

## The impact of short-term predator removal on vole dynamics in an arctic-alpine landscape

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During 1991–95, mammalian predators (weasel, *Mustela nivalis*, stoat, *M. erminea*, mink, *M. vison*, and red fox, *Vulpes vulpes*) were excluded in late summers from a 2 ha piece of a north Norwegian mountain slope. The enclosure extended from an outpost of luxuriant sub-arctic birch forest to a typical arctic-alpine habitat complex, including productive willow scrublands, tundra heaths, dry ridges and snow-beds. The enclosure thus encompassed the entire range of habitat conditions encountered in a typical north Fennoscandian mountain and tundra landscapes. During 1991–95, the enclosure was predator-proof from late July to late September. In wintertime and in early summer, the enclosure was accessible to mammalian predators. Vole dynamics in the short-term enclosure were compared to dynamics in five reference areas with similar habitat conditions.

In 1991, when vole densities were rising in the area, neither collective vole densities nor densities of individual vole species differed significantly between the enclosure and the replicated controls. Spring densities of voles were never significantly different between the enclosure and the controls. With respect to autumnal densities of voles, however, the enclosure was a statistical outlier in the peak year 1992 and throughout the gradual decline phase of 1993–95. In the peak year, the difference in collective vole densities was modest (30%), but increased to two-fold during the first two decline years and was almost four-fold in the crash year of 1995. The strongest response was displayed by field voles (*Microtus agrestis*), hypothesized to be the pivotal prey species of weasels, especially by females and young individuals, i.e. by the functional categories especially sensitive to mammalian predation. These results are consistent with the hypothesis that predation plays a pivotal role for the regulation of herbivorous mammals in relatively productive arctic-alpine habitats.

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One of the major controversies in ecology concerns the role of predators in the regulation of herbivore populations and communities in terrestrial ecosystems. Several authors argue that the mortality inflicted by predators on herbivores is either compensatory or insufficient to have major population dynamical consequences. Instead of being regulated 'from above', i.e. by their natural enemies, herbivores are supposedly limited 'from below' (White 1978), by climatically triggered changes in food quality (Kalela 1962, Tast and Kalela 1971, Selås 1997)

by the induction of plant defenses (Haukioja and Hakala 1975, Rhoades 1985, Seldal et al. 1994, Plesner Jensen and Doncaster 1999) or by being locked in a predator–prey interaction with their food plants, where herbivores are in predator's role (Lack 1954, Myllymäki 1977, Rosenzweig and Abramsky 1980, Caughley and Lawton 1981, Caughley and Gunn 1993, Paine 2000, Turchin and Batzli 2001). Another group of ecologists emphasizes lateral factors – social interactions between herbivores – and maintain that these factors alone

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suffice to regulate herbivore populations (Chitty 1960, Krebs and Myers 1974, Krebs 1978a, b). A third group argues that predation is pivotal for the dynamics of herbivores, at least in relatively productive ecosystems, where the vegetation can sustain fairly high consumer densities (Hairston et al. 1960, L. Oksanen et al. 1981, L. Oksanen and T. Oksanen 1981, 2000, Erlinge et al. 1983, Henttonen et al. 1987, Bergerud et al. 1988, L. Oksanen 1990, Hanski et al. 1991, 1993, 2001, Korpimäki et al. 1991, 1994, Messier 1994, Hanski and Korpimäki 1995, Krebs et al. 1995, Crête and Manseau 1996, Korpimäki and Krebs 1996, Turchin and Hanski 1997, Crête 1999, Turchin et al. 2000, T. Oksanen et al. 2001, Norrdahl and Korpimäki 2002).

Critical predictions differentiating between these conjectures concern dynamics in the absence of predators. If herbivores are regulated 'from below' or by lateral factors, similar dynamics should be displayed in the presence and in the absence of predators. Conversely, if predation plays a central role in the regulation of herbivores, their dynamics in presence and absence of predators should be radically different. Unfortunately, however, to exclude predators from a piece of fairly natural terrestrial landscape is easier said than done. Closing all sub-terranean entrances that smallest predators might utilize is tough enough a task, so is the construction of a fence, which remains operative in all seasons. These technical problems are multiplied by the perceived need to control predation removal experiments for the so-called 'Krebs effect' or 'fence effect' (Krebs et al. 1969), i.e. against supposed consequences of arrested dispersal.

We agree with Ostfeld (1994) that the concept of 'fence effect' should be critically analyzed, and we should realize that predators have not been adequately studied in studies supposedly demonstrating the existence of a 'fence effect'. Thus, undocumented removal of some predator (e.g. the shrew *Blarina brevicauda*, which has high mortality in the context of vole trapping) could account for the 'fence effect'. It is also hard to see how dispersal per se could regulate herbivore populations, as the movement of animals from site A to site B has no obvious impact on population dynamics on a larger spatial scale. Moreover, everything else being equal, immigration and emigration rates should be equal for each habitat patch. Thus, blocking both processes should not influence population dynamics on local scale, either. The 'fence effect' could become an issue only in situations, where the fenced area consists of better habitats than typical for the landscape as a whole, so that the fence blocks a natural tendency for net emigration from the area. An adequate control against the 'fence effect' in the context of predator removal experiments is thus to conduct the experiments in a landscape scale, so that the normal habitat selection processes is possible within the fenced area.

