

## Predators indirectly protect tundra plants by reducing herbivore abundance

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The role of predators in controlling herbivores and indirectly affecting plant abundance is controversial, and some have argued that such trophic cascades are rare in terrestrial habitats. To examine the potential of trophic cascades in a shrubby tundra ecosystem, vole densities, plant damage and plant cover were examined in areas with and without small mammal predators. On islands without predators, vole densities and plant damage were up to five times higher compared with predator-rich mainland habitats. As a consequence, the abundance of three out of five dwarf shrub species was substantially reduced on predator-free islands, providing evidence for strong cascading effects in a rather large-scale terrestrial system. Herbs on the other hand were not affected by the increased herbivory on islands. This suggests that the strength of trophic cascades also depends on the interaction between plant type and seasonality.

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Whether or not predators control herbivore populations and thereby indirectly provide protection for plants is a central question both for basic and applied ecology, and is currently a hot debate (Strong 1992, Polis 1994, Brett and Goldman 1996, Pace et al. 1999, Persson 1999, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, Bell et al. 2003). Such indirect top-down effects, trophic cascades, were suggested more than 40 years ago as an explanation for the apparent green-ness of the world (Hairston et al. 1960). However, while large-scale trophic cascades have frequently been observed in aquatic and marine ecosystems (Strong 1992, Brett and Goldman 1996), evidence from natural terrestrial systems derives, with few exceptions (McLaren and Peterson 1994, Sinclair et al. 2000, Terborgh et al. 2001,

Norrdahl et al. 2002), only from small-scale studies (Polis et al. 2000, Schmitz et al. 2000, Halaj and Wise 2001). It has therefore been suggested that trophic cascades are rare in terrestrial systems because these systems have reticulate and complex food webs, are spatially heterogeneous, show variable prey population dynamics and have variably edible prey (Strong 1992, Polis 1994, 1999, Polis and Strong 1996, Chase 2000, Polis et al. 2000).

In northern ecosystems, e.g. in northern Fennoscandia, earlier studies have shown that both herbivore–plant and predator–herbivore interactions may be strong (Chitty et al. 1968, Boonstra and Krebs 1977, Oksanen and Oksanen 1981, 1992, Henttonen et al. 1987, Oksanen and Moen 1994, Norrdahl and Korpi-

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mäki 1995, Korpimäki and Krebs 1996, Hambäck and Ekerholm 1997, Klemola et al. 1997, 2000, Turchin et al. 2000), providing a potential for trophic cascades. Previous observations also suggest that plant damage, in presence of vole predators, is limited to only a few plant species, despite the ability of many vole species to reduce total plant biomass drastically (Moen et al. 1993, Klemola et al. 2000). Nevertheless, this system has three characteristics that Polis et al. (2000) suggested to preclude the possibility of a trophic cascade. First, the system is certainly heterogeneous at several spatial scales with high animal movement rates between patches (Oksanen and Oksanen 1992, Hambäck et al. 1998, Oksanen et al. 1999). Second, vole populations fluctuate strongly with peak intervals of three to five years (Henttonen et al. 1987, Oksanen and Oksanen 1992, Hanski et al. 1993, Hörnfeldt 1994, Ekerholm et al. 2001). Third, the plant community includes both species that are highly edible to voles, such as several herb species, and species that are rather inedible, such as several evergreen shrubs. Based on this information we should expect a rather weak or even absent trophic cascade. This was also the outcome of the only study that has experimentally examined whether predation on voles could explain their limited effect on plant biomass (Norrdahl et al. 2002), and the authors prescribed this lack of effect to the strong seasonality of the system. Interestingly, they argued that this occurred because their system contained mostly forbs and grasses, species that are highly edible to voles (Kalela 1957, Bergeron and Jodoin 1987, Moen et al. 1993, Hjältén et al. 1996). In contrast, the few less edible plants were heavily affected by the increased vole herbivory.

