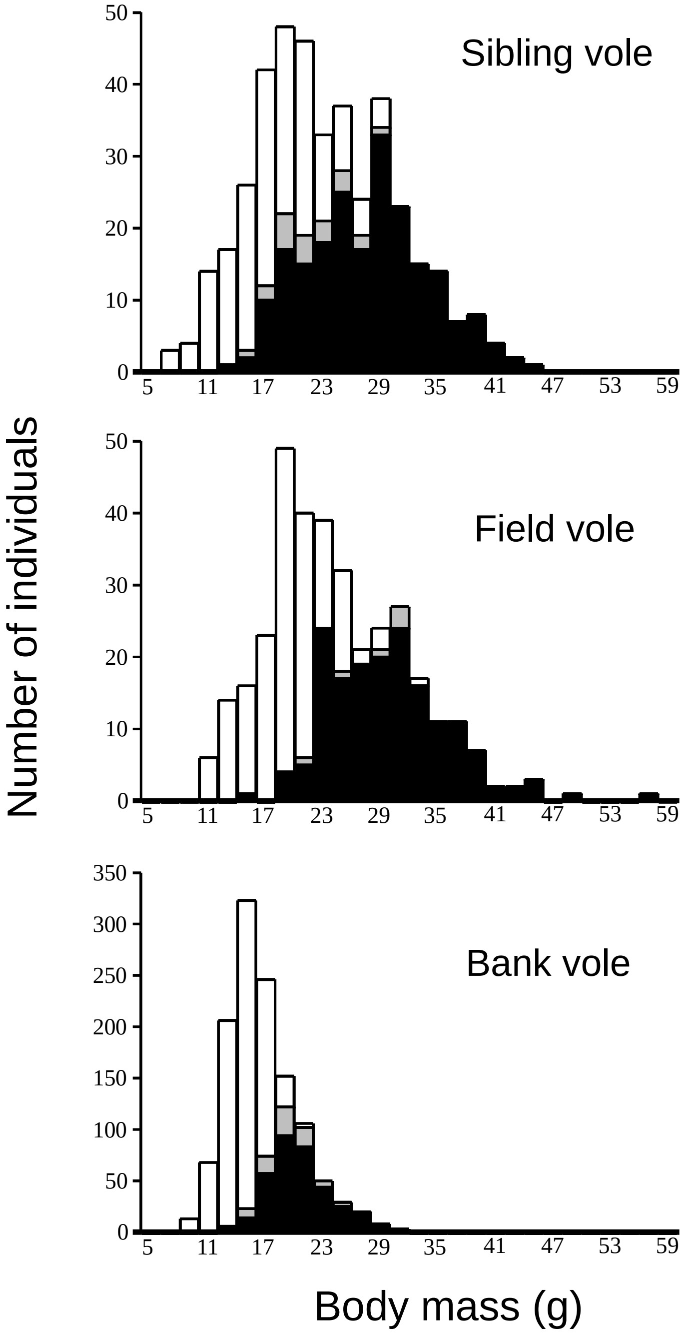

Fig. 3. The maturity and weight distribution in three species of voles (the sibling vole, the field vole and the bank vole) in the autumn. Black bars: mature individuals, grey bars: post-mature individuals, and white bars: immature individuals. Voles were snap-trapped in the Lapua-Kauhava region, western Finland, in 1984-1992 (**IV**).

Numerical response of the least weasel (V)

Weasels as specialist predators are expected to show a delayed numerical response to changes in their prey (Korpimäki et al. 1991). Even if weasels are capable of fast reproduction they cannot keep up with the rate of increase in voles, which leads to the time lag in weasels' response. I observed captive weasels to produce regularly two litters per year, especially if the first litter was born early in the season, or if the first litter died at an early phase of the nursing period. Young weasels are known to be able to reproduce in the year of their birth, but among the 65 litters produced during this study, only one was produced by a young female born earlier in the season. No clear evidence for winter breeding was obtained, even if the breeding season was long, litters being born from March until August. Litter sizes tended to decrease during the breeding season. The mean litter size was 5.1 with equal sex ratio of weaned young.