Our initial ambition was to perform a landscape-scale, long-term predator exclusion experiment in the outback of northernmost Norway. Unfortunately, however, the technical challenges proved overwhelming (below). As the ideal design turned out infeasible, we approached the problem with a combination of two techniques. First, we used the possibility of maintaining a predator-proof fence for short periods in late summer. Second, we introduced voles to small islands, isolated from the mainland and its predators by long stretches of water or ice (Hambäck et al. 2004). These two experiments complement each other, as the island work provides a long term perspective, whereas the enclosure study, to be reported here, gives direct evidence concerning the impact of predator removal to vole dynamics.

## Material and methods

### Study area, its habitats, and its microtines

The study was conducted on a south facing escarpment slope (the slope sub-area of T. Oksanen et al. 1999) in the Joatka research area, Alta, Finnmark, Norway, (69°45'N, 24°00'E at altitudes ranging from 400 to 650 m.a.s.l.). The lower parts of the slope are occupied by productive, herb-rich willow scrublands, and, at lowest altitudes, by outposts of luxuriant mountain birch (*Betula pubescens* ssp. *czerepanowi*) forest, with an understory of tall herbs (*Cicerbita alpina*, *Cirsium helenioides*, *Filipendula ulmaria*). The middle parts are dominated by moderately productive habitats (mainly herb-rich dwarf birch heaths), whereas unproductive habitats (dry arctic-alpine heaths and late snow-beds) prevail in the upper part.

Vole dynamics in the area have been cyclic, with peaks in 1978–79, 1982–84, 1987–88, 1992, and 1997–98, and crash years in 1975, 1980, 1985, 1990, 1995 and 2000 (Turchin et al. 2000, Ekerholm et al. 2001, L. Oksanen and J. Dahlgren, unpubl.). All four vole species present in the area – gray-sided voles (*Clethrionomys rufocanus*), red voles (*C. rutilus*), field voles (*Microtus agrestis*) and root voles (*M. oeconomus*) – are regularly trapped on the slope (see above). Lemmings (*Lemmus lemmus*), which have only had two sharp outbreaks during the past 25 years (in 1978 and in 1988, Turchin et al. 2000, Ekerholm et al. 2001), have been uncommon on the slope even in outbreak years (T. Oksanen 1993).

### The composition of the predator guild and over-all vole dynamics in the area

During the 1988 peak 5 stoats (*Mustela erminea*) and 7 weasels (*M. nivalis*) were captured in our vole traps in the 5-ha piece of slope which was being divided to the fence and the main control. In addition, the slope

harbored four pairs of rough-legged buzzards (*Buteo lagopus*), the nearest one breeding just 400 m from the enclosure. In the fall of 1988, a hawk owl (*Surnia ulula*) was recurrently observed in the fence and in its surroundings. Red foxes (*Vulpes vulpes*) were uncommon, due to the impacts of sarcoptic mange. Arctic foxes (*Alopex lagopus*) have remained virtually absent since 1982.

In 1990, the invasion of the American mink (*M. vison*) and the simultaneous recovery of red foxes was accompanied by a major change in the predator community. Thereafter, weasels were only occasionally captured in our live traps, and even our snow-tracking data (T. Oksanen et al. 1992, 1999, L. Oksanen et al. 1997) indicated that stoats had become numerically dominating small mustelids, probably because of the impact of minks on the delicate competitive balance between stoats and weasels (Hanski and Henttonen 1996, T. Oksanen and Henttonen 1996, T. Oksanen et al. 2001). Minks and foxes were active on our control grids in 1991 and 1992, making it necessary to cover vole traps with rocks. The change in the community of mammalian predators was associated with increased seasonality in the numerical dynamics of voles. Vole declines became gradual (Ekerholm et al. 2001), spring densities were never high and, consequently, breeding densities of avian predators remained modest even in peak years (L. Oksanen et al. 1997, Fig. 18.2), but one pair of rough-legged buzzards nevertheless bred in the vicinity of the enclosure in 1992 it was frequently seen hunting there.

### Experimental design in the pilot phase

The pilot phase of this study was performed in 1988–90, with the ambition to initiate a long-term predator removal experiment. The original design of the experiment was to exclude all mammalian predators for a period of 2–3 years from a piece of mountain slope, embracing the entire range of habitat variation available in the landscape. The response predicted by all variants of the predation hypothesis was so dramatic that we regarded replication and use of inferential statistics as superfluous. Hence, we constructed an elongate enclosure of 2 ha on a steep escarpment slope (about 250 m long and 100 to 50 m wide) stretching from luxuriant birch forest at 500 m a.s.l. to arctic–alpine barrens at the 600 m contour, thus including the whole productivity range found in the study area (Fig. 1). The rest of the concave part of the slope (size: 3 ha) was used as control (habitat distribution as in the enclosure, Fig. 1, Table 1). The fence was built in 1988. It was 2 to 4 meters high (depending on snow conditions), constructed of mink cage net with a mesh size of 12.5 mm. The top 30 cm were covered by shingled plates of steel on the outside, to prevent predators from climbing into the area. The net was dug at least 20 cm down to the mineral soil to block sub-terrestrial entrances to the enclosure.