In this study, we further examined the relation between seasonality and edibility for the strength of trophic cascades. We thus compared the effect of grey-sided voles (*Clethrionomys rufocanus*) on shrubby tundra vegetation between island and mainland areas over a three year period. The islands used in this study had strongly reduced predator densities, with only scattered observations of non-breeding avian predators during the study period, while mainland areas had a diverse set of predators. In order to compare effects between island and mainland, we estimated vole numbers, vole herbivory and effects on plant cover. The latter effect was examined by erecting vole exclosures on island and mainland areas, and compare responses in and outside exclosures. The predictions for the experiment are straightforward. If trophic interactions are strong we should expect increased vole numbers, increased vole herbivory and reduced plant cover on islands compared with the mainland. Moreover, as our study system is dominated by dwarf shrubs, in comparison with the herb-dominated system studied by Norrdahl et al. (2002), we could expect stronger effects on plant cover than found in their study.

## Material and methods

### Study area and design

The study was conducted in the Joatkanjávrit research area on Finnmarksvidda in northernmost Norway (69°45'N, 24°30'E) from autumn 1991 to spring 1994. We used three islands in lake Iesjávri as predator-free areas and two mainland reference areas. Island sizes ranged from 0.6 to 1.3 ha (Hambäck and Ekerholm 1997), and their vegetation was dominated by either productive, low arctic scrublands, or by barren heaths with patches of scrubland along the shoreline. Mainland reference areas were selected such that the mainland and island vegetation was similar, one area was at the more productive end compared with islands and the other at the less productive end. Thus, one mainland locality was situated in a moist and nutrient-rich slope occupied by productive scrublands, while the other was situated in a generally barren lowland with scrublands along streams (S1-4 and L1-4 in Oksanen et al. 1999, respectively). Both localities were about 10 km from the lake. The nutrient-rich slope was characterized by generally high mammalian and avian predator densities, and even in the more barren area, activity of mammalian predators was high during the decline of vole populations (Oksanen and Oksanen 1992, Oksanen et al. 1999). The islands were on the other hand isolated from the predator-rich control area (and from corresponding ones on the other side of the lake) by 10 km of unproductive tundra habitats with very low mammalian and avian predator densities (Oksanen and Oksanen 1992) and, in addition, by 0.5 to 3 km of water (July–September) or ice (October–June). No mammalian predators were trapped on the islands during the study, although the multiple capture traps we used also capture stoats and weasels (all weasels captured on the mainland and a large fraction of trapped stoats have been caught in these traps, Oksanen and Oksanen 1992, Oksanen et al. 1999), and except for gulls no avian predators were breeding on any study island during our study period. Long-tailed jaegers move on the lake in spring and fall and one pair was breeding on the mainland only 500 m from one island in 1994. The only mammalian predators occasionally observed on the lake (spotted, tracked or identified by their scats) were red and arctic foxes. Even their presence was sporadic and restricted to late winter. Thus, the islands were not totally predation-free, but the presence of predators was occasional and the small mustelids, assumed to drive the cycles on the mainland in accordance to the advocates of the predation hypothesis (Oksanen 1990, Korpimäki et al. 1991, Oksanen and Oksanen 1992, Hanski et al. 1993), were absent.

As compared to excluding predators through fencing (Norrdahl et al. 2002), mainland-island comparisons have both advantages and disadvantages. The main disadvantage is that randomization is impossible. Strictly

speaking, introductions to islands are thus in the borderline terrain between experiments and comparisons of spatial patterns. The main advantages are technical. Predator-proof fencing is expensive and, to our experience, works only in summer at high latitudes. Islands, in turn, occur for free as replicates, and treeless islands are protected by their invisibility even in winter. Moreover, dispersing out of islands across the frozen lake is a trivial task for a dispersion-motivated vole, especially in spring, when weather is warm and the ice is black. Even the swimming distances from our experimental islands to mainland and to larger islands (3 km to 100 m) are short as compared to the swimming capacity of voles (Pokki 1981). Thus, the much-discussed fence effect (Krebs et al. 1969, Ostfeld 1994) can a priori be eliminated as an alternative explanation for eventual mainland–island differences in vole-vegetation dynamics. Predator proof fences and island–mainland comparisons thus have different strengths and weaknesses. Hence, we have used both approaches in concert, where the predator enclosure experiment, conducted on the nutrient-rich slope, serve as a control for the inherent weaknesses of the island-mainland comparison. As the results from our predator enclosure experiment is reported in another paper (Ekerholm et al. 2004) we will primarily focus this paper on the island-mainland comparison.

