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Experimental tests of predation and food hypotheses for population cycles of voles

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Pronounced population cycles are characteristic of many herbivorous small mammals in northern latitudes. Although delayed density-dependent effects of predation and food shortage are often proposed as factors driving population cycles, firm evidence for causality is rare because sufficiently replicated, large-scale field experiments are lacking. We conducted two experiments on *Microtus* voles in four large predator-proof enclosures and four unfenced control areas in western Finland. Predator exclusion induced rapid population growth and increased the peak abundance of voles over 20-fold until the enclosed populations crashed during the second winter due to food shortage. Thereafter, voles introduced to enclosures which had suffered heavy grazing increased to higher densities than voles in previously ungrazed control areas which were exposed to predators. We concluded that predation inhibits an increase in vole populations until predation pressure declines, thus maintaining the low phase of the cycle, but also that population cycles in voles are not primarily driven by plant–herbivore interactions.

Keywords: three- to five-year population cycles; predator exclusion; field experiment; *Microtus*; small mustelids; delayed effects

1. INTRODUCTION

Vole and lemming populations fluctuate in short-term (three- to five-year) cycles and snowshoe hare populations in long-term (nine- to ten-year) cycles in Arctic and boreal ecosystems (e.g. Elton 1942; Hansson & Henttonen 1988; Keith 1990; Norrdahl 1995). Recent studies have suggested that the most obvious extrinsic factors likely to operate in a delayed density-dependent manner, as required for the cyclic population dynamics of herbivores (Royama 1992), are high mortality from specialist predators (Hansson 1987; Henttonen *et al*. 1987; Korpimäki *et al*. 1991; Hanski *et al*. 1993; Korpimäki & Norrdahl 1998), poor reproduction or death due to a reduction in high-quality food (Seldal *et al*. 1994; Agrell *et al*. 1995; Plesner Jensen & Doncaster 1999) or the interactive effects of predation and food shortage (Krebs *et al*. 1995; Hansson 1999). In contrast, intrinsic explanations assume that population growth is self-regulated within the population (e.g. Chitty 1960, 1967; Krebs *et al*. 1973; Charnov & Finerty 1980). At present, the senescence–maternal effects hypothesis remains the most plausible of intrinsic explanations for population cycles in small mammals (Boonstra *et al*. 1998). This hypothesis proposes that a detrimental change (e.g. a shift in the age structure of reproductive females) in maternal quality occurs in the peak phase, carries over several generations and leads to population decline and a subsequent low phase of the population cycle (Boonstra 1994; Boonstra *et al*. 1998; Tkadlec & Zejda 1998).

Despite intensive research, even the most popular explanatory hypotheses about population cycles in voles remain largely untested by sufficiently replicated field experiments (Stenseth & Ims 1993; Batzli 1996; Korpimäki & Krebs 1996; Boonstra *et al*. 1998). Therefore, we tested the predation hypothesis for the cyclic low experimentally by excluding all main mammalian and avian predators for voles in large enclosures. Because the founder voles for the experiment originated from populations in the low phase of the cycle, we also assessed the relevancy of intrinsic hypotheses which assume that low quality of voles rather than predation maintains populations at low densities (Boonstra *et al*. 1998). In the second enclosure experiment, we then tested food-mediated delayed effects by examining the combined effects of predator exclusion and previously high vole density on the population growth of voles.

2. METHODS

Field voles (*Microtus agrestis*) and sibling voles (*Microtus rossiaemeridionalis*) are the most abundant small rodents in the Alajoki study area (flat, uniform, agricultural farmland in Lapua, western Finland, 63° N, 23° E) and exhibit three- to five-year cycles in density (Korpimäki & Norrdahl 1991*a*; Korpimäki *et al*. 1991; Norrdahl & Korpimäki 1995*a*) (figure 1). Predation by least weasels (*Mustela nivalis nivalis*) and stoats (*Mustela erminea*) appears to be a major cause of mortality for the *Microtus* (Norrdahl & Korpimäki 1995*a*, 1998) and the densities of these small mustelids track vole densities with a six- to 12-month lag (Korpimäki *et al*. 1991). The breeding densities of avian predators (the Eurasian kestrel *Falco tinnunculus*, the short-eared owl *Asio flammeus*, the long-eared owl *Asio otus* and Tengmalm's owl *Aegolius funereus*) track vole densities without an obvious time-lag and their predation rates on voles are directly density dependent (Korpimäki & Norrdahl 1989, 1991*a*,*b*).

