Interactions between gray-sided voles (*Clethrionomys rufocanus*) and vegetation in the Fennoscandian tundra.

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List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numbers.


II. Dahlgren J., Oksanen L., Olofsson J. and Oksanen T. Recovery of low arctic tundra vegetation following heavy grazing by gray-sided voles (*Clethrionomys rufocanus*). Manuscript.


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Background

The enigma of the green world has fascinated ecologists for decades. Each plant is exploited by some herbivores, and their population growth could potentially lead to decimation of plant biomass, unless the collective density of herbivores is controlled by the collective action of predators or unless the low quality or heterogeneity of the terrestrial vegetation makes it invulnerable to herbivory (Strong 1992, Polis and Strong 1996). In their Green World Hypothesis Hairston et al. (1960; Hairston and Hairston 1993) advocated the former explanation, pioneering the trophic cascade approach – a theme that has become increasingly popular in current community ecology (Knight et al. 2005; Croll et al. 2005). Experimental studies concerning the strength of trophic cascades in terrestrial ecosystems have so far primarily focused on folivorous insects and their predators. In these food webs, predation only seem to influence the abundance of palatable plants (Schmitz et al. 2000; 2004; Halaj and Wise 2001; Shurin et al. 2002; Borer et al. 2004). However, evidence from islands and experimental systems indicates that the regulatory impact of predators on herbivorous mammals and their subsequent effect on the vegetation can be strong (Potvin and Breton 1992; McLaren and Peterson 1994; Terborgh et al. 2001; 2006; Norrdahl et al. 2002; Hambäck et al. 2004).

Oksanen et al. (1981) extended the Green World Hypothesis by considering the impact of primary productivity on interactions within the endotherm branches of terrestrial grazing chains. Their conjecture is customarily referred to as the Exploitation Ecosystem Hypothesis (EEH). EEH is based on the assumption that herbivorous and predatory endotherms have the potential to regulate their resources. However, the potential of predators to control herbivorous mammals is predicted to be realized only in fairly productive habitats, where the vegetation can absorb the impacts of relatively numerous herbivores. In widespread, unproductive habitats, herbivores are predicted to be food limited, as even herbivore densities too sparse to support predators are dense enough to profoundly deplete their forage. The strong interaction is in those ecosystems should thus be between herbivorous mammals and plants. High importance of herbivory has indeed been proposed by several ecologists specialized in arctic, alpine or arid ecosystems (Tihomirov 1959, Caughley and Gunn 1993). At intermediate productivities, herbivorous endotherms are predicted to be controlled by predators, but the direct effects of herbivores on vegetation are still predicted to be pronounced. Therefore, plant biomass should respond negatively to removal of predators and positively to the removal of herbivores (Fig.1). My main study system, islands in and mainland sites close to the lake Iešjávri, should represent an area with such intermediate productivity.
Introduction to plant-herbivore interactions
Herbivores influence plant communities through a wide range of mechanisms. They often directly reduce the abundance of the most preferred plants (Harper 1969, Crawley 1990). Many plants have thus developed mechanical and chemical defense mechanisms to protect themselves from being eaten (Crawley 1983, Rausher 2001). However, the effect of herbivory on plants depends not only on the plant palatability, but also on plant tolerance or resilience (Strauss and Agrawal 1999, Rausher 2001, Del Wal and Crawely 2005). Plants with a high capacity to regrow can thus be favored by intense grazing, even if they were preferred food plants for the herbivore (Del Wal and Crawley 2005). Resistance and tolerance represent two general strategies of plant defense against herbivores (Leimu and Koricheva 2006). Since resources are limited and resistance and tolerance are likely to impose conflicting demands on plants, the occurrence of trade offs between these two strategies has usually been assumed (Herms and Mattson 1992, Leimu and Koricheva 2006). Besides these direct impacts, herbivores influence the vegetation even indirectly (Mulder 1999). Herbivores can increase or decrease the abundance of plants by altering competitive interactions between plants (Mulder and Ruess 1998, Zaches et al. 2001), physical conditions (Brooker and van der Wal 2003, van der Wal and Brooker 2004) or nutrient availability (Pastor et al. 1993, Zimov et al. 1995, de Mazancourt et al. 1998, van der Wal et al. 2004).
The impact of herbivores on the vegetation depends on their density (Huntly 1991) in relation to the growth rate of plants (Grime 1979). In areas characterized by pronounced fluctuations of herbivore populations, the long-term effects of herbivores on vegetation will thus depend both on the effects of herbivores during periods of high density and the recovery of vegetation during periods of low herbivore density. If the same plants, which are depleted when herbivores are dense, recover when herbivores are sparse, the vegetation will simply fluctuate between different states (Jefferies et al 1994). Given a trade off between ability to grow and defend (Herms and Mattson 1992, Leimu and Koricheva 2006), fluctuating levels of herbivory are expected to favor tolerant and resilient plants, whereas recurrent, strong herbivory should favor heavily defended and thus unpalatable plants.