### Introduction and monitoring of vole numbers

Before the start of the study there were no voles on any island, even though islands had been occupied by voles during previous vole peak-years (Oksanen and Oksanen 1981, Oksanen et al. 1987). During summer 1991, we therefore caught grey-sided voles in areas surrounding the lake and placed them on the islands, at initial densities equal to that in the mainland areas (35 voles per ha). This density corresponds to the middle phase of population rise in the best habitats on the nutrient-rich slope and a vole peak in typical habitat complexes of the lowland tundra (Oksanen et al. 1999) and taiga (Henttonen et al. 1987). We thereafter estimated vole densities through live-trapping two times each year, at the beginning of summer (early July) and in early autumn (end of August), on both islands and in the two mainland reference areas. To trap voles, we used Ugglan special multiple live capture vole trap in grids with traps at 10-m intervals. In each mainland area, traps were placed in four trap grids, separated by at least 500 m, while trap grids on islands included the entire island. Traps were left open between trapping occasions, and at the start of a trapping period we closed and baited traps with crushed oats. On mainland grids, each second row was activated at a time, and trapping lasted for 96 hours. On islands, the method had to be modified due to logistic constraints. All traps were activated simulta-

neously to provide the same trapping effort in shorter time, and then checked every eight hours for 48 hours. Voles were individually marked, and vole numbers were determined as the minimum number alive at any given trapping period. We tested the differences in vole density between localities from 1991–1994 with multivariate repeated-measures ANOVA on  $\log_e$ -transformed values, using trap grids as replicates (i.e. three grids in each mainland locality and three islands). In this and subsequent test, we checked residuals but in no cases did these deviate significantly from normality.

### Vole herbivory

To estimate the shoot mortality due to vole herbivory (i.e. the proportion of cut shoots), we marked 240 bilberry (*Vaccinium myrtillus*) shoots, sub-divided into 12 plots at the start of the study, in all trap grids in mainland localities and on islands (Hambäck and Ekerholm 1997, Oksanen et al. 1999). Plots were dispersed across the area in four clusters, and plots within each cluster were separated by at least 5 m. Plots were revisited in spring and autumn each year to count cut shoots and to mark new shoots, such that each plot always had 20 marked bilberry shoots. Vole damage in this area is easy to score as voles usually cut the entire shoot and carry it to the nest for consumption. Partial damage is rare and could safely be ignored. If a shoot had died from other causes we noted this and marked a new shoot. The proportion cut shoots is calculated as (cut shoots)/(marked shoots–lost shoots). The differences in shoot mortality between localities were tested with a factorial ANOVA on  $\log_e$ -transformed values, using time and locality as factors.

### Plant cover

We assessed the effect of voles on plant abundance by studying changes in plant cover in open plots and in vole enclosures. For logistic reasons, we only used the slope area in comparisons of plant cover. At each location, we selected eight to ten permanent plots, at least 1 m<sup>2</sup>. All permanent plots were selected such that it was possible to build vole proof fences around the plot. An additional criterion was that all plots should include bilberry. Therefore no plots were placed in either the most barren or the most lush habitats. Every second plot on each island or in the slope were randomly assigned as enclosure and the remaining plots were left open. The enclosure nets had a mesh size of 2 × 2 cm and were dug down 15 cm, leaving 85 cm above ground. During the course of the experiment no enclosure showed signs of intrusion by voles. We estimated plant cover in the plots through a modified point intercept method. This index correlates well with plant biomass for single species in

such habitats (Jonasson 1988). We used a transparent plastic table with randomly distributed points as template in low vegetation and a measurement tape with randomly distributed points as template in higher vegetation. On each plot we counted the number of contacts to the pin of each plant species at each point, usually contact with a leaf. For species with very small leaves (e.g. *Empetrum hermaphroditum*), the unit was a shoot. The effect of excluding voles on plant cover was compared between islands and mainland from 1992 to 1994 with a multivariate repeated measures ANOVA, with localities nested under the main/island treatment (data transformed as  $w = \log_e(x+1)$ ). In the plant cover analyses, we compared responses of three major vascular plant groups; deciduous shrubs, evergreen shrubs and herbs. In addition, we compared responses for five shrubs that occurred commonly in most areas and that had about equal initial densities in mainland and island areas. In all analyses, we only included plots with a non-zero starting density of a species.