In spite of being over snowed in its upper parts, the fence did exclude small predators in the first winter, as the entrance routes were at high altitudes, where small mustelids do not normally move (T. Oksanen et al. 1992). Thus, no tracks were found inside the enclosure that winter. Unfortunately, however, even low-altitude

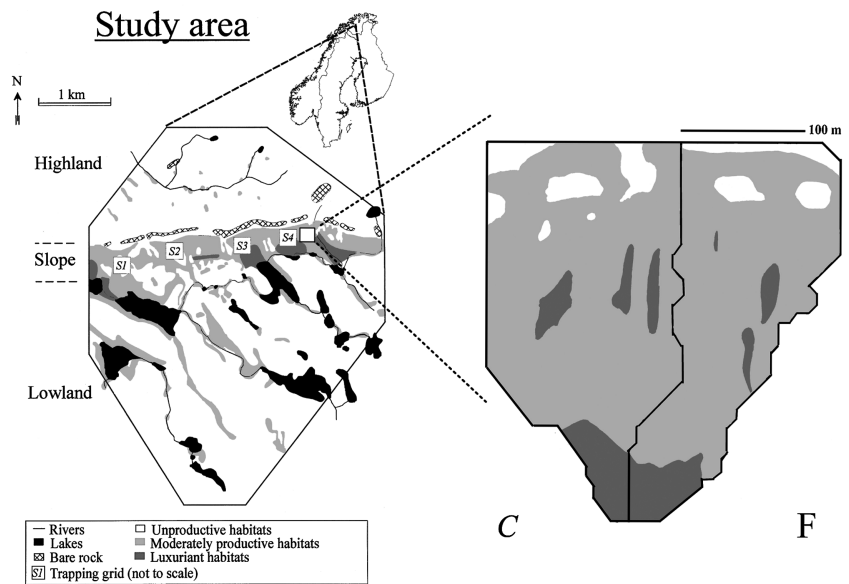


Fig. 1. Location of study area and distribution of major habitat categories in the area as a whole and within the enclosure and the main control during 1991–95 (F denotes fence, C denotes main control, S1–S4 denotes the smaller control areas on the slope).

Table 1. Percentages of different habitat categories in the enclosure and on controls. C(main) refers to the main control, C(S1)–C(S4) denotes the smaller control grids. Percentages for the enclosure and mean percentages for the controls are printed in bold to make comparisons easier. ‘Luxuriant habitats’ refers to willow scrublands and birch woodlands with tall herbs. ‘Moderate habitats’ refers to dry meadows, herb-rich scrublands, willow mires, cloudberry bogs, billberry heaths (with or without birches) and to moist and nutrient-rich early to moderate snow-beds. ‘Unproductive habitats’ refers to ridge heaths, lichen heaths, late snow-beds (regardless to edaphic conditions), and to dry and nutrient-poor snow beds.

Habitat ↓ Grid →	Enclosure	C(main)	C(S1)	C(S2)	C(S3)	C(S4)	C mean
Luxuriant	<b>9</b>	10	14	30	58	31	<b>29</b>
Moderate	<b>83</b>	84	68	64	42	61	<b>64</b>
Unproductive	<b>8</b>	6	18	6	0	8	<b>8</b>

parts of the fence were severely damaged during the snowmelt, allowing predators to enter in spring 1989 before any trapping could be conducted. When the trapping sites were snow-free, a stoat was already repeatedly trapped in the enclosure. The stoat was removed in the context of spring (June) trapping, and the upper part of the fence was totally reconstructed during the summer, now in a site where snow does not accumulate. Unfortunately, this place turned out to be sensitive to avalanches, which destroyed the fence in March 1990.

### Experimental design during the main experimental period, 1991–95

From 1991 on, we managed to get the fence repaired by mid-July, when the last snowfields had disappeared. The period of effective exclusion ended in late fall, as the predators had now learned to enter the enclosure via the spots, where the first snowdrifts covered the fence. The effective duration of the treatment was thus just 5 to 6 weeks. Consequently, replicated controls were needed to document the response of voles to this short-term treatment. We thus selected four more controls, stretching from the luxuriant base of the slope to arctic–alpine habitats higher up (length 150 m width 40 m). Distributions of the three main habitat categories in the enclosure and the controls (derived from vegetation mapping) are presented in Table 1. The habitat distributions in the enclosure and on the main control were identical, whereas the additional controls were characterized by higher fraction of luxuriant habitats. This made the design conservative by introducing a bias against detecting positive impacts of predator exclusion, especially so for *Microtus* spp, primarily found in the most luxuriant habitats (Viitala 1977, Ekerholm et al. 2001). Although unplanned and initially undesired, the change in design made it easier to evaluate the direct impacts of predator removal, as abnormally high vole densities were now avoided (Ford and Pitelka 1984, Yodzis 1989).

In spite of its size, the enclosure was not large enough to safeguard vole populations against random

extinctions, and for voles, the fence turned out to be a real barrier even before it had been repaired after snowmelt damages. To prevent the predator enclosure from becoming also a vole enclosure, following policy was applied. If a given species was found from the main control but not from the enclosure, one male and one female were moved from the main control to the enclosure. This was done twice: in 1993 for the red vole and in 1995 for the field vole.

### Trapping and density estimation

Lemming variants of Ugglan Special multiple capture live traps (with broad flippers and open entrances) were permanently laid out on all grids in a 10 by 10 m network (310 trap stations in the enclosure, 456 trap stations on the main control, 80 trap stations in each of the additional controls). The traps were left lying on the sites with back doors open and became thus a part of the runway systems of rodents, which profoundly increases their trapping efficiency (Viitala 1977). Trapping was conducted in the second half of June, immediately after snow had disappeared from the slope (except for genuine snow-beds), and in the first two weeks of September. Any predators captured in the enclosure were removed even during the spring (late June) trapping session. Trapping sessions lasted for 96 hours (12 trap rounds), with ‘odd’ rows activated during the first 48 hours, ‘even’ rows during the last 48 h. Traps were activated day and night, baited with oats, and checked at intervals of 8 h. Captured animals were permanently marked, weighed, sexed and aged on the basis of molt patterns.