Manipulation of food quality or quantity for females during the onset of the breeding season did not affect mating frequency, but there was a tendency for smaller litter sizes and lower survival of the young when the females had low quality food or restricted diet during the mating period. These results are not necessarily in disagreement with the previous studies reporting lack of observations of reproduction in weasels when food was scarce (Erlinge 1974, Tapper 1979). But present results indicate that the observed lack of successful reproduction is caused by high mortality of juveniles or embryos, rather than the suppression of breeding itself. In this respect weasels differ from the other main predators of small mammals, owls and raptors, which often skip a breeding opportunity when food availability is low (e.g. Newton 1979, Mikkola 1983).

Experimental test of the predation hypothesis (VI)

The experimental test of the predation hypothesis did not produce any conclusive evidence either for or against the hypothesis. The vole populations in two of the three study areas did not show any effect of experimental weasel augmentation, while there was a treatment effect in one of the areas. In the Lake Pielinen experimental island, the field vole population decreased or remained at the constant level (depending on the method of analysis) during the first year following the start of weasel additions, while the field vole population increased in the control island. Also, the structures of field vole populations were different between the experimental and control islands in Lake Pielinen, the experimental island showing male-biased sex ratio. A possible explanation for such biased sex ratio is a higher predation rate on female than on male field voles (Cushing 1985, Klemola et al. 1997).

The lack of the treatment effect in the other two areas was associated with generally low densities of field voles in these areas compared to the Lake Pielinen study area. Naturally, no effect of increased weasel abundance is likely to be detected if vole populations are constantly at a low level, even in the control areas. The field vole is expected to be the main prey of the least weasel, and therefore any possible effect of weasel augmentation should be first or primarily seen in the field vole dynamics (Henttonen 1987, Hanski and Henttonen 1996), and only later on (if the effect is strong enough) in the dynamics of bank voles.

In the grouse censuses conducted once per year in the study areas, the grouse densities tended to be at a lower level in the experimental islands than in the control islands following weasel additions. The possible effect of weasel additions could be due to increased predation on the grouse chicks. It is possible that captive-born weasels released to the islands actually preferred grouse chicks, because in a captivity considerable part of their diet was chicks. The effect on grouse numbers was greatest in the Lake Päijänne study area, where more weasels were released than in the other two study areas.

The interpretation of the results of this experiment was further complicated by the irregular dynamics of voles in the study areas during this study. The formerly regular 3 yr or 3-4 yr vole cycles as revealed by owl ringing data and mustelid tracking indices for the nearby areas, turned to something much irregular during this study, making it difficult to determine the best possible time for the start of supplementary weasel introductions.

Moreover, the constantly low densities in some of the study areas prevented the detection of any change cause by the introduction of weasels. The results suggest that the irregular dynamics are not a local phenomenon, but are possibly connected to increased irregularity of vole population dynamics over larger areas (e.g. Hansson 1999, Henttonen 2001; see also **I**). In the case of Lake Saimaa, however, the obvious lack of regular cycle was probably due to the presence of large numbers of generalist predators, mainly domestic cats, in the study area. High density of generalist predators is expected to dampen the population fluctuations of voles (Hansson 1988, Hanski et al. 1991). I radio-tracked field voles and sibling voles in the control and experimental islands in Lake Saimaa and found that the mortality of voles in both islands was high. During the 22 days of tracking in September-October in 1997, 9 out of 20 and 11 out of 17 voles were killed by predators in the experimental and control islands, respectively. The main mortality factor found to be predation by avian predators, followed by mortality caused by the least weasel. Voles that disappeared completely (7) were considered to have been killed and taken away by avian predators or large mammalian predators (e.g. cats, foxes, and raccoon dogs). Because no voles with malfunctioning radio-transmitters were found in extensive trappings, I excluded the possibility of broken radio-transmitters, and because voles could not be located within ca. 0.5-1 km radius from the point of last fix, I practically ruled out the possibility of dispersal as a cause of disappearance

Another factor that made the interpretation of the experimental results difficult was the surprisingly high mortality of released weasels: only 56% of seventeen radio-tracked released weasels survived during the radio-tracking period (P. Hellstedt, unpublished; maximum duration of tracking was 25 days). Regardless of the reasons for such high mortality rates, whether they are due to the captive-born origin of weasels or naturally high mortality of young inexperienced weasels, the high mortality reduced the treatment effect in the experimental populations. Additionally, the general difficulty of estimating weasel density further complicates the evaluation of the results. Reliable estimates of natural weasel densities are largely lacking in the literature, and the ones that exist vary greatly.