According to the carbon/nutrient balance (CNB) hypothesis (Bryant et al. 1983, Coley et al. 1985), the optimal allocation to herbivore deterrent carbon-based secondary metabolites (CBSMs) is correlated to the relative availability of carbon and nitrogen. Although the carbon/nutrient balance hypothesis can predict the effect of fluctuations in carbon and nitrogen availability on chemical defenses in some cases, it has failed in others (Hartely et al. 1995, Koricheva et al. 1998). The carbon/nutrient balance hypothesis has been criticized for lacking a clear physiological mechanism, and for not considering the effects of genotype on the phenotype of a plant (Hamilton et al. 2001). Changes in CBSMs may also be masked by the rapid turnover of some of these metabolites (Reichardt et al. 1991). However, the carbon/nutrient balance hypothesis seems to be able to predict the response for metabolic end-products and compounds with slow turnover rates such as condensed tannins fairly well (Reichardt et al. 1991, Keinänen et al. 1999).

Herbivore damage may induce changes in C/N ratio and levels of carbon-based secondary metabolites in plants and thus their subsequent susceptibility to other herbivores. The effects of initial herbivore damage on the palatability of plants clearly depends on the type of damage caused (Lehtilä et al. 2000), and is linked to parallel changes in plant chemistry or growth characteristics. For instance, insect defoliation during the growing season tends to reduce subsequent herbivore performance (den Herder et al. 2004, Nykänen and Koricheva 2004). Winter browsing, on the other hand, has been found to reduce the number of meristems per plant, resulting in fewer but more vigorous shoots (Price 1991, Bryant et al. 1991, Bryant 2003). These regrowing shoots have often higher levels of N and lower C/N ratios than the removed shoots, and may thus be more susceptible to herbivory in the future (Danell and Huss-Danell 1985, Danell et al. 1985, Haukioja 1990, Hjältén and Price 1996, Roininen et al. 1997, Lehtilä et
The intensity of herbivory may also strongly affect the susceptibility of plants to subsequent herbivory (Wallin and Raffa 1999, Wallin and Raffa 2001). Although the relationship between the intensity of herbivory and subsequent levels of plant defense compounds may be linearly positive or negative (Mattson and Haack 1987, Waring 1987), plant defense levels may also be maximized by intermediate levels of herbivory. Proximately, this may be caused by damage induced limitations of precursor availability for biosynthesis of defensive metabolites or activation of compensative responses. A likely ultimate reason is a trade-off between resistance and resilience, making it adaptive for heavily damaged plants to prioritize resilience (Oksanen 1990).

Behavior and life history of herbivores (Hambäck and Beckerman 2003) as well as food web interactions (Ohgushi 2005) may also affect the level of herbivory on target plants. Moreover, herbivores can alter competitive interactions between plants and availability of nutrient in soil and their by influence the chemistry of plants that they do not directly browse (Agrawal 2004).

The responses of plants to herbivory have even animal ecological ramifications. A substantial number of ecologists have remained skeptical to the idea that vole cycles are driven by predation and, instead, propose various hypotheses based on time-delayed changes in food quality (Seldal et al. 1994, Jensen and Doncaster 1999) or interactions between climate, plant reproduction and plant defenses (Selås 1997, 2006). A shared prediction of all these hypotheses is that vole cycles should display their normal course even in the absence of predators, and voles should not exert essentially stronger impact on plants on predator-free islands than the mainland. Even if my primary scope was not to study population cycles, papers I - III, allowing for comparisons between vole dynamics in presence of predators and in their virtual absence, are relevant for these hypotheses, too.

The aims of this thesis were to study:

- the strength of trophic cascades in a tundra ecosystem.

- the effect of gray-sided voles (Clethrionomys rufocanus) on the plant community composition in low artic tundra vegetation in presence and absence of predators.

- how gray-sided voles affect the quantity and quality of bilberries, their main winter food plants.
Outlines of the study system

I studied interactions between the gray-sided vole and the vegetation, on predator-free islands in the freshwater archipelago of Lake Iešjávri and in the mainland surrounding the lake (Paper I, II, III and V).