In estimation of vole numbers from trapping data, two different approaches are currently used. The Nordic tradition is to estimate vole numbers by means of asymptotic enumeration. In previous studies (Viitala 1977, Henttonen et al. 1987, Löfgren 1995, T. Oksanen et al. 1999), it has been found that the accumulated number of captured voles reaches an asymptote after about 96 hours of continuous trapping with Ugglan Special multiple capture live traps (Löfgren 1995, Fig. 4). Thereafter, the number of new captures stabilizes at a low level, indicating that unmarked individuals are either

dispersers or newly weaned juveniles. In this kind of a situation, enumeration and standard CMR methods (Capture and Mark, Krebs 1989) yield practically identical values for systems where the premises of CMR methods are satisfied (compare the enumeration results of Henttonen et al. 1987 with the Mark indices of Previot-Julliard et al. 1999, computed from the same data).

Discussing the relative merits of the two approaches is beyond the point of the present paper. It is, however, worthwhile to note one frequently overlooked limitation of CRM-indices (McKelvey and Pearson 2001). These indices require estimation of a large number of parameters from a limited data-set. Each estimation procedure is subject to error. We have little if any knowledge of the statistical behavior of these errors, not to talk about the statistical properties of their combined impact on population estimates. While CRM estimates doubtlessly come, at average, closer to true values than enumeration results, there is a substantial risk for some individual values to be quite incorrect, as also found in trials where CRM-estimates of the same population were computed after different numbers of checking rounds (J. Dahlgren and D. Rosengren, unpubl.). In the absence of treatment replication, it is vital to avoid the risk of large errors in individual population estimates, while a slight underestimation of the densities of all trapped populations does not bias comparisons between the treatment and the controls. Consequently, we chose to use enumeration.

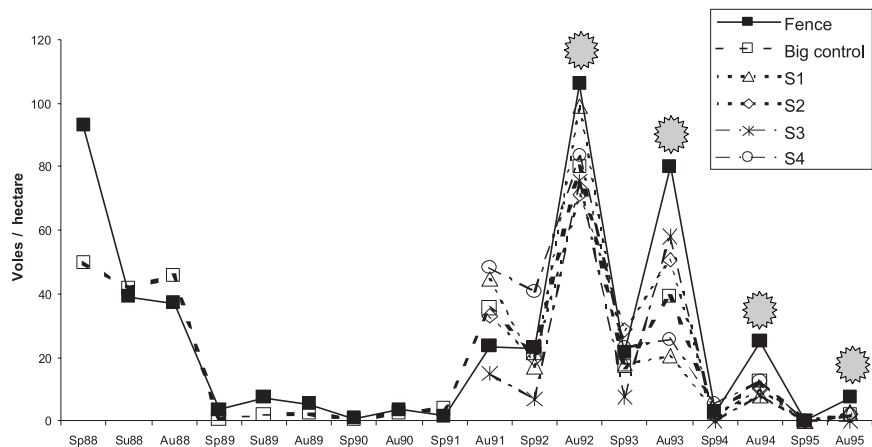
The effective sizes of the additional controls were estimated for each season and for the main functional categories (mature males, mature females, immature in post-juvenile or pre-adult molt and juveniles) by adding a perimeter zone corresponding to their mean observed home range radius within the grid (T. Oksanen et al. 1999). The effective sizes of the additional controls thus

obtained are conservative, because the home ranges of most mature individuals included areas outside the grids, leading to underestimation of home range radii. Consequently, our estimates of vole densities for the additional controls are likely to be somewhat inflated, creating a bias against detecting positive effects of predator exclusion.

### Statistical tests

For the pilot study in 1988–90, no statistics were computed. The results of the experiment will only be presented as a graph concerning the collective vole densities in the enclosure and on the main control. For the period 1991–95, we checked whether the enclosure was a statistical outlier by means of a t-test. The tests for different years were assumed to be statistically independent, since there was ample of time for predators to eliminate all traces of past treatment effect during the period when the enclosure was accessible for predators. To make the test conservative, we consistently used two-tailed tests, although the use of one-tailed tests could be motivated by the existence of a priori predictions. The test was first conducted for collective vole densities. If the enclosure was a statistical outlier with respect to collective vole densities, we proceeded to perform corresponding tests on different species and on the following three functional categories: males in adult or pre-adult moult, females in adult or pre-adult moult and young individuals (in post-juvenile moult or in juvenile pelage), which had been born when the fence was working. The magnitudes of significant treatment effects (effect sizes) were computed as  $(E_i - C_i) / C_i$ , where  $E_i$  is the population density of category  $i$  in the enclosure and  $C_i$  is the same category's mean density on the controls.

Fig. 2. Vole densities in the enclosure and on the main control during spring 1988–95, and in the added smaller control areas during autumn 1991–95. Spring (S) and autumnal (A) densities are shown for all four vole species pooled together (vole individuals per hectare). S1, S2, S3 and S4 are names used for the smaller control areas respectively. Complementary summer trapping periods were added in 1988 and 1989. The sun symbol refers to significant differences between the fence and the control ( $p < 0.05$ ).