(a) *Enclosures and control areas*

We chose four distinct agricultural field areas. We constructed a 1-ha predator-proof enclosure in each, which was divided by fencing into two 0.5-ha sub-enclosures to avoid a failure of the whole replicate in case a fence broke (hereafter, the result for an enclosure is the average of the values from two sub-enclosures). Adjacent unfenced 1-ha areas served as controls where predators had free access. The pairs of enclosures and their control areas were within 12 km^2 and at least 1.5 km apart. The sizes of the sites

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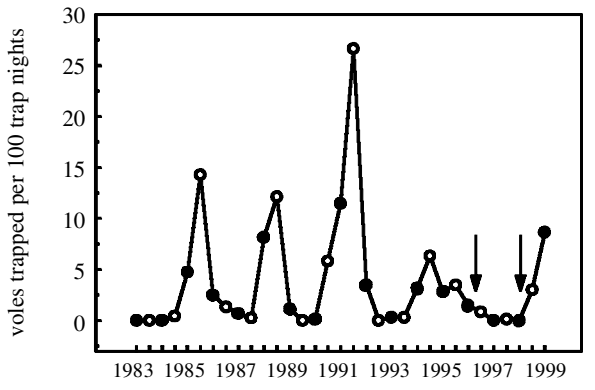

Figure 1. Index of density for cyclic populations of *Microtus* at the Alajoki farmland which reached around 150–200 voles ha^{-1} during peak phases. Spring (filled circles) and autumn (open circles) snap trapping was conducted in sites located within 1–10 km of the enclosures and control areas used in the experiments. Arrows denote the onsets of the first (July 1996) and second experiments (May 1998), respectively.

were 150 m × 65 m (two enclosures and three controls), 110 m × 95 m (one enclosure) and 250 m × 40 m (one enclosure and one control). The enclosures were constructed using hardware cloth (12.7 mm mesh) which extended 0.5 m below ground and 1.3 m above ground. We fastened a 40 cm wide metal sheet on the upper edge of the fence to prevent climbing by mammalian predators. To prevent access of avian predators, we covered the enclosures with nylon net (10 cm mesh). The fences effectively excluded all predators except some occasional visits by small mustelids, owls, shrikes and adders. The few predators that we detected in the enclosures were rapidly captured and removed.

Two site pairs (NE and SE) had ceased cultivation more than ten years, and two site pairs (NW and SW) ceased one year, before our experiment. The old fallow fields were dominated by grasses (*Elymus repens*, *Phalaris arundinacea*, *Deschampsia cespitosa* and *Calamagrostis* spp.) and dicotyledons (*Epilobium angustifolium*, *Filipendula ulmaria* and *Urtica dioica*), and the young fallow fields were dominated by grasses (*E. repens*, *Phleum pratense* and *D. cespitosa*) and thistle (*Cirsium arvense*).

When the first experiment started in July 1996, the initial abundance of voles was estimated by live trapping. Where field vole abundance was lower than six pairs per hectare in an enclosure or control area (the initial abundance was three, or less than three, voles in three enclosures and three controls), we complemented founder populations to six pairs with field voles trapped from agricultural fields nearby. In addition, two enclosures had a founder population (two pairs) of sibling voles. After the second trapping period in September 1996, additional field voles (three to four of both males and females) were reintroduced to each enclosure and control area to strengthen the populations before winter.

Before the second experiment in May 1998, *Microtus* voles were removed from the control areas by live trapping (all enclosure populations were extinct at that time) (figure 2). Thereafter, we introduced eight pairs of field voles to each enclosure and control area. These voles were mainly captured in several other farmlands of southern and central Finland (Karvia (62° N, 22° E), Konnevesi (62° N, 26° E), Toijala (61° N, 24° E) and Valkeakoski (61° N, 24° E)) because of the low natural density of voles in the Alajoki study area (figure 1) (controls in figure 2).