In terms of biomass and impact on plant communities, the gray-sided vole is the dominating herbivorous mammal of the North Fennoscandian inland tundra (Andersson and Jonasson 1986, Oksanen et al. 1999, Ekerholm et al. 2001, Olofsson et al. 2004). As typical for rodents in arctic and boreal regions (Hanski et al. 1993) it displays pronounced multi-annual density fluctuations (Ekerholm et al. 2001, Hörfeldt 2004). The prominent role of gray-sided voles in these ecosystems depends ultimately on the low nutrient availability and the dry and cold climate, which contributes to the dominance of a few dwarf shrub species (Kalliola 1939, Oksanen and Virtanen 1995), which are unpalatable in winter for other herbivores capable of removing the snow or to moving within it – the reindeer (*Rangifer tarandus*), the Norwegian lemming (*Lemmus lemmus*) and the root vole (*Microtus oeconomus*). For gray-sided voles, the palatability of these dwarf shrubs varies from species to species. The crowberry (*Empetrum nigrum*) is regarded as largely unpalatable and the bilberry (*Vaccinium myrtillus*) is highly palatable and considered to be the most important winter food plant for gray-sided voles (Aleksandrova et al. 1964, Kalela 1957, Ericson 1977, Tolvanen et al. 1992, Hambäck and Ekerholm 1997, Hambäck et al. 1998, 2002). In addition to the studies in northern Norway, I studied the effect of simulated herbivore damage and fertilization on quantity and quality of bilberry twigs in Svartberget research park (Paper IV).

Iešjávri
Lake Iešjávri is situated on Finnmarksvidda in northernmost Norway (69°45´N, 24°30´E, 390 m.a.s.l.). Biogeographically, the area belongs to the weakly continental sector of the hemiarctic zone (Oksanen and Virtanen 1995), where lichen-dwarf birch tundra prevails, but outposts of birch forest are found in sites with favorable microclimate. Snowmelt is rapid, occurring around June 10th. The growing season starts about a week later, when the topsoil has thawed. The break up of ice on larger lakes normally happens between June 20th and 25th. The fall starts in late August and the winter usually arrives in late September. The area consists of fairly flat Pre-Cambrian bedrock. Numerous shallow lakes have been created in the end of the Ice Age; the largest of these is Iešjávri. Along its shorelines, glaci-fluvial ridges form long peninsulas and rise here and there as elongated islands, with sizes ranging from 0.02 to 105 ha. Channels
wide enough to substantially influence movements of voles and their mammalian predators separate many islands from the mainland.

All islands consist of three primary habitats: hummock bogs (1) i.e. moist habitats with dense vegetation dominated by cloudberry (*Rubus chamaemorus*) and several dwarf shrubs; bilberry, artic blueberry (*Vaccinium uliginosum*), lingonberry (*Vaccinium vitis-idaea*), crowberry and dwarf birch (*Betula nana*). The ground is covered by a thick moss layer, dominated by *Hylocomnium splendens* on hummocks and *Polytricum ssp.* or *Sphagnum ssp.* in depressions. (2) drier sites mainly occupied by lichen heaths and dominated by the same dwarf shrubs as for (1), but at lower coverage. (3) windswept areas on top of the ridges where the lichen cover is thin and the dwarf shrub cover consists of scattered plots of lingonberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum nigrum*). For more details see Hambäck and Ekerholm (1997).

Hummock bogs form the preferred habitat of gray-sided voles (Ekerholm et al. 2001), the overwhelmingly dominant rodent species in the region (Oksanen et al. 1999; Ekerholm et al. 2001). For this reason and because its critical position on the productivity axis (see Fig. 1), I chose the hummock bog as the focal habitat of my study. All large islands harbor populations of gray-sided voles, but the species is seldom found on small islands more than 200 m from mainland. Except for lemmings during peak years, no other rodents occur in this habitat in significant numbers. Reindeer, (*Rangifer tarandus*) migrate through the mainland in early winter, but do not enter the islands, as the lake is then only partially frozen. Hares (*Lepus timidus*) and grouses (*Lagopus lagopus*) occur in moderate numbers on the mainland and on large islands. In winter, they move freely in the entire archipelago, but can then only consume tops of tall shrubs and plants growing on wind-blown ridges, as neither hares nor grouses can remove the tightly packed tundra snow.