Experiments on the role of predation in vole population dynamics

Even if vole population dynamics have been extensively studied, experiments on the impact of predation on vole populations have not been frequently reported. Sih and his co-workers (1985) have reviewed the general literature about predation experiments. They searched experimental studies on predation in seven high-quality scientific journals in the years 1965-1984. None of 139 studies used mammals as a prey, while the number of all predator manipulation experiments had increased in a sigmoid fashion during the 20-year period. Since the review of Sih et al. (1985), several experiments on predation involving small mammals have been completed. Nonetheless, Korpimäki and Krebs (1996) expressed their concern of lack of experiments on the role of predation in vole population dynamics. At the moment, the situation has improved and several competent experiments have been completed (Appendix).

Experimental studies involving mammals at the population level are subject to many difficulties. Experiments need to be carried out at a relatively large spatial scale, even if experiments are concerned with small mammals. Also, most interesting small mammal populations cycle, and the cycle length is at least three years long, requiring a long-term experiments. Because of these logistic difficulties, conducting proper experiments on the effects of predation on small mammal population dynamics is a matter of ample resources and plenty of hard work. Thorough and reliable experiments are thus rare, not because of a lacking interest, but because of the massive efforts required. Also noteworthy, some of the large-scale experiments in Appendix were actually done for other reasons than to test any specific hypothesis about predation (e.g. van Wijngaarden and Bruijins 1961, Kildemoes 1985, Steen et al. 1990).

Unfortunately, most experimental tests of the effect of predation on small mammal populations have lacked some crucial elements. In many cases, there were neither proper controls nor enough replicates. In case where those requirements were met, the temporal or spatial scales were typically too small to make the experiment truly relevant for the dynamics of natural populations (Appendix). In other cases, the experimental design allowed some unwanted predators to enter the experimental area, or the impact of some predators was ignored. In enclosure experiments where the prey is prevented from dispersing, one should consider the role of the ‘fence-effect’, which might lead to abnormally high small mammal densities (Krebs et al. 1969, see also Ostfeld 1994) that could mask the possible effect of predator exclusion.

In theory, one way to conduct an experiment on the role of predation in vole population dynamics at the population level is to manipulate prey abundance in large unenclosed areas. But in the case of voles, the number of animals would be so large that such manipulation would not be possible at a sufficiently large scale. A more plausible option is to manipulate the numbers of predators. Predator manipulation experiments can be categorised into three classes: removal, exclusion and introduction experiments. In the following, I will review the existing experiments of these three different types. The experiments are summarised in the Appendix.

Removal experiments

In removal experiments, all predators or some groups of predators are removed from unfenced areas. Complete removal of predators is usually difficult and hence only a reduction of predator numbers can be achieved in practice.

A large-scale removal experiment was conducted on two large islands (18.0 and 23.5 km^2) in the northern Baltic Sea by Marcström et al. (1988, 1989). The original idea was to study the alternative prey hypothesis by reducing the numbers of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). From 1976 to 1980, foxes and martens were killed in one island and from 1980 to 1984 on another one. The numbers of tetraonids, arctic hares (*Lepus timidus*) and voles were monitored during the 9-year study, which lasted for two 4-year population cycles for voles. Both the numbers of tetraonids and hares increased during the experimental reduction of predators. There was no significant effect on vole numbers, which was to be expected, because the red fox and the marten are generalist predators (see section ‘Role of predators’).

In the beginning of last century a massive countrywide predator extermination program was started in Norway. The government of Norway paid a bounty to hunters for all medium-sized mammalian predators, owls and raptors. Bounty program and propaganda against all predators led to a large-scale reduction in the numbers of these predators. Steen et al. (1990) reported the apparent consequences of this ‘unplanned experiment’ influencing small mammal populations. They observed loss of cyclicity for approximately 20 years, in addition to the loss of large-scale regional synchrony in voles and lemmings (see also Högstedt et al. 1991 for an alternative explanation).

Erkki Korpimäki and his research group have done a series of experiments in western Finland, where they have reduced densities of small mustelids and/or breeding avian predators in 3-5 (2-4 km^2) experimental plots (Norrdahl and Korpimäki 1995c, 1996, Klemola et al. 1997, Korpimäki and Norrdahl 1998, Korpimäki et al. 2002). The main conclusion drawn from these experiments was that reduction of both predator types had some marked effects on vole population dynamics in all phases of vole cycle. Their results also suggested that the regional synchrony in small mammal cycles is driven by nomadic avian predators (Norrdahl and Korpimäki 1996), and that the presence of mustelid predators slowed down population growth of *Microtus* voles (Klemola et al. 1997).