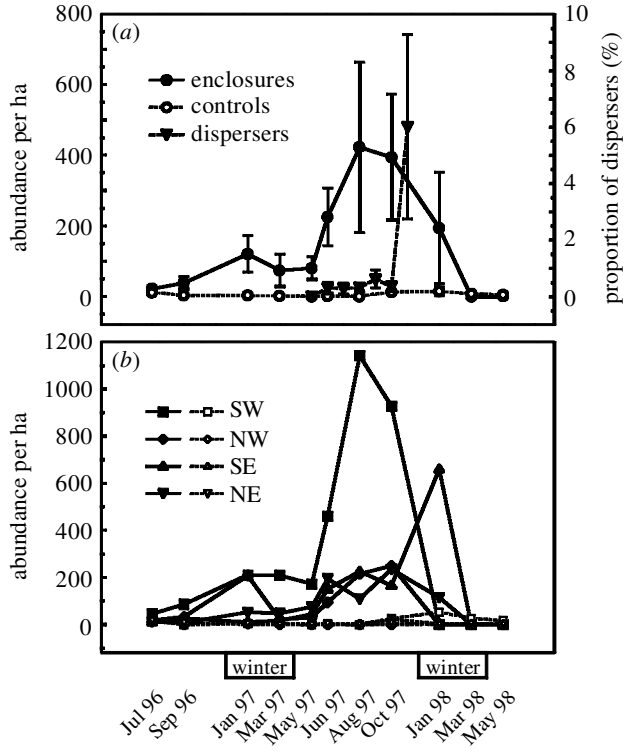

Figure 2. (*a*) Mean (± s.e., $n = 4$) estimates of the abundance of voles and the proportion of voles presumed to be dispersers from the enclosed populations in the first experiment, and (*b*) estimates for each enclosure (filled symbols) and control area (open symbols). When populations crashed only a single vole was trapped from the enclosures in March 1998 and the next trapping period confirmed that all enclosure populations were extinct.

(b) *Trapping procedures and estimation of vole abundances*

In the first experiment, we monitored the vole abundances using live trapping in the enclosures and control areas six times per year. We marked each vole individually by toe clipping when first captured. Sex, body mass and reproductive condition were recorded before release at the point of capture. The trapping grids consisted of 100 trap stations at 10 m intervals. Each trapping station had one (two in summer 1997 because of high vole numbers in the enclosures) multiple-capture Ugglan live trap covered by a plastic box (40 cm × 30 cm × 25 cm). The shelter reduced exposure to rain, wind and temperature extremes and made it possible to conduct subnivean winter trappings. We trapped one enclosure–control pair simultaneously, after which we transferred the traps to the next site pair. The traps were set for three days and checked three times per day. Using this schedule we avoided almost all trap mortality. We estimated the abundance of voles in each trapping period separately for each sub-enclosure and control area using a jackknife estimator for the model M_h in the program CAPTURE (Otis *et al.* 1978). We calculated separate estimates for both *Microtus* species and pooled their abundances.

In the second experiment, we live trapped monthly. At the end of this experiment, live-trapped voles were killed by cervical dislocation for autopsy. We extended the final trapping period by snap trapping to obtain larger samples. Ninety Finnish metal snap traps designed for house mice and baited with bread were set at 10 m intervals for three days after live

trapping and were checked once a day. For the final abundance of voles, a removal estimator was applied (Pollock & Otto's for model M_{bh} in the program CAPTURE) (Otis *et al.* 1978; Pollock & Otto 1983), combining three-day live- and three-day snap-trapping data by treating all live-trapped voles captured during the same day as voles snap trapped in one day.