Two species of vole predators are frequently found in hummock bogs: long-tailed jaegers, (*Stercorarius longicaudus*), breeding there during years of high vole numbers, and stoats, (*Mustela erminea*) which are especially numerous during vole declines (Oksanen et al. 1992, 1997, 1999, Aunapuu and Oksanen 2003). All these predators are found on the large islands, too. Stoats have never been seen, tracked or trapped, on the smaller islands, but they are visited by arriving flocks of migrating jaegers. In years with low vole densities in the mainland, jaegers stay in flocks and moves on the lake even in summer. Conversely, in peak vole years, these flocks quickly break to pairs which settle on the mainland and large islands.
Svartberget
Svartberget is an experimental forest situated in northern Sweden (64°14′N, 19°46′E), 70 km NW of Umeå. The experimental area is located in the middle boreal zone (Ahti et al. 1968) in a late successional Norway spruce (*Picea abies*) forest of bilberry type, *sensu* Kalliola (1973). As compared to the hummock bogs of Finnmarksvidda, the main difference is the replacement of dwarf birch shrubs by spruces. The field layer is dominated by the same ericaceous dwarf shrubs - bilberry and lingonberry, and even the co-dominants, the twinflower (*Linnea borealis*) and Wavy Hair-grass (*Deschampsia flexuosa*) are common in both areas. The difference abundance relationships of field layer plants between the hummock bogs of Iešjávri and the spruce forests of Svartberget reflect primarily the difference between weakly paludified and non-paludified habitats. Even on Svartberget, cloudberry, arctic blueberry and crowberry abound in peatlands.

Methods

Vole trapping
On the predator-free islands of Iešjávri, I studied vole populations by live-trapping, using grids with trapping stations at intervals of 10 m, which covered the entire habitable areas, excluding only the vegetation-free shoreline and the windblown ridges covering the center of the largest predator-free island (Paper I, II, III and V). A similar grid was established in a hummock bog on the big control island (used in paper I), the only island which was equally isolated as the predator-free islands and shared their physical conditions but had nevertheless the main predators present. In addition, reference areas of 90 by 40 m were established on the mainland close to the shore of different sides of the lake to ensure that there were no spatial gradients in vole dynamics, which could bias the experiment. Moreover, four islands were kept permanently vole-free by continuously operating traps and were subjected to removal trapping if voles were found.

Each station had an Ugglan Special multiple capture trap. Spring trapping was conducted immediately after the ice breakup in June-July. Fall trapping was carried out between August 25th and September 15th. During each trapping session, traps were activated, baited with crushed oats and checked for every 8h during a 48h period on the predator-free islands with closed populations and during 96h period in the mainland reference grids and on the control island. The average percentage of voles captured at least twice during the same trapping session was 76% (range 68% to 84%) for mainland reference grids and 78% (range 71% to 85%) for predator-free islands, indicating that vole censuses were
equally complete on all grids. Between the trapping sessions, the traps were lying in the runways with back doors open, which improves trapping efficiency (Viitala 1977).

Due to the high recapture rates (see also Löfgren 1995; Oksanen et al. 1999), and the similarity of recapture percentages between mainland and island grids, we decided to estimate population sizes by direct enumeration. When converting numbers to densities, we added a 9 m perimeter zone to the effective trapping areas of the control island and the mainland reference grids, corresponding to the perimeter zone found by Oksanen et al. (1999) for juveniles. This gave an effective grid size of 0.6 ha. We deliberately chose this minimum estimate of effective grid size to ensure that the vole density estimates for control and reference areas were, if anything, inflated, making our comparisons conservative. Moreover, we estimated vole densities on predator-free islands for entire habitable island areas, which deflated our estimates of vole densities in hummock bogs of the largest predator-free island.

Plants
In Paper I, I studied the direct impacts of voles and the indirect impacts of predators on hummock bog vegetation. To eliminate the impacts of grazing history, I used vegetation blocks transplanted from the control island, with both voles and predators, to the treatments (predator-free islands and vole-free islands) and back to the control. I used eighty transplanted vegetation blocks (size 70 by 70 cm, depth at least 30 cm), excavated from a hummock bog in the isthmus of the control island, slightly outside the control grid. I randomly assigned the excavated plots to the different treatments (no voles, voles but no predators, voles and predators).

Changes in the vegetation (paper I, II and IV) were monitored with the point frequency method (Jonasson 1988), with 100 sampling points per square (50 in paper IV). We recorded all contacts between green parts of vascular plants and the pin (diameter 2 mm) separately, except for crowberry, for which branches were treated as units. Regression functions between plant biomass and number of point intercepts were estimated from 90 additional plots that were investigated both with the point intercept method and harvested for plant biomass.

The effects of voles on bilberry twigs (in paper III) were studied by marking individual ramets in permanent plots. Twenty bilberry ramets were marked in each permanent plot in summer 2000. The numbers of live, dead and missing ramets were then recorded annually in the beginning of the summer and all dead
or missing ramets were replaced by marking the nearest ramets, so that the number of marked ramets was still twenty in the beginning of every winter.

The age structure of bilberry ramets (in paper III) was recorded in random plots (0.25 m × 0.25 m) at all sites. All bilberry ramets within the square were counted and cut at ground level. If there were less then five ramets in a plot, the ramets closest to the plots were collected to get five ramets. These additional ramets were used for estimating the age structure of bilberry only, and were not used for estimating population density. The age of each ramet was determined by retrospective aging techniques (Tolvanen 1995). Thereafter the ramet was dried at 40°C for 48 hours and weighed.