## Results

### The pilot phase of the experiment (1988–90)

Before the closure of the fence, several small mustelids were trapped in the enclosure and the main control (L. Oksanen and T. Oksanen 1992), and vole numbers in the enclosure were rapidly declining. On the main control, winter survival was poor and spring densities were on the level typical for post-crash springs. Out of an autumnal stock of 137 voles, only two survived to June 1989, giving an overall survival rate of 1.5%. In the enclosure, where 74 voles were found alive in fall, 7 voles survived, giving a survival rate of 9.5% (Fig. 2). In summer 1989, vole populations in the enclosure increased after the removal of the stoat, but stabilized later on (Fig. 2). The fence was then repaired in the lower parts, where predator activity was highest, but the repair work along the upper edge was going on. The enclosure was thus accessible for a predator smart enough to make a detour via the alpine habitats.

### The main experimental period (1991–95)

There were no significant differences in spring vole densities between the enclosure and the control. In 1991, when vole densities were rising, and the density of mammalian predators was low (T. Oksanen et al. 1999), even autumnal densities in the enclosure and on controls were similar (Fig. 2). During the peak year 1992, vole densities in the enclosure were significantly but not dramatically above the control level. (Fig. 2, Table 2). During the peak year, different functional categories responded differently to the exclusion of mammalian predators. Young voles showed a positive and relatively strong treatment response, whereas old males showed a significant and negative response to the treatment (Table 2). During the decline years (1993–95)

the difference in collective autumnal densities of voles between the enclosure and the controls was consistently significant, densities in the enclosure being at least twice as high as the average for the controls (Fig. 2, Table 2). The magnitude of the difference culminated in the crash year 1995, although in this year, the absolute numbers were so low that the direct impacts of moving two voles from the main control to the enclosure contributed to the magnitude contrast. The strongest positive responses were shown by old females. The responses of young voles were consistently positive and strong in 1994 and 1995. Even males then responded positively to the exclusion of mammalian predators (Table 2).

The positive treatment effects on collective vole densities were primarily generated by field voles (Fig. 3, Table 2), especially by reproducing females and by young individuals (Table 2). Root voles were initially absent from the grids, invading them in 1992. In 1994, when root voles already were present on all grids in spring, they displayed the strongest positive response to the treatment (Fig. 4, Table 2). Gray-sided voles did not show significant responses to the treatment during the peak, but a statistically significant positive response was observed in 1993 (Fig. 5, Table 2). Red voles occurred in low numbers in 1991 and 1992. They disappeared from the enclosure during winter 1991–92, and their re-introduction in 1992 failed. As they were present on all controls in autumn 1992, the negative treatment effect then obtained for them in 1992 was statistically significant (Fig. 6, Table 2).

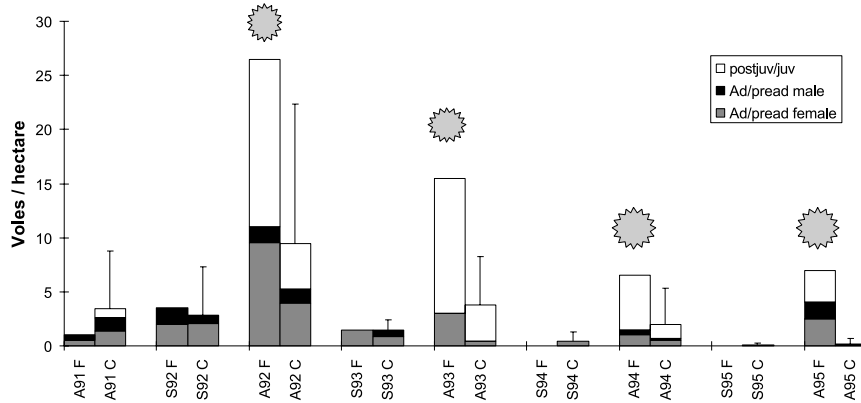
## Discussion

The results reported above show that even short-term fencing during a decline of a cyclic vole population is followed by enhanced seasonal recovery and that the impact is strong enough to override the normal spatial

Table 2. Effect sizes, i.e. magnitudes of statistically significant ( $p < 0.05$ ) treatment effects on collective vole densities, main functional categories (all species combined), the different vole species trapped and functional categories of field voles. 'Old' refers to individuals in adult or pre-adult moult, 'young' refers to individuals in post-juvenile moult or in juvenile pelage. Effect sizes were computed as  $(E_i - C_i) / C_i$ , where  $E_i$  is the population density of category  $i$  in the enclosure and  $C_i$  is its mean density on the controls. Effect sizes for which  $p < 0.01$  are written in bold style.