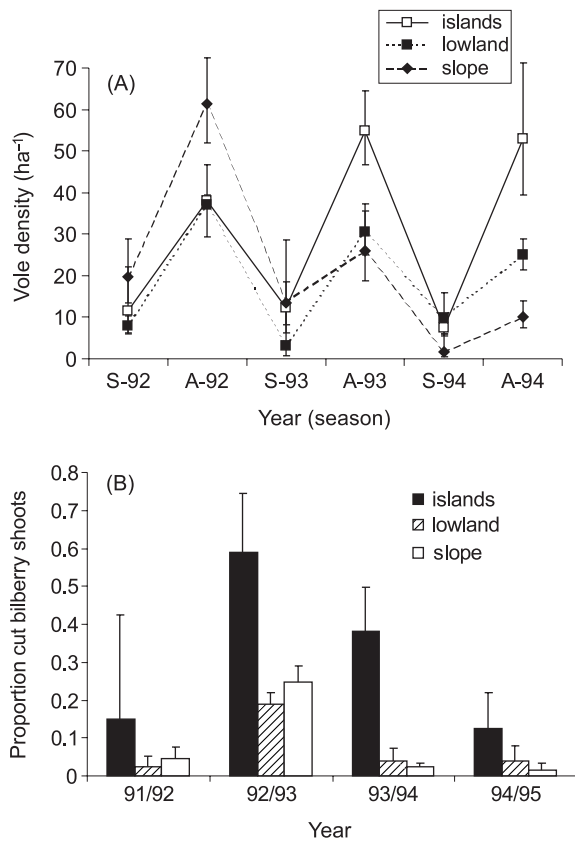


Fig. 1. Population densities of grey-sided voles (A, mean  $\pm$  SE,  $N = 3$ ) and the proportion cut bilberry (*Vaccinium myrtillus*) shoots (B, mean  $\pm$  1 SE,  $N = 3$ ) on islands and in two mainland reference areas.

## Results

Vole densities in the two mainland locations decreased throughout the study period, particularly in the slope area, while densities on predator-free islands increased (Fig. 1A). This resulted in a significant location-by-time interaction, and at the end of the study vole densities were between 2 and 5 times higher on islands compared with mainland areas (Location  $F_{2,8} = 3.8$ ,  $P = 0.07$ ; Time  $df = 2,7$  (num,den), Wilks' lambda = 0.3,  $P < 0.5$ ; Location-by-time  $df = 4,14$ , Wilks' lambda = 0.2,  $P < 0.05$ ). As a consequence of increased vole densities, rates of shoot mortality due to vole herbivory were each year about 4 times higher on bilberry shoots growing on islands compared with shoots in either mainland location (Fig. 1B, Model  $F_{11,36} = 4.6$ ,  $P < 0.001$ ; Year  $F_{3,36} = 7.5$ ,  $P < 0.001$ ; Location  $F_{2,36} = 11.8$ ,  $P < 0.001$ ; Location-by-year  $F_{6,36} = 0.7$ ,  $P > 0.6$ ). Due to increased

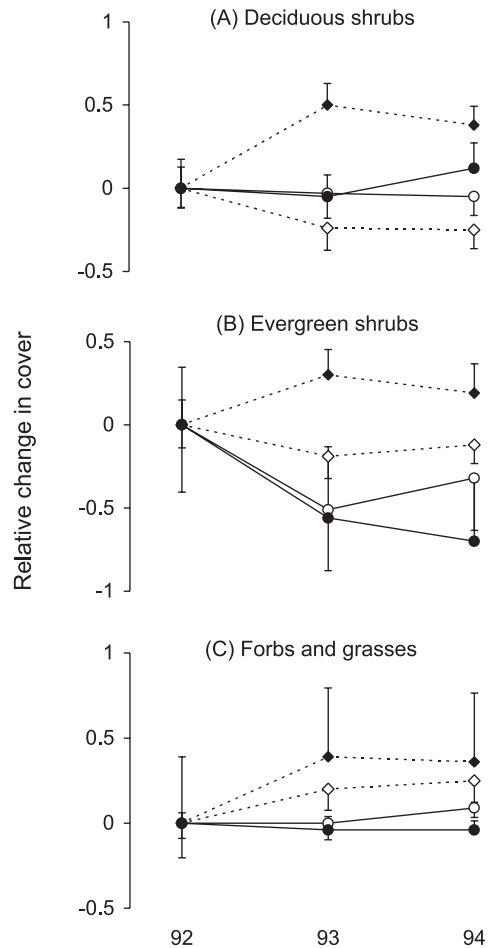


Fig. 2. Cover of deciduous shrubs (A), evergreen shrubs (B) and herbs (C) on islands (dotted line), mainland (solid line), and in (filled symbol) and outside (empty symbol) vole-proof fences. In all plots the value for 1992 is set to 0 to show changes better ( $\pm$  SE, for statistical significances see Table 1).