Grazing pressure on willows (paper V) was estimated by marking willow twigs on each island in the autumn and counting the number of marked twigs that had been cut by voles in the spring. To study insect herbivory on *Salix glauca*, we randomly collected leaves and twigs from each of our study sites at the peak of the growing season. I then estimated the proportion of the tissue consumed by invertebrate herbivores on leaves from each site. Shoot length, leaf size and number of leaves per shoot were recorded from ten current-year shoots in each site.

**Preference trials**
In preference trials (in paper III and IV), a number of bilberry twigs from the different treatments were offered to each vole simultaneously, along with rabbit pellets, a less preferred food source. The shoots were fixed in foam designed to hold flower arrangements in place (Oasis), so that they were standing in an upright position, similar to the natural situation. Preference by the voles was recorded as the number of shoots of each type cut at the end of the trial. The voles were collected in the Iešjávri area at the beginning of September 2001 and were kept in separate cages in a greenhouse at a temperature of 7–10 °C until the experiment started. During this time, the voles were fed on rabbit pellets and potatoes. The voles used in the preference trial were all post-juveniles or pre-adults that had been born during the summer and had not yet reproduced. The sex ratio was even and their weight varied between 18 and 27 g.

**Chemical analyses**
The bilberry ramets (paper IV) and willow leafs (paper V) collected for chemical analyzes were homogenized in liquid nitrogen and 20 mg of the powder was extracted with methanol as described by Witzell et al. (2003). The HPLC-equipment was of a Merck Hitachi (LaChrom) L-7100 pump, L-7200
autosampler, L-7360 column oven (set at 30 °C), and L-7455 diode array detector. The compounds were separated on a Chromolith™ (RP-18e 100-4.6) column. The mobile phase consisted of water (A, pH adjusted to 2.5 with H3O4P) and methanol (B). The elution profile was 12–15% B in A at 0–2 min, 15–23% B in A at 2–8 min; 23–35% B in A at 8–12 min; 35–70% B in A at 12–24 min, followed by rinsing and equilibration to initial conditions. The flow rate was 2 ml/min. The compounds were tentatively identified on basis of their spectral characters (200–400 nm). Epicatechin and vanillic acid were quantified against corresponding pure standards, cinnamic acid derivatives were quantified as chlorogenic acid equivalents and flavonoids as isoquercitrin equivalents. The standard compounds were purchased from Sigma (Sigma Chemical Co., MO, USA) and Extrasynthese (Genay, France). Condensed tannins were determined by the vanillin–HCl assay (Sun et al. 1998), and concentrations of carbon and nitrogen were analysed in the same samples of shoots. For this purpose, 5 mg of the milled shoots from each treatment was used. Carbon and nitrogen concentrations were analysed by an elemental analyser (2400 CHN analyzer, Perkin Elmer, Norwalk, CT).

**Paper I**

I investigated the importance of a trophic cascade in tundra ecosystems. During 2001-2003, populations of gray-sided voles fluctuated seasonally on predator-free islands as expected for populations limited by winter food (Klemola et al. 2003). Autumn densities were several times higher than autumn densities on the control island. Vole densities on the control island increased from levels below trappability in spring 2000 to slightly less than 100 voles per hectare in autumn 2002, and started thereafter to decline. The change from rise to decline was associated with the appearance of stoats in my traps on the mainland reference grids and conformed to the expected dynamics of rodent populations interacting with specialized predators (Hanski et al. 1991; Turchin et al. 2000; Klemola et al. 2003). The high vole densities on predator-free islands indicate that in the presence of predators, even peak densities are substantially depressed. My findings are thus consistent with previous results emphasizing the role of predation for the regulation of herbivorous mammals (Hanski et al. 2001, Crête and Manseau 1996, Korpimäki and Norrdahl 1998; Krebs et al. 2001, Hanski and Henttonen 2002; Klemola et al. 2003, Korpimäki et al. 2005).

