

Interactions between gray-sided voles (*Clethrionomys rufocanus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant

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Abstract We compared the abundance, population structure and palatability of bilberry ramets on vole-free islands, islands with voles but no predators (predator-free islands) and mainland sites with both voles and predators. As expected, bilberry biomass was strongly correlated with the herbivory pressure exerted by the voles, since it was significantly lower on the mainland, and much (>80%) lower on the predator-free islands, than on the vole-free islands. However, another finding, which conflicts with hypotheses postulating that herbivory generally induces plant defenses, was that voles preferred ramets from predator-free islands. Bilberry plants were fairly tolerant to grazing since they compensated for some of the lost tissue by producing more new ramets. This response should promote stability in the plant–herbivore interaction by reducing the impact of past grazing on current food production and thus minimizing time delays in the interactions that could potentially generate population cycles.

Keywords Voles · Bilberry · Plant defense

Introduction

Despite decades of research, opinions concerning the causes of population cycles of voles still diverge (Graham and Lambin 2002; Korpimäki 2003; Hörnfeldt 2004). Recent work on the dynamics of vole populations in boreal and arctic ecosystems supports the specialist predator hypothesis (Korpimäki et al. 2004, 2005; Ekerholm et al. 2004). In the absence of predators, however, vole densities can rise and have significant impact on their winter food plants, suggesting that their numbers may crash due to food limitation in such cases (Norrdahl et al. 2002; Dahlgren 2006). In addition to such readily observable direct effects, grazing may induce changes in plant quality, which could potentially explain the regular population fluctuations of voles (Haukioja and Hakala 1975; Batzli 1983; Lindroth and Batzli 1986; Seldal et al. 1994; Jensen and Doncaster 1999; Kent et al. 2005).

Microtines can reach high densities during the summer, due to their high reproductive potential (Oksanen 1990) and the richness of the plants like herbs and grasses that are available then (Norrdahl et al. 2002). However, the seasonal increase in vole densities cannot match the pulse in primary production during the summer. Thus, voles only have minor effects on their preferred summer food plants, even in predator-free experimental systems (Hambäck and Ekerholm 1997). However, the high vole populations that build up during summer can have major effects on their food plants during the winter, when primary production ceases (Norrdahl et al. 2002; Olofsson et al. 2004; Dahlgren 2006). Thus, if voles are limited by food quantity, this limitation should be imposed during the winter when the food supply is lowest (Boutin 1990; Robbins 1992; Turchin and Batzli 2001; Ergon et al. 2004).

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The gray-sided vole (*Clethrionomys rufocanus*) is the most common vole in tundra ecosystems of northern Fennoscandia (Andersson and Jonasson 1986; Oksanen et al. 1999; Ekerholm et al. 2001; Olofsson et al. 2004) where the vegetation is dominated by a few dwarf shrub species (Kalliola 1939), one of which is bilberry (*Vaccinium myrtillus*). Bilberry is considered to be the most important winter food plant for gray-sided voles, although they also consume other dwarf shrub species (Kalela 1957; Ericson 1977; Tolvanen et al. 1992; Hambäck and Ekerholm 1997; Hambäck et al. 1998, 2002; Strengbom et al. 2003). Vole herbivory has been found to severely reduce the abundance of bilberry twigs in these ecosystems (Hambäck and Ekerholm 1997; Hambäck et al. 2004; Olofsson et al. 2004; Dahlgren 2006). In addition, grazing simulation experiments (Strengbom et al. 2003) and descriptive studies (Oksanen et al. 1987) have shown that herbivory may reduce the level of phenolics and increase the levels of nitrogen in bilberry ramets. These findings indicate that gray-sided voles not only reduce the quantity of their winter food but also increase its quality. However, the quality of a plant as a food for an herbivore is often difficult to estimate by chemical measurements (Strengbom et al. 2003), because even proteins can have defensive functions (Seldal et al. 1994). Thus, preference or performance tests are needed to assess the quality of a plant for a specific herbivore.