Table 1. Statistical tests on the cover of deciduous shrubs, evergreen shrubs, herbs and five shrub species comparing islands and the mainland reference area (P-values in parantheses, NS equals  $P > 0.2$ ). Entries for between-subject effects (without time) are sums of squares attributed to each effect in the ANOVA. Entry for within-subject effects (with time) are Wilks' lambda, and df for these tests is the maximum. For the following species the denominator df had to be adjusted as plots without a plant initially were excluded from the analyses; EVS (-4), F&G (-1), Bn (-16), Eh (-13), Vm (-15), Vu (-15) and Vv (-6). MS- and F-values of test statistics can be calculated from the figures given and are omitted for brevity.

Effect	(max df)	Deciduous shrubs	Evergreen shrubs	Forbs and grasses	<i>Betula nana</i>	<i>Empetrum hermaphroditum</i>	<i>Vaccinium myrtillus</i>	<i>V. uliginosum</i>	<i>V. vitis-idaea</i>
Main/Island (MI)	1	1.1 (0.12)	218.6 (0.0001)	178.2 (0.0001)	0.5 NS	126.5 (0.0001)	33.1 (0.0001)	5.1 NS	36.8 (0.001)
Fence (F)	1	0.1 NS	<0.1 NS	0.6 NS	0.7 NS	0.2 NS	0.2 NS	1.7 NS	0.7 NS
Location (L(MI))	3	0.7 NS	5.4 NS	13.0 (0.04)	25.8 (0.14)	4.8 NS	7.2 (0.06)	19.5 NS	2.7 NS
MI-by-F	1	<0.1 NS	1.1 NS	<0.1 NS	5.6 NS	0.3 NS	3.0 (0.08)	0.7 NS	<0.1 NS
F-by-L(MI)	3	4.4 (0.03)	3.0 NS	4.1 NS	1.7 NS	1.6 NS	9.2 (0.03)	4.6 NS	0.9 NS
Error	20	14.2	41.6	43.5	70.4	21.0	29.0	80.9	28.2
Time (T)	(2,32)	0.91 NS	0.74 (0.01)	0.74 (0.01)	0.64 (0.03)	0.38 (0.0001)	0.90 (0.19)	0.76 (0.10)	0.88 (0.18)
MI-by-T	(2,32)	0.82 (0.04)	0.65 (0.002)	0.78 (0.02)	0.68 (0.05)	0.41 (0.0002)	0.81 (0.04)	0.78 (0.12)	0.66 (0.005)
F-by-T	(2,32)	0.41 (0.001)	0.81 (0.05)	0.97 NS	0.45 (0.002)	0.90 NS	0.81 (0.04)	0.97 NS	0.96 NS
L(MI)-by-T	(6,64)	0.77 (0.20)	0.78 NS	0.66 (0.04)	0.77 NS	0.49 (0.03)	0.87 NS	0.85 NS	0.86 NS
MI-by-F-by-T	(2,32)	0.50 (0.0001)	0.87 (0.14)	0.95 NS	0.59 (0.02)	0.73 (0.05)	0.77 (0.02)	0.99 NS	0.97 NS
F-by-L(MI)-by-T	(6,64)	0.74 (0.12)	0.62 (0.03)	0.63 (0.02)	0.93 NS	0.52 (0.04)	0.81 NS	0.77 NS	0.69 (0.12)

rates of herbivory, the cover of deciduous shrubs was reduced on islands relative to the mainland location as indicated by a significant mainland/island-by-fence-by-time interaction, with a similar tendency for evergreen shrubs (Fig. 2, Table 1). In the test of species, two deciduous shrubs (*Vaccinium myrtillus* and *Betula nana*) as well as one evergreen shrub (*Empetrum hermaphroditum*)