Vegetation blocks transferred from scrubland habitats on an island with predators present, to similar habitats on predator-free islands were devastated by vole grazing. Conversely, plant biomass increased in blocks transferred to vole-free islands. My results indicate that predators protect tundra vegetation through
a trophic cascade, in spite of the diversity of plant types and the initial 
abundance of tannin-loaded evergreen ericaceous dwarf shrubs. Recall that the 
ocurrence of unpalatable species and the diversity of defensive strategies in 
vascular plants has been a standard critique against simple models of food web 
dynamics (Leibold 1989; 1996; Strong 1992; Polis and Strong 1996; Polis 1999; 
Chase et al. 2000). Yet, the impacts of the absence of predators cascaded to the 
entire plant community, leading to pronounced decline in community level plant 
biomass. Moreover, the plant biomass displayed a positive response to the 
removal of voles on the control island as well. Thus, herbivorous mammals 
fluence plant biomass of low arctic scrublands even in the presence of 
predators, but the impact of herbivores is pronouncedly strengthened in the 
absence of predators. These results are in accordance with the predictions from 
the Exploitation Ecosystems Hypothesis (EEH) (Oksanen et al. 1981; Oksanen 
and Oksanen 2000).

On the predator-free islands, the largest declines were recorded for evergreens 
and for bilberry. The other deciduous plants common enough to be analyzed 
separately coped better with the increasing grazing pressure, and the herbaceous 
dwarf cornel (*Cornus sueccia*) benefited from the absence of predators. Bilberry 
was decimated even in the presence of predators and persisted at its initial levels 
on vole-free islands only. The contrasts between the vole removal and predator 
removal treatments were significant for five out of seven woody plants: bog 
rosemary (*Andromeda polifolia*), dwarf birch, crowberry, lingonberry, and 
bilberry, implying that these species respond consistently negatively to 
increasing herbivory pressure. The least palatable plants (i.e. evergreen 
ericaceous dwarf shrubs) turned out to be especially dependent of predators. The 
only species, which clearly gained from the absence of predators, was the 
palatable, herbaceous, dwarf cornel. In the arctic, low palatability is thus an 
advantage only in the presence of predators.

**Paper II**

This study focused on the recovery of low artic scrubland vegetation following 
ten years of intensive grazing of gray-sided voles. This study shows that the 
collective biomass of vascular plants recovered completely within only three 
years, when voles were excluded. Although most plants that dominated in 
ungrazed vegetation recovered rapidly in exclosures, the vegetation did not 
simply return to its initial state.

The contrast between exclosures and open plots was significant for one 
evergreen dwarf shrub, crowberry, two deciduous dwarf shrubs, bilberry and
artic blueberry and for one herbaceous plant, cloudberry. The contrast was almost significant for lingonberry. No significant effects were detected for the two other species common enough to be tested statistically, i.e. dwarf birch and dwarf-cornel.

The most spectacular (4.6 fold) increase in the vole exclosures was observed for the evergreen crowberry, the least palatable species (Aleksandrova et al. 1964) included in this study. This result contradicts the predictions of Herms and Mattson (1992) and was unexpected, as crowberry was the only tundra plant that recovered poorly from disturbance in an earlier experiment (Olofsson et al. 2005). The type of disturbance does, however, differ between these two studies. In the study by Olofsson et al. (2005) disturbance was severe, removing all aboveground plant organs and damaging roots. To be able to grow back in these plots, crowberry either had to re-grow from remaining roots and rhizomes or colonize the plots by seeds. In the present study, voles damaged only erect aboveground shoots. Remaining semi prostrate twigs had most leaf bearing shoots close to the ground. When voles were excluded, these flat crowberry mats could expand rapidly, making the poor ability of crowberry to recover from rhizomes or seeds irrelevant. While the evergreen crowberry increased substantially, the other formerly abundant evergreen dwarf shrub, the lingonberry, responded only weakly to vole exclusion. The contrasting response of these two evergreen, tannin accumulating species could be explained by the difference between their growth forms. Lingonberry remained vulnerable because of its stereotypic growth form with erect shoots growing from a horizontal rhizome. In sites where lingonberry had been depleted by voles, it had no horizontal, leaf bearing shoots ready for expansion but had to re-grow from below-ground rhizomes. Moreover, crowberry could reduce damages by changing its growth form, whereas lingonberry continuously exposed its erect shoots to browsing, which gradually exhausted its energy reserves.

Both herbs abundant enough to be included in this study, i.e. cloudberry and dwarf cornel, increased in exclosures, even if the contrast between exclosures and open plots was not statistically significant. Summer herbivory by voles may thus be more important on these predator-free islands than previously reported (Hambäck and Ekerholm 1997). The collective results from paper I and II indicate that the response to vole herbivory of herbaceous plants can vary depending on the initial situation and time scale. It seems likely that pronounced, multi-annual fluctuation in grazing pressure is maximally favorable for most herbaceous plants, as such a situation prevents erect woody plants from gradually excluding herbaceous plants and allows herbaceous plants to take advantage of their main asset: ability to recover and to expand quickly during the grazing-free periods. Paradoxically, however, this kind of grazing even
favors the evergreen, woody crowberry, which can become both grazing-resistant and very resilient when it has suffered its initial losses and changed its growth form from semi-erect to trailing.