(c) *Dispersal barriers*

Because northern least weasels are often smaller (30–50 g) (Korpimäki *et al.* 1991) than large *Microtus* individuals (up to 60 g), it was not feasible to construct fences permeable to voles only for year-round study. Therefore, the tendency for voles to disperse from enclosures was assessed using dispersal barriers (e.g. Desy & Batzli 1989). A 4-m wide and 40–65-m long mowed strip of ground was maintained along one edge of each sub-enclosure during the growing season of plants in 1997 and 1998. The outer 1 m of the strip was also treated with herbicide (Roundup®) to eliminate any green vegetation. Eight live traps per sub-enclosure were set on the strip along the fence and checked three times per day during regular trapping periods. We conducted additional three-day trapping inside the dispersal barriers between the trapping periods in summer and autumn 1997, but trapping in the dispersal barriers was not possible during periods of snow cover. Voles captured in the dispersal barriers for the first time were returned to the enclosures but voles captured for a second time during the same trapping period were considered as dispersers and removed from the enclosures.

(d) *Winter food adequacy*

We assessed winter food by counting green shoots of wintering grasses and dicotyledons from permanent sampling plots (2 m × 2 m) in the enclosures and control areas during the first experiment. Half of the plots were fenced to protect them against grazing by small mammals. Six protected and six unprotected (three in each sub-enclosure) plots were located in each enclosure, and five protected and five unprotected plots in each control area. One randomized quadrat of size 0.5 m × 0.5 m per plot was used to estimate shoot numbers. In addition to permanent plots, we counted the number of green shoots from 20 randomly selected unprotected quadrats (0.5 m × 0.5 m; ten in each sub-enclosure). All these censuses were done within two days in late April 1997 and 1998 after the snow melt and before plants had started to grow.

(e) *Predation impact in control areas*

The abundances of small mustelids within 1–2 km^2 of each control area were estimated by snow tracking in December 1996. Four lines (900–1700 m) were searched per control area after a snowfall so that tracks were only one to two days old (for details of the methods, see Korpimäki *et al.* (1991)). In addition, 11 adult voles were radio-collared to determine the proximate causes of vole mortality in the control areas in October 1997 (for details of the methods, see Norrdahl & Korpimäki (1995*a*)).

3. RESULTS

(a) *Experiment 1*

Predator exclusion induced a rapid increase in vole abundances which did not occur in the control areas (figure 2). From the onset of the first experiment until the second winter, predator exclusion had a significant effect (repeated-measures ANOVA for log + 1-transformed vole abundances: treatment $F_{1,6} = 49.5$ and $p < 0.001$, treatment × time $F_{7,42} = 5.9$ and $p < 0.001$, and time $F_{7,42} = 13.3$ and $p < 0.001$). Predator exclusion increased the peak abundance of voles in the enclosures by >20-fold compared to the controls. Despite the high densities, the proportion of reproducing (visibly pregnant or lactating) individuals of all potentially reproductive (≥20 g) females remained high in the enclosures throughout the second summer and autumn (in 1997): the mean percentages (±s.e., $n = 4$) were 56 ± 20 for May, 61 ± 11 for June, 79 ± 6 for August and 71 ± 15 for September–October. The scarcity of voles in the controls prevented between-treatment comparisons of the reproductive rate. The enclosure populations then crashed during the second winter (figure 2). Starvation appeared to be the cause of death in all five emaciated vole carcasses found during the crash as no signs of infectious diseases were identified in laboratory analyses at the National Veterinary and Food Research Institute in Helsinki, Finland.