In Scotland, where the field vole exhibits 3-4 yr cycle in abundance (Lambin et al. 2000), Graham (2001) conducted an experiment in which she reduced the numbers of common weasels in three 5-12 ha clear-cuts in order to test the specialist predator hypothesis. She concluded that weasels do not drive the field vole population cycle in her study area, as there was no delay in weasels' numerical response. Graham (2001) also concluded that even if the removal of weasels did not change the population dynamics of field voles, removal increased adult survival but reduced juvenile survival.

Exclusion experiments

Many of the population-level experiments on predation have been conducted using exclosures. A typical exclosure experiment involves a pen to keep the potential prey species inside and the various predators outside. During the experiment, changes in population size and demography are recorded and compared with a control population.

Predation, food and cover were manipulated in declining populations of *Microtus towsendii* in Vancouver, Canada (Taitt et al. 1981, Taitt and Krebs 1983). Unfenced populations with increased cover had higher survival than populations with less cover. The addition of cover and netting reduced predation by the great blue heron (*Ardea herodias*). Taitt and Krebs (1983) concluded that the start of the spring decline was a result of predation, while the latter part of the decline was due to density-dependent dispersal.

Erlinge (1987) conducted a study in southern Sweden, where the vole populations are generally non-cyclic. This study was conducted in one 0.5 ha exclosure, which was permeable to voles and weasels. Weasels killed some individuals in the experimental population, despite continuous removal trapping. Results confirmed Erlinge's and his co-workers' (1984) earlier observations that predation was the primary cause of the spring decline in field vole populations.

Desy with her colleagues (Desy and Batzli 1989, Desy et al. 1990) manipulated both food and predation in their experiment on populations of the prairie vole (*Microtus ochrocaster*) in Illinois, USA. They used eight 0.13 ha pens. Predator exclusion significantly increased adult survival, recruitment and density of voles. Predator exclusion and supplemental food increased vole density more than did predator exclusion alone.

Ylönen et al. (1991) conducted an experiment in which they excluded all avian predators from two 0.5 ha pens in central Finland and tried to keep small mustelids away by trapping for eight months. They did not find any effect of this manipulation on bank vole populations, which they attributed to the great abundance of voles outside the exclosures. The study was done in a peak year of the vole cycle.

Reid and co-workers (1995) fenced a non-cyclic collared lemming (*Dicrostonyx kilangmiutak*) population in Canada. They had one 11.4 ha exclosure, which excluded avian predators, and large and medium-sized mammals, but allowed lemmigs and other small mammals to move freely. Predatory ground squirrels and stoats were removed from the exclosure by continuous trapping in summer. Predation was the most important mortality factor in the surrounding control populations, and population density remained higher in the exclosure than outside. Also in Canada, Wilson et al. (1999) studied cyclic collared lemmings (*Dicrostonyx groenlandicus*) following a similar experimental design as Reid et al. (1995)

during the peak and decline years of lemmings. They found predation to be the main mortality factor during three summers, but the survival of lemmings was significantly higher in the exclosure only during the population decline. They concluded that predation was necessary to limit the population during the peak and decline summers, and that predation extended the duration of decline.

Lin and Batzli (1995) performed an experiment, in which they manipulated fenced populations of the prairie vole in order to let different groups of predators to enter six different types of 0.01 ha exclosures in Illinois, USA. Larger carnivores were the most important predator group, and the study supported the notion that resident generalist predators respond quickly to an increase in the density of voles and may prolong the low density phase in vole dynamics.

Carlsen (1999) set up an experiment in which he manipulated predation in eight clearings (0.6-1 ha) in Denmark. Four of the study plots were covered with a net to prevent avian predators and, to some extent, medium size mammalian predators from entering the area, while four plots had nest boxes and perches to increase the presence of avian predators. Results showed increased survival of field voles in predator exclosures in winter and consequently higher population density. Attraction of avian predators did not have significant effect.