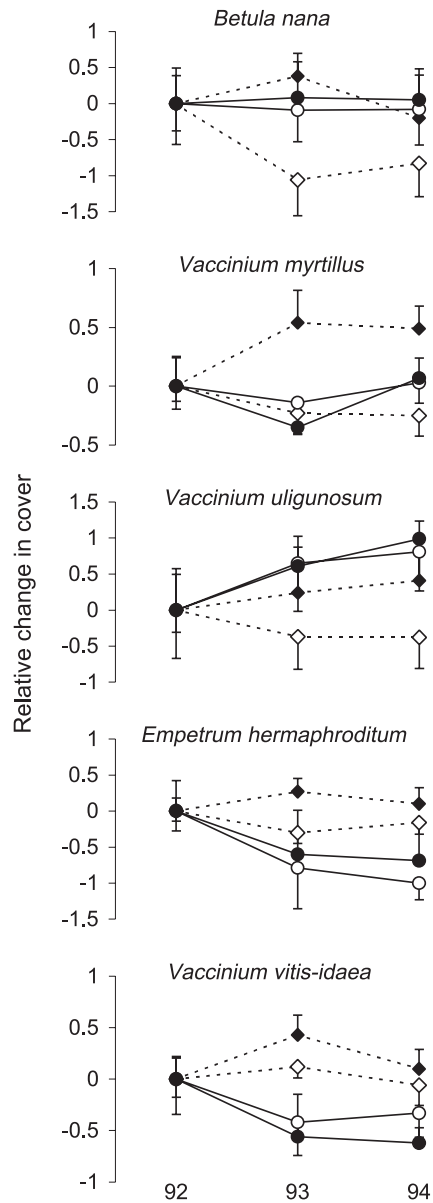


Fig. 3. Cover of five common shrub species on islands (dotted line), mainland (solid line), and in (filled symbol) and outside (empty symbol) vole-proof fences. The five shrub species include three deciduous species (*Betula nana*, *Vaccinium myrtillus*, *V. uliginosum*) and two evergreen species (*Empetrum hermaphroditum*, *V. vitis-idaea*). In all plots the value for 1992 is set to 0 to show changes better ( $\pm$ SE, for statistical significances see Table 1).

tum) were significantly reduced on islands relative to the mainland location (Fig. 3, Table 1). The effect magnitude was larger for deciduous shrubs, and the cover for the most affected plant species was reduced by more than 50% after three seasons.

## Discussion

There is an intense current discussion about trophic cascades in terrestrial systems (Persson 1999, Chase 2000, Polis et al. 2000, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002), but the focus of the debate has shifted from a presence-absence discussion to a discussion about when trophic cascades are strong and when they are weak. This paper adds one piece in the puzzle by showing that the strength of trophic cascades depends on within-year dynamics. It is evident from our short-term experiment that the increased vole densities on predator-free islands have negative effects only on winter food plants but not on summer food plants. In this study, vole densities and vole herbivory on bilberry were increased with up to five times on islands compared with the mainland. Increased herbivory was also apparent on other shrub species, although this was not systematically quantified in all areas. On two islands, annual shoots of *Salix glauca* and *Vaccinium vitis-idaea* were almost completely consumed by voles, while the few mountain birch (*Betula pubescens* ssp. *czerepanowii*) individuals were almost completely debarked on the most heavily affected island. Similar damage was not observed on these plant species in any mainland area. As a consequence of the intense herbivory, the cover of dwarf shrubs was reduced up to 50 percent on islands (Fig. 2). On the other hand, herbaceous plants were not negatively influenced by increased vole densities on the islands (Hambäck and Ekerholm 1997).

The mechanism underlying the different responses by summer and winter food plants is most likely the pulsed plant production and seasonal bottlenecks for voles (Hambäck and Ekerholm 1997). Many small mammals are especially sensitive to seasonal bottlenecks as they often store very little fat and only survive a few days without food (Robbins 1992). Vole individuals may consequently face serious food shortage during the long winter, in this area nine months of the year, if not killed by predators before starvation. In spring, voles therefore have low densities, as was also observed in this study, and are unable to track the sudden increase in plant production. By the time voles reach high numbers, the grasses and forbs have ceased production and withdrawn their resources below-ground. Voles are therefore generally not limited by food during summer and herbivory rates during this period are consequently low in strongly seasonal envi-

ronments (Ericson 1977, Andersson and Jonasson 1986, Bergeron and Jodoin 1987, Moen 1990, Hambäck and Ekerholm 1997, Norrdahl et al. 2002).