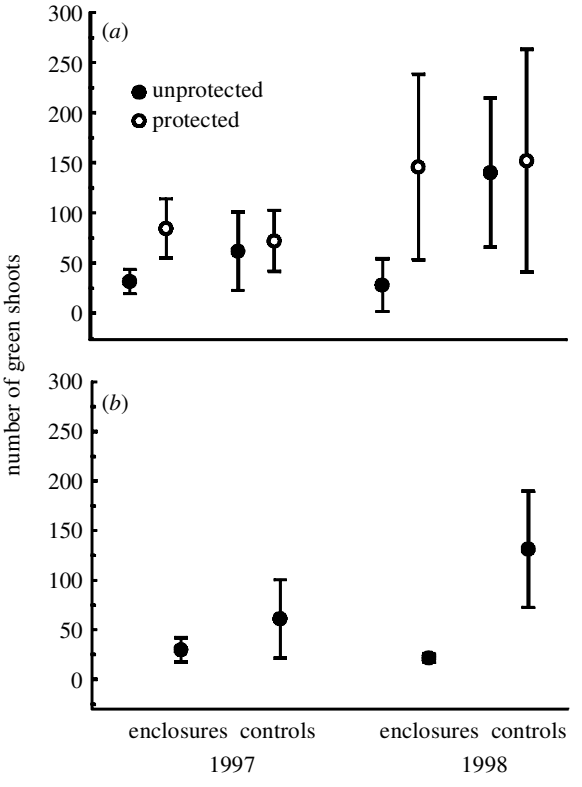

Figure 3. The mean (95% confidence limits, $n = 4$) number of green shoots (grasses and dicotyledons pooled) in the enclosures and control areas in (*a*) the permanent sampling plots and (*b*) randomly in selected quadrats. The means (number of shoots 0.25 m^{-2}) for each study site were used as observations. A three-way ANOVA for the permanent plots showed significant effects of treatment ($F_{1,24} = 6.1$ and $p = 0.021$), protection ($F_{1,24} = 12.3$ and $p = 0.002$), year ($F_{1,24} = 15.4$ and $p = 0.001$) and treatment × protection ($F_{1,24} = 7.3$ and $p = 0.012$). A two-way ANOVA for the random quadrats also showed significant effects (treatment $F_{1,12} = 38.9$ and $p < 0.001$, year $F_{1,12} = 7.5$ and $p = 0.018$, and treatment × year $F_{1,12} = 12.1$ and $p = 0.005$).

After both winters, the number of green shoots of plants was significantly lower in the enclosures than in the control areas (figure 3), suggesting grazing in the enclosures reduced the food availability. The number of

green shoots in the enclosures was also lower in unprotected than grazing-protected plots, but this difference did not occur in the control areas (figure 3). Shoots in unprotected plots in the enclosures were also more damaged (*ca.* 90% of shoots were clipped by voles) than shoots in the controls or in protected plots (<10%).

The tendency for voles to disperse remained low at low and intermediate densities of enclosed voles and only increased when the grazing pressure in the enclosures reached very high levels after the end of the growing season (figure 2*a*). In 1997, from June to October we captured 139 voles in the dispersal sinks, 110 of which were young males, and removed 26 animals, 22 of which were young males. Substantial numbers of females (91 out of 176 voles) were captured in the dispersal sinks only when food resources were declining in November (figure 2*a*). This change towards females was significant among presumed dispersers (from 15 to 56%; $G^2=14.0$ and $p=0.001$) and also among all voles captured in the dispersal sinks (from 14 to 52%; $G^2=52.9$ and $p=0.001$) between June and October (low proportion of dispersers), and November (high proportion of dispersers) (figure 2*a*).

The snow tracking of predators in the controls showed mean (±s.e., $n=4$) abundance indexes (the number of individuals crossing track lines per kilometre) of 0.5 ± 0.2 for stoats and 0.1 ± 0.1 for least weasels in December 1996. We also made repeated observations of small mustelids, including a female least weasel with young in 1996 (SW control area) and two litters of stoats in 1997 (SE and SW). In addition, three other mammalian species and ten avian predator species were observed hunting at the control areas. The numbers of avian predator nests within 12 km^2 of the enclosures and their control areas were six, four and three nests for kestrels and four, three and zero nests for short-eared owls from 1996 to 1998, respectively. Moreover, radio-collared voles showed 45% (five out of 11) mortality due to predation (four out of five by small mustelids) during a three-week surveillance in October 1997.

(b) *Experiment 2*

During the summer, all introduced populations increased in the enclosures (figure 4), and the log-transformed abundance of voles was significantly higher in the enclosures than in the controls at the end of the experiment ($F_{1,6}=8.7$ and $p=0.026$) (repeated-measures ANOVA for the entire experiment: treatment $F_{1,6}=5.0$ and $p=0.066$, treatment × time $F_{4,24}=1.8$ and $p=0.162$, and time $F_{4,24}=6.2$ and $p=0.001$). No voles were trapped twice in the dispersal barriers and removed during this experiment.