Unit of computation	Fall 1992	Fall 1993	Fall 1994	Fall 1995
All categories, all species combined voles	+0.33	<b>+1.04</b>	+1.00	<b>+2.87</b>
Young voles	+0.58	+0.66	+1.53	<b>+1.43</b>
Old females	–	+4.04	–	+18.2
Old males	–0.64	+1.50	+2.28	+3.05
Species, all categories combined				
Root voles	–	–	+5.45	–
Field voles	+1.82	+3.07	+2.23	+34.0
Gray-sided voles	–	+0.93	–	–
Red voles	–1.00	–	–	–
Field voles, categories				
Young voles	+2.66	+2.66	+2.73	<b>+41.86</b>
Old females	+1.39	+6.5	–	+34.71
Old males	–	–	–	+20.43

Fig. 3. Average autumnal vole densities during 1991–94 and their standard errors on mainland grids, on control islands and on food supplemented islands. The entries used in computations were means for the whole period for each island or grid. The two unproductive islands without supplemental food had identical averages. According to ANOVA based on logarithmically transferred densities,



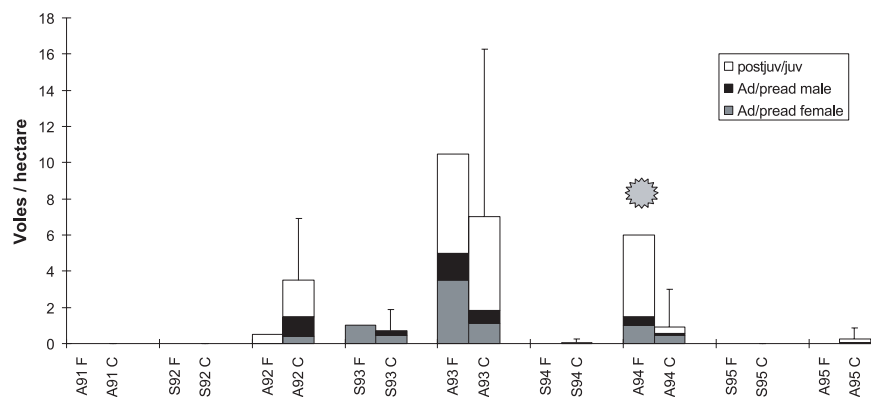
the impact of productivity was highly significant ( $p < 0.001$ ), so was the treatment effect, when the mainland, the control islands and the food supplemented islands were regarded as separate treatments. (A fully factorial analysis was not possible due to the absence of food supplemented mainland grids.) The interaction between productivity and the treatment variable was non-significant ( $p = 0.642$ ). According to Turkey's post-hoc test, both food-supplemented and control islands differ significantly from the mainland when the impact of productivity is accounted for ( $p < 0.001$  in both cases). The corresponding difference between food-supplemented and control islands approached statistical significance ( $p = 0.078$ ).

variation in vole dynamics, making its documentation possible without treatment replication. To our understanding, the 'fence effect' (Krebs et al. 1969), does not provide a plausible explanation for this result. Besides the arguments discussed in introduction (Ostfeld 1994), there are three more reasons to reject the 'fence effect' as a plausible reason for the treatment effect. First, the difference between the enclosure and the controls was weak in the peak year, when densities were highest and the occurrence of a 'fence effect' had been maximally plausible. The strongest contrasts between the enclosure and the controls were observed during the later stages of the decline, when there was amply of empty space for dispersers to settle within the enclosure. Second, on the inside of the fence, the woody poles reached to the upper edge. Hence, a vole really motivated to leave the fence could have climbed up along the posts and jumped down

to the other side. Third, our results were consistent with those of Korpimäki and Norrdahl 1998, obtained without fencing, and with those of Klemola et al. (2000a, b), obtained by using large, replicated predator exclosures with dispersal sinks (Desy and Batzli 1989, Korpimäki et al. 2002). To our understanding, exclusion of mammalian predators is thus the only logical explanation for the contrast between the enclosure and the controls.

Even the responses of different species and functional categories to the treatment are consistent with the interpretation that the removal of mammalian predators accounts for the documented differences between the enclosure and the controls. Reproducing female field voles and their young showed the strongest and the most consistently positive treatment effects (compare with Korpimäki et al. 1994, Korpimäki and Norrdahl 1998). The low statistical power of the tests probably accounts

Fig. 4. Spring (S) and autumnal (A) densities of root voles shown as functional groups and totals (individuals per hectare) in the enclosure (F) and on controls (C) (mean+1 SD), during autumn 1991–95. The standard deviations are based on the means of all functional groups pooled together. The sun symbol refers to significant differences between the fence and the control ( $p < 0.05$ ).



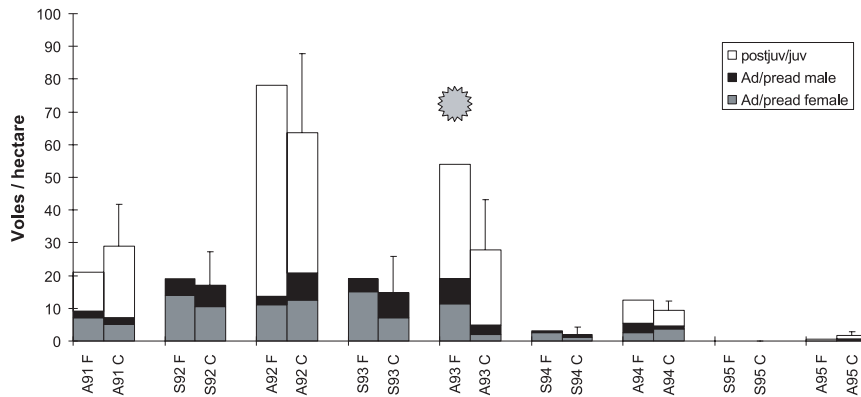


Fig. 5. Spring (S) and autumnal (A) densities of grey-sided voles shown as functional groups and totals (individuals per hectare) in the enclosure (F) and on controls (C) (mean+1 SD), during autumn 1991–95. The standard deviations are based on the means of all functional groups pooled together. The sun symbol refers to significant differences between the fence and the control ( $p < 0.05$ ).