Klemola et al. (2000) conducted an experiment in western Finland in which they had four 1-ha exclosures that prevented entry by mammalian and avian predators. Predator exclusion induced rapid population growth of *Microtus* voles, after which their numbers crashed due to food shortage. Klemola et al. (2000) concluded that predation prevented the increase in the surrounding vole populations and is the cause of the low phase of the vole cycle. Furthermore, they concluded that population cycles of voles are not driven by plant-herbivore interactions based on the results of a follow-up experiment. O. Huitu et al. (unpublished manuscript) have run an experiment in the same exclosures, in which predators were excluded and voles were fed during the winter. Their results indicate that vole populations that succeeded in escaping from predators' control are mainly limited by winter food supply.

Introduction experiments

In introduction experiments, predators are introduced in the study area in order to influence prey population dynamics. Often introduction areas are unfenced, but introductions onto islands that are to some extent isolated by water are relatively common.

Oksanen and Oksanen (1981, see also Oksanen 1983) introduced one male least weasel onto a 13-ha island in northern Norway. Grey-sided voles had been released on the experimental island and on two smaller control islets in the previous year. Oksanen and Oksanen (1981) studied vole populations for three weeks after the release of the weasel, and they found that the experimental population declined by 43%, whereas the control populations increased by 97%. They concluded that weasel predation was the cause of this difference in survival rate, because there were only a few observations of other predators in the islands during the study period. They also inferred considerable surplus killing by the weasel.

In 1931, 102 weasels and 9 stoats were released on the Terschelling island in the Netherlands to control water voles in forest plantations (van Wijngaarden and Bruijins 1961, King and Moors 1979). Weasels disappeared within three years, but stoats, despite their low initial numbers, increased greatly and they drove the water vole population to extinction within five years, and reduced the population of rabbits (*Oryctolagus cuniculus*) to a low level. During shortage of the favoured food, stoats turned to alternative prey, making considerable damage to the local bird populations. Kildemoes (1985) reported on a similar case, where six male stoats were released to a Danish island of 46 ha in order to control the water vole. The stoats were successful in their job, and the first effects of stoats on the vole populations were seen in a few months. Sullivan and Sullivan (1980) attempted to use stoats as a control agent of Oregon voles (*Microtus oregoni*) and deer mice (*Peromyscus maniculatus*) in forest plantations in British Columbia, Canada. They introduced seven stoats into a 1 ha study plot, within which the Oregon vole and deer mouse populations were monitored during one year. Stoats were released into middle of the study plot in three occasions during one month in the autumn. No significant effect was observed between the experimental and control populations of rodents. However, the deer mouse population in the experimental plot started to decline two weeks before the control population, and the vole population in experimental plot failed to recover after the decline. Failure to obtain significant result was probably caused by high density of stoats in the study areas. As expected, stoats moved out from the small experimental plot quickly and two of them returned the same area where they had been originally captured (0.87 and 3.75 km from experimental plot).

The effects of adder (*Vipera berus*) predation on field vole populations was studied in six small islands (1-12 ha) in the Baltic. Lindell and Forsman (1996) experimentally manipulated the density of adders on four islands. Two islands were used as controls. The vole density was lowest on an island with experimentally increased adder population. In the control island the density was intermediate, whereas islands with the lowest adder density displayed the highest vole density. The differences were statistically non-significant, probably because the vole densities happened to greatly decline just before the experiment and remained at a low level during the entire experiment.

Lomolino (1984) studied the effects of a predatory shrew, the short-tailed shrew (*Blarina brevicauda*), on meadow vole (*Microtus pennsylvanicus*) populations in the Thousand Islands Region, USA. He introduced the short-tailed shrew on three islands (0.13-0.43 ha) occupied by meadow voles. The short-tailed shrew had a negative effect on vole densities. Populations of meadow voles declined or failed to increase until shrews became extinct. The impact of the predator was primarily caused by short-tailed shrew predation on juvenile voles. Lomolino (1984) concluded that short-tailed shrew predation was the main reason for the absence of meadow voles in some islands.

Viability of the predation hypothesis

Most of the studies reviewed and summarised in Appendix show that predation does have an effect on the dynamics of voles. In cases were no significant effect was found, the authors usually have an explanation for this (Ylönen et al. 1991, Lindell and Forsman 1996), or the reasons were obvious when the experimental design was critically examined. For example, in the experiment of Sullivan and Sullivan (1980), lack of significant treatment effect was obviously caused by rapid dispersal of introduced stoats from the very small study areas. The removal study of Marcström et al. (1988, 1989) showed no effect on vole population dynamics because only the generalist predator numbers were reduced. In Scotland (Graham 2001), even though the field vole populations are cyclic, they differ considerably from the Fennoscandian cyclic populations. Most notably, the amplitude is much greater in Fennoscandia, primarily due to much lower densities during the low phase of the cycle. If vole densities are constantly over 50 ind./ha, as in Scotland, there is no reason to assume a distinct numerical response in weasels. Considering all the studies in Appendix, the impact of predation on small mammals varied greatly from absence or only minor effect to total removal of the main prey species by the predator (van Wijngaarden and Bruijins 1961). Naturally, variations in the impacts of predators on prey is expected, because of dissimilarities in the experimental designs, the predator-prey communities, and the abiotic environmental conditions.