**Paper III**

This study focuses on the interaction between gray-sided voles and their main winter food plant bilberry (Kalela 1957, Ericson 1977, Tolvanen et al. 1992, Hambäck and Ekerholm 1997, Hambäck et al. 1998, 2002). The fraction of bilberry ramets cut by herbivores was higher on predator-free islands than on mainland sites, and lowest on vole-free islands throughout the study period. On the predator free islands, between 50% and 80% of bilberry ramets were cut every year. The intense herbivory on bilberry twigs from the dense populations of gray-sided voles had by the end of the study reduced the biomass of bilberry twigs by almost 90% on the predator-free islands and by more than 50% on the mainland with predators present. Corresponding impact have been reported from other boreal and arctic ecosystems (Ericson 1977, Andersson and Jonasson 1986, Ericson and Oksanen 1987. Tolvanen 1994, Hambäck and Ekerholm 1997, Grellmann 2002, Hambäck et al. 2004, Olofsson et al. 2004, Paper I).

However, although up to 80% of the bilberry ramets were eaten repeatedly for many years on the predator-free islands, the species persisted. Bilberry compensated for lost tissue by producing new ramets. After ten years of heavy grazing, bilberry still produced twice as many ramets on predator-free islands than on vole-free islands. After single defoliation events, plants might compensate for the lost tissue by reallocation of resources from belowground nutrient and carbon reserves (Chapin 1980). However, considering the long duration of this experiment, the compensatory regrowth of bilberry could hardly depend of stored resources from before the introduction of voles. It seems more likely that the ramets produced in spring were able to store enough carbohydrates and nutrients in the rhizomes during the summer, to provide resources for new ramets in the next spring. Instead of going extinct, bilberry thus became functionally herbaceous on the predator-free islands.

Bilberry leaves and ramets contain a wide rage of different defense substances (Laine and Henttonen 1987, Oksanen et al. 1987, Hambäck et al 2002, Strengbom et al. 2003) and several studies have considered grazing-induced or other changes in the forage quality of bilberry as a factor that could explain the multi-annual fluctuations in microtine populations (Laine and Henttonen 1987, Selås 1997, 2006). However, these defense substances do not seem to be especially deterrent for gray-sided voles, as up to 80% of bilberry ramets were eaten year after year on the predator-free islands. Moreover, even though other
plants have been found to respond to herbivory by inducing defense substances (Agrawal 1998), the palatability of bilberry increased due to vole herbivory. A preference trial revealed that bilberry ramets from predator-free islands were more preferred by gray-sided voles than ramets from mainland sites, and ramets from mainland sites were more preferred than ramets from vole-free islands. These results are in agreement with previous studies using chemical analyses; which show that simulated and real vole grazing increase the N content and reduces phenols and tannin levels in bilberry ramets (Laine and Henttonen 1987, Oksanen et al. 1987, Paper IV).

**Paper IV**

This study focused on effects of simulated damage and fertilization on the quality and quantity of bilberry twigs as food for gray-sided voles. I addressed this question by combining long-term field experiments with preference-trials and chemical measurements.

Four years of clipping reduced the abundance of bilberry twigs, regardless whether it was combined with fertilization or not. Clipping and fertilization induced changes in the growth form as well as in levels of phenols. Fertilization increased shoot size while clipping decreased it. Tannin levels were highest in the control treatment, lowest in the fertilized treatment and intermediate in damage and damage plus fertilization treatments. Reductions in condensed tannin and phenolic acid concentrations following fertilization appear to be a common phenomenon, and our results are in accordance with the general concept of the carbon/nutrient balance hypothesis (Bryant et al. 1983, Coley et al. 1985) as well as with reported responses of several woody plant species to fertilization, including birches (Graglia et al. 2001), aspen (Bryant et al. 1987) and spruce (Hartely et al. 1995). There were no significant effects of fertilization on plant nitrogen content. The preference trial revealed that voles preferred the fertilized bilberry shoots. The unfertilized and damaged bilberry twigs were the least preferred shoots by gray-sided voles. The low palatability of these shoots cannot be explained either by tannin or nitrogen levels. The small size of the shoots might explain why they were not chosen by gray-sided voles. The results were in apparent conflict with the results of the other preference trial (paper III), where gray-sided voles preferred the small bilberry shoots from the predator free islands. However, clipping by hand and clipping by voles are different treatments, as voles return easily available nutrient to the vegetation as urine and faeces. Therefore, the treatment “fertilization plus clipping”, which was preferred by gray-sided voles, probably amounted to the best simulation of the effects of voles. Changes in plant growth-form are commonly reported
following herbivory or pruning (Danell and Huss-Danell 1985, Danell et al. 1985, Price 1991, Roininen et al. 1997). The results obtained in papers III and IV indicate that grazing impacts on growth form and chemistry of plants have partially conflicting impacts on the food choice of voles, and the impact of clipping without fertilization is entirely different from the impact of vole herbivory.