for the fact that the treatment effect for gray-sided voles was significant in 1993 only. The two categories that responded negatively to the treatment in the peak year of 1992 can be regarded as exceptions that confirm the rule. Old males tend to be especially mobile and are thus likely targets for avian predation (Korpimäki 1981, 1985; recall that in 1992, rough legged buzzards, bred in the vicinity of the enclosure and were frequently hunting there). Red voles, in turn, can be regarded as agile and elusive apparent competition specialists (Holt 1977, L. Oksanen 1992), whose small size and specialization to high quality plant products makes them competitively inferior to other voles (Henttonen et al. 1977; notice that the converse results of Sundell et al. 2004, concerning the relation of *Microtus* voles and agile, climbing *Clethrionomys* species to predation were obtained in meadows and willow scrublands, which are not suitable for climbing).

Detailed discussion on magnitudes of treatment effects would require interval estimates for the treatment means, which we could not obtain, as treatment replication was technically and economically infeasible. We tackled this source of uncertainty by making several

choices that biased the study against finding significant treatment effects (Material and methods). This was done in order to ensure that only large treatment effects could be statistically detected and to allow us attach the words ‘at least’ to our estimates of effect sizes. While the exact magnitudes of treatment effects remain opaque, the results nevertheless tell that a short-term removal of predators sufficed to profoundly strengthen the summer recoveries of voles during the gradual vole decline of 1993–95. In combination with the experiments of Korpimäki and Norrdahl (1998), Klemola et al. (2000a, b), Norrdahl et al. 2002 and Hambäck et al. (2004) the results reported above thus indicate that predation plays a major role in the regulation of north Fennoscandian vole populations as proposed by several authors (L. Oksanen and T. Oksanen 1981, 2000, Henttonen et al. 1987, L. Oksanen 1990, Hanski et al. 1991, 2001, Korpimäki et al. 1991, 2003, Korpimäki and Krebs 1996, Turchin and Hanski 1997, T. Oksanen et al. 2000, 2001, Turchin et al. 2000, Norrdahl and Korpimäki 2002).

The impacts short term predator removal reported here become especially instructive when seen in combi-

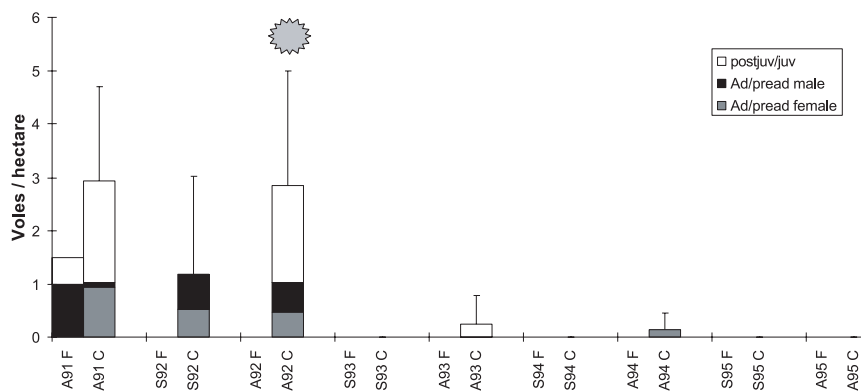


Fig. 6. Spring (S) and autumnal (A) densities of red voles shown as functional groups and totals (individuals per hectare) in the enclosure (F) and on controls (C) (mean+1 SD), during autumn 1991–95. The standard deviations are based on the means of all functional groups pooled together. The sun symbol refers to significant differences between the fence and the control ( $p < 0.05$ ).

nation with the results of island experiment of Hambäck et al. (2004), where voles were allowed to live in virtual absence of predators, while dispersal across the lake (frozen from early October to late June) was hardly a problem (Pokki 1981). On all islands, voles exerted strong impacts on the woody vegetation. In the absence of predators, neither social regulation nor changes in plant quality (Selås 1977, Seldal et al. 1994, Plesner Jensen and Doncaster 1999) sufficed to stop the growth of vole populations to the level sufficient to cause acute depletion of winter resources.

Nevertheless, the message of our results in the intensified debate concerning the role of predation in dynamics of cyclic vole populations (Graham and Lambin 2002, Oli 2003a, b, Korpimäki et al. 2003, Lambin and Graham 2003) is not entirely straightforward. Our fence excluded all mammalian predators. As strict specialists (weasels) remained rather uncommon during the 1993–95 decline and even stoats reached high densities first in 1994 (Aunapuu 1998, Aunapuu and Oksanen 2003), the results reported for 1992 and 1993 concern mainly the impacts of exclusion of generalists (red foxes and minks), which are not normally regarded as likely candidates for the delayed density-dependence that must in one or another way be responsible for population cycles (May and Oster 1976, May 1981). Interaction between voles and generalists may, however, generate cyclic dynamics (T. Oksanen et al. 2001), and the characteristics of the ‘new dynamics’, following the invasion of American minks in 1990 – gradual declines and a pronounced seasonal component in the fluctuations (Fig. 2, T. Oksanen and Henttonen 1996, Ekerholm et al. 2001) – correspond to the predicted impacts of increased prevalence of generalists.