A surprisingly small number of experimental studies has been conducted on truly cyclic populations (see Appendix). In these studies, definite conclusions were usually not drawn about the cause of cyclicity. The strongest experimental evidence so far for a critical role of avian and mammalian predators in shaping cyclic vole dynamics in Fennoscandia is comes from western Finland (e.g. Norrdahl and Korpimäki 1995c, 1996, Korpimäki and Norrdahl 1998, Korpimäki et al. 2002) and from Norway (Steen et al. 1990). In contrast, Graham (2001) concludes that predation does not cause the cycles in the Scottish field vole populations (but see above comments concerning important dissimilarities in the vole cycles in Scotland versus In Fennoscandia). Erlinge’s (1987) results from an experiment done with non-cyclic populations in southern Sweden are consistent with the predictions of the predation hypothesis. He concluded that predation by abundant generalist predators was the main cause of non-cyclicity in southern Sweden. An experiment conducted by Oksanen and Oksanen (1981) showed that weasels might have a large role in shaping vole dynamics. Unfortunately, their results are not very conclusive, because the short-term experiment was not replicated and even the presence of the released weasel on the experimental island during the experiment was not verified. Wilson et al. (1999) suggest that predators play an important role in the dynamics of collared lemming populations, whereas several studies conducted on the Norwegian lemming indicate that food supply is the most important factor to maintain cyclic dynamics (Oksanen and Oksanen 1992, Turchin et al. 2000).

Despite the partly contradictory results of the previous studies, and the ones reported in this thesis, the bulk of recent experimental results, both observational and theoretical, point toward an important role of predation in northern small mammal population dynamics. In spite of the recent significant accumulation of information regarding the predation hypothesis, we unfortunately still lack of sufficient evidence to conclude that the long-standing puzzle of microtine cycles has been finally solved. In my opinion, the questions that need most attention in the future are the relative importance of different functional groups of predators, the numerical response of small mustelids, and the cause of the Chitty effect. Also, the mechanisms causing the decrease in the growth rate in dense vole populations should be more rigorously investigated to explain why predator populations, with slower intrinsic growth rate, can catch up numerically with their prey, and even cause its decline. To what extent is the pooled predation rate by the entire predatory guild sufficient for this purpose, and what is the role of the increased presence of predators on suppressed growth of prey population (i.e. indirect effects of predator presence)? The answer to question about the decrease in growth rate of prey does not change the predictions of predation hypothesis, because the predation hypothesis does not assume any particular mechanism for slowing down the growth of vole population. Another subject that has been largely neglected in experimental studies is the nature of predation during the winter.

Conclusions

I have studied various components of predation that influence cyclic vole populations in Finland. In the first study (**I**), the vole populations dynamics were studied at large spatial scale by using ringing data on vole-eating avian predators. The study showed a latitudinal (and longitudinal) gradient in cycle length and large-scale spatial synchrony of vole populations. One possible synchronising factor is predation of voles by mobile avian predators. Another potential mechanism that may synchronise vole populations at large scale is spatially-correlated climatic perturbations combined with similar structure of density dependence in the vole populations (the Moran effect). In contrast to previous studies, I found that cyclicity of vole dynamics was more regular in southern than northern Finland.