**Paper V**

The purpose of this study was to evaluate the relationships between gray-sided voles and the chemistry, growth characters and subsequent susceptibility of northern willows (*Salix glauca*) to invertebrate herbivory.

Vole density correlated positively with nitrogen concentrations in the leaves, with number of leaves per shoot, with leaf size, and with shoot length. Moreover, there was a negative correlation between vole densities and the C:N ratio in leaves as well. This is in accordance with the results of several previous studies (Roininen et al. 1988, Roininen et al. 1994, Roininen et al. 1997, Stein et al. 1992, Hjältén and Price 1996, Olofsson and Strelgbohm 2000), which show that the plants at sites with high herbivore densities tended to have larger leaves with higher N concentration and lower C/N ratios than plants at sites with lower herbivore densities. However, there was no correlation between vole densities and leaf concentrations of C, condensed tannins or any of the individual phenolic compounds that were analyzed. The higher nutrient content of browsed plants may result from increased allocation of resources per remaining meristem, driven by increases in the root/shoot ratio (Bryant et al. 1991b, Bryant 2003). However, voles might also indirectly enhance N contents in willows, by enhancing the N turnover or by reducing root competition from other plants. Voles may thus enhance the subsequent palatability of willows, both directly and indirectly.
Conclusions

In the absence of predators, vole densities in a low arctic scrubland increased several fold and voles dramatically reduced the abundance of vascular plants. Even though the plant community consisted of a diverse set of plant types with vastly different allocations of reduced carbon to secondary compounds, the impacts of predators cascaded all the way down to community level plant biomass. Plant biomass increased when voles were removed, even in the mainland, where predators were present. In this system, herbivorous mammals thus influence plant biomass even in the presence of predators, but the impact of herbivores is much stronger when predators are absent. (Fig. 2)

![Figure 2](image-url)

**Figure 2.** A schematic view over the main interactions studied in this thesis. Interactions between herbivores and plants in the presence and absence of predators, within and between trophic levels. The sizes of the arrows represent strength of an interaction.

In the absence of predators, voles damaged both preferred food plants (bilberry) and strongly defended plants (crowberry). In the presence of predators, however
voles decreased the abundance of the most preferred species only. (Fig. 2) Thus, differences in palatability between plants matter even under arctic winter conditions, as long as predators are present. Herbivores are selective as long as forage is not depleted. When herbivory is intense enough to generate acute shortage of winter forage, all available plants are consumed independent of palatability and the only successful plant strategy is resilience.

Nevertheless, when the vegetation recovered from intense grazing it did not simply return to its ungrazed state. Herbaceous plants that had gained from the heavy impacts of voles on woody plants kept on increasing, whereas the recovery of dwarf shrubs was quite heterogeneous. The strongest recovery was displayed by crowberry, the least palatable ericaceous dwarf shrub abundant enough to be analyzed individually. The resilience of plants in this ecosystem cannot thus be understood as a problem of carbon allocation but seems to be primarily determined by their over-all morphology. Plants insisting in production of erect shoots and placing most of their reserves above ground recovered poorly, whereas herbaceous plants with subterranean rhizomes and creeping woody plants recovered strongly.

Gray-sided voles influenced bilberry, their main winter food plants, even in presence of predators, but the effect was much stronger when predators were absent. However, although most bilberry ramets were eaten repeatedly for many years on the predator-free islands, the species persisted. Bilberry compensated for lost tissue by producing new ramets. After ten years of heavy grazing, bilberry still produced twice as many ramets on predator-free islands than on vole-free islands, demonstrating that a highly palatable woody plant can survive intense winter herbivory by becoming a “functional herb”. In any case, the new ramets produced after heavy winter browsing were high quality food for gray-sided voles. The interaction between gray-sided voles and bilberry twigs thus lacks time-delays, which can generate multi annual population cycles.

Food limited herbivores favor plants, which do not expose their resource-storing organs to herbivores. Whether this is achieved by being herbaceous, by a persistently trailing habit, or by a flexible growth strategy, where a plant shifts from semi-erect to prostrate growth form after being grazed is a tactical matter, reflecting to the same strategy: to avoid a growth form where a single bite in winter would deprive large amounts of foliage from its support and connection to roots. The advantages of different tactical solutions to this strategic problem cannot be inferred from the defense strategy or growth form without considering the frequency, intensity and timing of the grazing as well as the state of the vegetation in the absence of grazing.
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