The low herbivory during the summer contrasts with the high herbivory during winter. As a consequence of food-limitation, voles consume also rather unpalatable plants during this period. Nevertheless, it is evident that palatability matters, at least in the short term. In this study, the effect on deciduous shrubs (*Betula nana*, *Vaccinium myrtillus* and *V. uliginosum*) was generally larger than on less palatable evergreen shrubs (*Empetrum hermaphroditum* and *V. vitis-idaea*, Fig. 3, Kalela 1957, Sonesson and Callaghan 1991). Yet, even evergreen shrubs were negatively affected at high vole densities, and more so than highly palatable forb species. Thus, in a strongly seasonal environment, where resident mammalian herbivores are saturated in summer and starving in winter, it may be 'better flee than poorly fight', i.e. the best option for plants to escape herbivory may be to spend the limiting season in the ground.

Our study complements the study by Norrdahl et al. (2002), showing that the results found in their study can be extended to another biome and to a more shrub-dominated habitat. It is evident that the stronger trophic cascade found in this study compared with theirs is related to differences in plant community structure. In both studies, food-limited voles had strong, negative impact on all woody plants, while impacts on herbaceous plants varied from weakly negative to positive. In our study system, initially dominated by woody plants, this translated immediately to a strong, community-level cascade. In their old-field system, the community level impact was weak in a short time frame. However, elimination of woody plants by voles from an old-field may stop secondary succession towards predominately woody vegetation (Pigott 1985, Manson et al. 2001). In a long time perspective, the impact of food limited voles on the vegetation may thus be even stronger in the old-field system of Norrdahl et al. (2002) than on the low arctic islands studied by us.

Both studies provide a useful extension of the trophic cascade theory at an experimental scale that is seldom observed. In fact, experimental evidence for large-scale trophic cascades in terrestrial systems has only rarely been documented, which is perhaps not surprising considering the labor intensity involved. The most convincing study is by Terborgh et al. (2001) that utilized relatively predator-free islands created by a hydroelectric impoundment in Venezuela. They found that densities of rodents, howler monkeys, iguanas and leaf-cutter ants were 10 to 100 times greater on islands compared with mainland areas after eight years. As a consequence, densities of seedlings and saplings of canopy trees were severely reduced on islands. Two other cases have been documented from Isle Royale

(McLaren and Peterson 1994) and the island of Anticosti (Potvin and Breton 1992), where a lack of predator control caused increased densities of moose (Isle Royale) or white-tailed deer (Anticosti) and pronounced effects on relatively palatable tree species and no effects on the least palatable trees. In contrast to these studies, experimental exclusion of mammalian predators of snowshoe hares in Yukon, Canada, did not lead to reduced plant biomasses despite higher herbivore numbers in predator exclosures (Krebs et al. 1995, Sinclair et al. 2000).

While the issue of community level terrestrial trophic cascades is far from settled, the results reported by ourselves and by Norrdahl et al. (2002) indicate that the absence of top predators will not simply favour unpalatable plants (Potvin and Breton 1992, McLaren and Peterson 1994, Power et al. 1996, Terborgh et al. 2001). Even herbaceous species, able to avoid herbivory through the use of temporal refuges, are favoured. The present study therefore extends the theory about species interactions in multitrophic systems into the realm of seasonal systems (Hambäck and Ekerholm 1997, Norrdahl et al. 2002). Seasonality effects, and temporal refuges, are generally not considered in models investigating tri-trophic systems. The importance of seasonal fluctuations for trophic interactions has been shown for other types of direct and indirect interactions, such as apparent competition (Hambäck and Ekerholm 1997, Abrams et al. 1998, Hambäck 1998), and it is clear that non-seasonal models are insufficient for understanding the consequences of species interactions in these systems (Oksanen 1990). The predictions made by these models on productivity–biomass relations (Oksanen et al. 1981, Abrams 1992) for strongly seasonal systems may therefore turn out most realistic if interpreted as referring to the biomass available at the end of the unfavorable season. Biomasses of herbaceous plants at the end of the favorable season are probably more directly connected to their productivity. To further understand these and other limitations of the trophic cascade hypothesis, additional large-scale experiments in terrestrial ecosystems are greatly needed. These studies may also show whether perceived differences between aquatic and terrestrial systems (Strong 1992, Polis et al. 2000) are due to systematic differences in some ecosystem properties or to an insufficient number of large-scale studies.

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