According to the predation hypothesis, the small mustelids, and particularly the least weasel, is the most important factor in maintaining the cyclic vole population dynamics. I have shown that the least weasel has that potential. The functional response of the least weasel to changes in vole abundance is of type II, which in theory has destabilising effect on population dynamics (**II**). The least weasel is an effective vole predator with a tendency to kill more prey individuals that would be needed by immediate requirements. Surplus killing further increases the effect of weasel predation on vole population dynamics. Weasel also kill different vole species according to their relative abundances, or even kill disproportionately more of the more abundant species, which increases the synchrony between vole species and may facilitate their coexistence (**III**). The effect of weasels on vole populations is even more pronounced if weasels prefer some functional categories of voles, for example breeding females. If changes in the size distribution of voles during the vole cycle is a consequence of predation by weasels, as suggested in paper (**IV**), the weasels could shape the population dynamics of voles even more than previously thought. If large-sized voles are especially vulnerable to weasel predation, vole population growth rate will be reduced, because the size of individual voles increases considerably at maturity. This is especially true for pregnant females that are likely to be more vulnerable to predation, because they cannot use as small holes as non-pregnant females to escape; they are also clumsier. The existence of fixed numbers of refuges for the prey is expected to have a stabilising effect on predator-prey dynamics, though this effect is not necessarily so strong that it would entirely stabilise cyclic dynamics (**IV**).

The least weasel has potential for fast reproduction. Young weasels can attain maturity and reproduce during the season of their birth. Weasels have large litters, and they may have two litters in the same season (**V**). There are some indications that they may even reproduce during the winter. Weasels mate and are ready to reproduce every year, but the breeding success is low in years of low food availability. The rapid growth rate of the least weasel makes it the numerically and functionally dominant vole predator. On the other hand, even if weasels have a fast intrinsic growth rate they cannot compete in this respect with voles, and it is therefore likely that weasels lag numerically behind a growing vole populations which started from a low density.

The main experiment of this thesis (**VI**) did not conclusively support nor reject the predation hypothesis. Captive-born weasels were introduced to three islands to eliminate the time lag in weasels' numerical response to changing vole populations. In one study area out of three, the expected treatment effect was found in field vole population dynamics and in population structure, but in the other two areas no effect of weasel additions was detected. The interpretation of the results was complicated by irregular dynamics and generally low density of the field vole in areas that formerly had cyclic dynamics, and by a surprisingly high mortality of the released weasels.

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Appendix. Literature review of predation experiments on small rodents.

Prey species	Manipulation	Cyclic or non-cyclic	Spatial scale	Temporal scale	Main results or conclusions	Controls	Replicates	Reference
Arvicola terrestris	Introduction of 102 weasels and 9 stoats on an island.	Non-cyclic	3000 ha	29 years	Weasels disappeared within 3 years and water voles within 5 years. Stoats maintained with alternative prey.	-	-	van Wijngaarden & Bruijns 1961
Microtus oregoni and *Peromyscus maniculatus*	Introduction of seven stoats in forest plantation.	Cyclic?	1 ha	1 year	In general, no effect on density. Earlier decline of deer mouse in experimental area. Recovery of voles after decline prevented.	1	-	Sullivan & Sullivan 1980
Clethrionomys rufocanus	Introduction of one male weasel on an island	Cyclic	13 ha	13 weeks	Survival on an experimental island decreased compared to control islets. Surplus killing of weasel.	2	-	Oksanen & Oksanen 1981
Microtus towsendii	Increase/reduction of cover and supplemented food	Cyclic	0.39 ha	9 months	Addition of cover reduced bird predation, female numbers increased and male decline was lower than in control population	2	-	Taitt et al. 1981
	Increase/reduction of cover and supplemented food. Exclusion of avian predators (herons) by net	Cyclic	0.39 ha	3 months	The first part of decline was due to predation and latter part due to density dependent dispersal. Both covered and netted population had higher density than control populations.	1	Net 4 Cover 2 Reduced cover -	Taitt & Krebs 1983
Microtus pennsylvanicus	Introduction of short-tailed shrew on the islands.	Non-cyclic?	0.13-0.43 ha	4 months	Experimental populations decreased or failed to increase until shrews became extinct, because of predation on juvenile voles.	2	3	Lomolino 1984
Arvicola terrestris	Introduction of six male stoats on an island.	Non-cyclic?	46 ha	16 months	Water vole populations declined.	-	-	Kildemoes 1985
Microtus agrestis	Exclosure: avian and mammalian predators. Weasels by trapping. Permeable for voles.	Non-cyclic	0.5 ha	8 months	Predation was the cause of the spring decline.	1	-	Erlinge 1987
Tetraonids, *Lepus timidus* (and voles)	Reduction of island population of red fox and marten	Cyclic	18 & 23 km^2	9 years	Tetraonids and hares increased. No effect on voles.	1	1 (2) 1 (2)	Mareström et al. 1988, 1989