4. DISCUSSION

The exclusion of all main predators induced an extensive difference in the vole abundances between the enclosure and control populations suggesting that predation maintains the low phase of the population cycle in voles. In contrast, the intrinsic explanations for the maintenance of the low phase were not supported because voles originating from the low phase started to reproduce and the populations increased when protected from predation. This should not have occurred if these voles were innately of low quality (Boonstra *et al.* 1998). Furthermore, our results suggest that population cycles in voles are not proximately driven by the delayed effects of food shortage, neither through quality nor quantity, because the introduced field voles increased to high abundances in previously overgrazed enclosures.

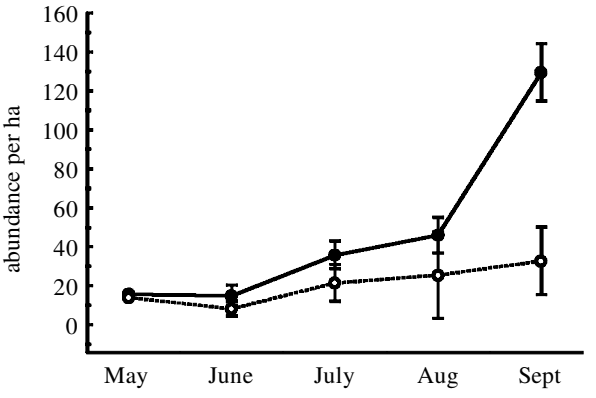

Figure 4. Mean (±s.e., $n=4$) estimates of the abundance of field voles in the enclosures (filled circles) and control areas (open circles) during the second experiment in 1998. Sibling voles were included if captured in the control areas.

The strong impact of predator exclusion was probably attributable to the exclusion of all predators rather than to either mammalian or avian predators or to generalist or specialist predators exclusively. Earlier field experiments by Norrdahl & Korpimäki (1995*b*) and Korpimäki & Norrdahl (1998) indicated that the removal of one subset of predators is not sufficient to prevent the crash phase of voles in our study area where the assemblage of vole-eating predators is diverse (Norrdahl & Korpimäki 1995*a*) and all predators should be considered when explaining the low phase.

We suggest that the overall predation pressure was high enough to maintain low vole densities in the control areas. Both mammalian and avian predators were frequently observed hunting in the study sites and they killed half the radio-collared voles within three weeks. In particular, stoats are able to survive periods of low vole abundances because they shift their diet to alternative prey (Korpimäki *et al.* 1991) and, according to our snow-tracking indices, they were more abundant than least weasels during the study. In addition, snow tracking in the vicinity (<25 km) of the experimental sites showed more than ten times higher abundances of both least weasels and stoats in spring 1997 than in spring 1998 when the voles began to increase (figure 1) (K. Norrdahl and E. Korpimäki, unpublished data). Trappings in other parts of the large (47 km^2) Alajoki farmland confirmed the regional synchronous low for an extended period (figure 1; T. Klemola, unpublished data), refuting the possibility that voles avoided the control areas employed for the experiments but concurrently increased in adjacent grasslands.

In earlier enclosure experiments with *Microtus* voles (Erlinge 1987; Desy & Batzli 1989), only short-term differences were demonstrated in the maximum densities between predator exclusion and control areas, whereas in our first experiment the dynamics of the manipulated vole populations were altered for 18 months. This

dramatic effect may be because we excluded all main predators, which was not the case in Erlinge's (1987) study or because we had larger enclosures than those (0.13 ha) used by Desy & Batzli (1989), providing more natural conditions for voles to reproduce. Similarly, using a large (11 ha) enclosure from which predators were excluded, Reid *et al.* (1995) concluded that predators limited summer population growth and prolonged the period of low density of collared lemmings (*Dicrostonyx kilangmiutak*) in northern Canada.