The viewpoints of Oli (2003a, b) and Lambin and Graham (2003) specifically address to the question whether predation is sufficient and necessary for the occurrence of multi-annual density fluctuations in microtine rodents. Their answer to both questions is negative. The multi-annual stability of island populations (Hambäck et al. 2004) might be seen as evidence for the necessity of predation for multi-annual density cycles in microtine rodents. However, a closer look at the islands (Ekerholm et al. 2003) reveals that behind the stable averages lie three entirely different island-specific dynamics: genuine multi-annual stability on two islands, a boom-crash syndrome on one island (where grazing conditions were especially favorable and where the woody vegetation was totally devastated during 1991–93), and gradual increase of voles on a fourth island.

Moreover, pronounced fluctuations of lemming populations are found in the least productive highland parts of our study area, where densities of all predators are chronically very low (T. Oksanen et al. 1992, 1999, L. Oksanen et al. 1997, Aunapuu and Oksanen 2003), so

are the rates of winter nest predation (zero in the crash winter of 1978–79 and 1.7% in the crash winter of 1988–89; numbers of nests inspected in the two crash winters 100 and 117, respectively; sources L. Oksanen et al. 1997, unpubl.). Even the sharp, short-lived peaks of lemmings and long periods of very low numbers indicate resource-limited dynamics (Turchin et al. 2000, Ekerholm et al. 2001), so does their massive impacts on the vegetation (Kalela 1971, L. Oksanen and T. Oksanen 1981, Moen et al. 1993). The boom-crash dynamics of lemmings and corresponding vole dynamics on the island with best winter grazing conditions suggest that predation is not a necessary condition for microtine cycles.

The live trapping study of T. Oksanen et al. (1999), using replicated grids for each landscape type, revealed that vole populations were relatively stable within the most heterogeneous part of our study area (dominated by barren tundra heaths, but with patches of more productive scrubland, too), in spite of the presence of predators and the predominance of small mustelids among them, which indicates that predation by small mustelids is not a necessary condition for population cycles, either. As a whole, the results obtained from our study area thus support the point of Oli (2003a, b) that predation by specialists is neither a necessary nor a sufficient condition for the occurrence of sustained population cycles in microtine rodents. Indeed, there are many kinds of consumer-resource interactions, which have the potential of generating cyclic dynamics (Hanski et al. 1991, 2001, Turchin et al. 2000, Turchin and Batzli 2001, T. Oksanen et al. 2001) but which can, depending on specific conditions, even create a locally stable consumer resource equilibrium (Rosenzweig 1971, Murdoch and Oaten 1975, Rosenzweig and Abramsky 1980, T. Oksanen et al. 2000, 2001). Hence, the search for necessary and/or sufficient conditions for oscillatory population dynamics will hardly become successful unless it is conducted on a relatively abstract level, with focus on those factors, which can destabilize different kinds of consumer-resource systems.

While we find many arguments of Graham and Lambin (2002), Oli (2003a, b) and Lambin and Graham (2003) agreeable and even rather trivial, we have difficulty to understand their tendency to discredit the experiments conducted by Korpimäki and Norrdahl (1998) and Klemola et al. (2000a, b), which to our judgment, convincingly show that predation plays a major role in the regulation of vole populations in the agricultural landscapes of central Fennoscandia. To attribute the results to the mysterious ‘fence effect’ seems dubious even in principle. Moreover, fencing was not used in the experiment of Korpimäki and Norrdahl (1998), and dispersal sinks were included in the design of Klemola et al. (2000a, b).

The current debate seems to suffer from the failure of the participants to realize that different ecologists working on cyclic populations of small mammals are asking different questions. The Kielder team appears to be primarily interested in the existence of oscillatory population dynamics. In this perspective, the crucial experiments are those, which lead to stability. Most northern European ecologists, in turn, try to identify the main sources of direct and time-delayed density dependence connected to the kind of population cycles characteristic for northern Fennoscandia, with high amplitude and very low minima, and high frequency of summer declines (Hansson and Henttonen 1985). In this context, the salient feature of a successful experiment is to impose pronounced changes on dynamics of treated populations (e.g. decrease or increases the amplitude of density fluctuations) or on collateral variables (e.g. the damage inflicted by voles on plants).

Our primary interest lies in dynamics of terrestrial food chains (L. Oksanen et al. 1981, L. Oksanen and T. Oksanen 2000), and in that context, limit cycles and stability are just modifications on the same theme. We study microtine rodents because they (along with reindeer/caribou) form the dominating part of arctic and subarctic-alpine herbivore communities (Wielgolaski 1975, Batzli et al. 1980). Hence, interaction between predators and the entire guild of microtine rodents are a crucial part of the dynamics of arctic-alpine food webs, having profound effects on plant populations and structure of plant communities (Sammul et al. 2000, 2004, Olofsson et al. 2002), and even on nutrient cycling and primary productivity (Batzli et al. 1980, Zimov et al. 1995, Olofsson et al. 2001, 2004, Olofsson and Oksanen 2002). For us, the bottom line of the present study and the island experiment of Hambäck et al. (2004) is that, in spite of its low average primary productivity, the low arctic life zone still harbors many habitats, where predators are persistently present and exert a controlling impact on the collective density of herbivorous mammals, curtailing their potentially strong impact on the vegetation and on ecosystem processes. It is up to other colleagues to judge, whether this finding has any implications for the search of necessary and sufficient conditions of sustained, regular density oscillations in microtine rodents.

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