Microtus orchrocaster	Exclosure: all predators (except short-tailed shrew). Supplemented food.	?	0.13 ha	3 years	Increased density, adult survival and recruitment. Food had additional effect on density.	1	(2)	Desy & Batzli 1989, Desy et al. 1990
Voles and lemmings	Reduction of medium-sized mammalian predators and raptors.	Cyclic	>100 000 km^2	ca. 20 years	Loss of cyclicity and regional synchrony	-	-	Steen et al. 1990
Clethrionomys glareolus	Exclosure: avian predators (weasels)	Cyclic	0.5 ha	8 months in peak year	No effect.	2	2	Ylönen et al. 1991
Microtus ochrocaster	Exclosure: different predator groups.	?	0.01 ha	1 year of low density	Large mammalian predators the most important group. Quick response of resident generalists.	1	-	Lin & Batzli 1995
Dicrostonyx kilangmiutak	Exclosure: avian, big and medium-sized predators (in summers).	Non- cyclic	11.4 ha	ca. 26 months	Survival better in exclosure. Predation limits summer growth of population	3	-	Reid et al. 1995
Dicrostonyx groelandicus	Exclosure: avian, big and medium-sized predators (in summers).	Cyclic	11 ha	ca. 25 months	Population decline was reversed in exclosure. Predation was necessary to limit the population in peak and decline summers.	3	-	Wilson et al. 1999
Microtus agrestis	Introduction and reduction of adders on islands.	Cyclic?	1-12 ha	2 years	No significant effects, but the lowest densities on introduction islands and the highest on reduction islands.	2	2	Lindell & Forsman 1996
Microtus rossiaemeridionalis, *M. agrestis*, *Clethrionomys glareolus*, *Sorex araneus*	Reduction of breeding avian predators.	Cyclic	3 km^2	4 years	Short-term changes in densities of common shrew and sibling vole.	4-5	4-5	Norrdahl & Korpimäki 1995c
Small mammals	Reduction of breeding avian predators.	Cyclic	3 km^2	4 years	Regional synchrony of small mammal cycles is driven by nomadic avian predators	4-5	4-5	Norrdahl & Korpimäki 1996
Microtus voles	Reducton of small mustelids and breeding avian predators.	Cyclic	2.5–3 km^2	4 months (in two crash years)	Mustelids slowed population growth of *Microtus* voles.	3	3	Klemola et al. 1997

Small rodents	Reduction of small mustelids and breeding avian predators.	Cyclic	2.5–3 km^2	4 months (in two crash years)	Only reduction of both avian predators and mustelids reversed the decline in densities of small rodents.	3	3	Korpimäki & Norrdahl 1998
Microtus voles	Exclosure: avian and mammalian predators	Cyclic	1 ha	22 (26) months	Enclosed populations increased rapidly to the peak densities and crashed due to the food shortage, while unfenced control populations remained at the low level.	4	4	Klemola et al. 2000
Microtus voles	Reduction of small mustelids and avian predators.	Cyclic	2.5-3 km^2	3 years	Increased vole densities in low and peak phases. Retarded initiation of decline phase.	4	4	Korpimäki et al. 2002
Microtus voles	Exclosure: avian and mammalian predators. Supplemented food in winter.	Cyclic	0.5-1 ha	2 years	Food supplementation increased vole density in exclosures, but not in unenclosed populations, and prevented deep decline in exclosures.	2	4 food and predation 4 predation 2 food	Huitu et al., in prep.
Microtus agrestis	Exclusion of avian predators and partly mammalian predators (not weasels). Attraction of avian predators with perches and nest boxes.	Non-cyclic?	0.6-1 ha	ca. 2 years	Generally higher densities in exclosures, especially in non-breeding season. Higher survival and proportion females in exclosures in winter. Attraction of avian predators had no effect.	4	4 exclosure 4 attraction	Carlsen 1999
Microtus agrestis	Reduction of common weasels	Cyclic	5-12 ha	2 years (30 months)	No effect on vole dynamics due to lack of delay in weasels' numerical response. Increase of adul survival, but decrease of juvenile survival	3	3	Graham 2001
Microtus agrestis and *Clethrionomys glareolus*	Addition of least weasels in islands.	Cyclic (previously)	5-10 km^2	16-24 months	No effect on *M. agrestis* on two out of three islands, while the third island showed effect on both structure and dynamics of population. No effect on *C. glareolus*.	3	3	Sundell 2002 (**VI**)