When studying high-density populations of *Microtus* voles, some investigators have found a 'fence effect' in which enclosed populations increase to abnormally high densities, overexploit their food resources and then crash, apparently because dispersal has been prevented (Krebs *et al.* 1969, 1973; Boonstra & Krebs 1977; but see Ostfeld 1994). These observations led to the conclusion that spacing behaviour plays a crucial role in the generation of vole cycles by preventing population growth at the peak phase. In our experiment, the voles overexploited their food supply and starved during the second winter, which might have been avoided with free emigration from the enclosures. However, because most dispersers are typically young males (Gaines & McClenaghan 1980; Sandell *et al.* 1990), we suggest that the generally low tendency for other voles to cross our dispersal barriers was a real phenomenon indicating that the need to disperse was low during increasing vole abundance, which reached the levels encountered under natural conditions. Consequently, we concluded that the rapid increase in the enclosure populations was more probably caused by predator exclusion rather than a substantial lack of dispersal opportunities. Because we argued that predation inhibits an increase in vole populations and maintains the low phase of the vole cycle, our conclusion and those of Krebs *et al.* (1969, 1973) and Boonstra & Krebs (1977), which discuss the peak phase, are not necessarily in disagreement.

In the second experiment, we used the four predator enclosures which had experienced severe grazing during the preceding autumn and winter, whereas the vole densities and, consequently, grazing pressure in the control areas had remained low for at least two preceding years. To produce a short-term population cycle of voles, the delay in the density-dependent feedback process should be approximately nine months (May 1981). The time-lags between the depletion of food resources in our first experiment and the onset or termination of our second experiment appeared to be four to eight or seven to 11 months, respectively. On the basis of the results and personal observations, we suggest that the detrimental food depletion started in late October 1997 in the NE, NW and SW enclosures and in February 1998 in the SE enclosure.

Despite the preceding reduction in food resources, the delayed effects on introduced voles remained undetected as the populations increased substantially during the second experiment. Moreover, autopsied voles showed that body condition and the reproduction of females were not detrimentally affected by the previously high density of voles (Klemola 1999). However, predator exclusion and previous heavy grazing occurred together in this experiment; therefore, we cannot assess their possible independent or additive contributions to the overall population growth of the voles. However, we suggest that the population increase in the second experiment again occurred because of predator exclusion and was not due to the positive effects of grazing on food plants which is typical in grasslands as a response to moderate levels of herbivory (McNaughton 1979, 1983). In our experiment, grazing was very intense and occurred most heavily outside the growing season of plants. Any possible negative (or positive) effects of a previously high density of voles may have been masked by the strong impact of predator exclusion. Nevertheless, our results concur with an earlier study on meadow voles (*Microtus pennsylvanicus*) which did not show a delay in population growth after a reduction in plant biomass (Ostfeld *et al.* 1993), but are in apparent disagreement with the experiment of Agrell *et al.* (1995) which found delayed effects of grazed food plants on the reproduction and body growth rate of field voles.

Reproducing females continued to be captured in the enclosures at very high vole densities until the termination of the growing season of plants, suggesting that food resources did not curtail population growth during summers. Instead, the quantitative estimation of the adequacy of winter food indicates that the vole populations in the enclosures suffered from a substantial shortage of winter food. However, we found this effect under extremely high densities and its relevancy to vole peaks of lower density is not known (but see Hansson 1999). If three-trophic-level interactions, including plants, herbivores and predators, influence population cycles in voles, food only contributes to a density decline in vole populations during winters but does not drive the cycles or cause the summer declines which are typical of cyclic populations of voles in Fennoscandia (e.g. figure 1; Hansson & Henttonen 1988).

Statistical analyses of time-series from cyclic populations of Fennoscandian rodents have shown second-order autoregressive dynamics which include both direct and delayed density-dependent mechanisms (e.g. Bjørnstad *et al.* 1995; Stenseth *et al.* 1996; Hansen *et al.* 1999). The findings presented here and those of others (Hansson 1987; Henttonen *et al.* 1987; Korpimäki *et al.* 1991; Hanski *et al.* 1993; Norrdahl & Korpimäki 1995*a*; Korpimäki & Norrdahl 1998) indicate that predation is a strong candidate for the delayed density dependence but it remains to be studied whether a winter food shortage accounts for the direct density dependence.

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