Despite intensive research, few experimental studies have examined predation and food limitation of vole populations simultaneously (but see Klemola et al. 2000a, b). The study presented here focuses on the interaction between gray-sided voles and their main winter food plant, bilberry, on predator-free islands in Lake Iešjávri and mainland habitats with predators in northern Norway. This is the first long-term investigation of the interaction between voles and their food plants to consider the effects of voles on the quality, quantity and population dynamics of the food plant. We predicted, on the basis of the considerations mentioned above, and previous experience, that voles should reduce the quantity but increase the quality of bilberry ramets on predator-free islands. In addition, we predicted that the effects of the voles on both the quantity and quality of bilberries would be weaker when predators were present. Due to the ambiguities of the chemistry-based approach, we assessed food quality directly in a preference trial. Moreover, we measured both the abundance and population structure of bilberry ramets in mainland areas with both voles and predators, on predator-free islands with voles, and on vole-free islands to evaluate the plants' capacity to re-grow following vole herbivory.

Materials and methods

This study was conducted on nine islands and four sites on the shores of Lake Iešjávri, Finnmarksvidda, in northernmost Norway (69°45', 24°30'). Biogeographically, the area is part of 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 microclimates. Snowmelt is rapid, occurring around 10 June. The growing season starts about a week later, when the topsoil has thawed. The break-up of ice on the lake normally starts in the second half of June. Plants start to develop autumn colors at the end of August and the ground is normally more or less covered by snow from the end of September. The size of the islands ranges from 0.03 to 5 ha, and they are all separated from the mainland by channels wide enough (300–1,600 m) to substantially hinder movements of voles and their mammalian predators.

All of the islands are elongated glaci-fluvial moraine ridges consisting of three primary habitats:

1. Hummock bogs, moist habitats with dense vegetation dominated by cloudberries (*Rubus chamaemorus*) and several dwarf shrubs—bilberry (*V. myrtillus*), arctic blueberry (*V. uliginosum*), lingonberry (*V. vitis-idaea*), crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) and dwarf birch (*Betula nana*)—ground covered by a thick moss layer, dominated by *Hylocomium splendens* on hummocks and *Polytrichum* ssp. or *Sphagnum* ssp. in depressions.
2. Drier sites mainly occupied by lichen heaths and dominated by the same dwarf shrubs as in hummock bogs, but at lower coverage.
3. Windswept areas on the top of the ridges where the lichen cover is thin and the dwarf shrub cover consists of scattered plots of lingonberry and crowberry. For more details see Hambäck and Ekerholm (1997).

Hummock bogs form the preferred habitat of the gray-sided vole (*C. rufocanus*) (Ekerholm et al. 2001), the overwhelmingly dominant rodent species in the region (Oksanen et al. 1999; Ekerholm et al. 2001). All large islands harbor populations of gray-sided voles, but the species is seldom found on small islands more than 200 m from the mainland or from a large island. Except for lemmings during outbreaks, no other rodents occur in this habitat in significant numbers. Reindeer (*Rangifer tarandus*) migrate through the mainland in early winter but do not cross the lake to the islands, since it is only partially frozen then. Furthermore, since reindeer

principally forage on lichens and graminoids in the winter season, they prefer other habitats. Hares (*Lepus timidus*) and grouse (*Lagopus lagopus*) occur in moderate numbers on both the mainland and large islands. In winter, they move freely throughout the entire archipelago.

Two species of vole predators are frequently found in hummock bogs on the mainland: long-tailed jaegers (*Stercorarius longicaudus*), which breed there during years when voles are abundant, and stoats (*Mustela erminea*), which are especially numerous at times when vole populations steeply decline. The habitat is also exploited by foxes (mainly *Vulpes vulpes*) (Oksanen and Oksanen 1992; Oksanen et al. 1999; Aunapuu and Oksanen 2003). However, the smaller islands are naturally free from mammalian predators. Stoats have never been seen, tracked or trapped on them. In spring, the smaller islands are visited by flocks of migrating jaegers, which stay on the lake throughout the entire summer in years when vole densities are low on the mainland. Avian predation may then occur on some of the small islands. However, the limited predation by jaegers probably has minor effects on the vole populations, and these islands are thus referred to as predation-free.

Gray-sided voles were introduced to four of these “predator-free” islands in 1991 or 1992 (Hambäck and Ekerholm 1997) and they have inhabited the islands since then. In addition, five islands have been assigned to a vole-free treatment and kept free from invading voles by snap trapping since 1995. There are no systematic differences between the vole-free islands and the four predator-free islands with respect to their size or isolation (Dahlgren 2006). Vole densities and the proportions of bilberry ramets that were cut were recorded from 2000 to 2003 at 13 study sites: one on each of the four “predator-free” islands with introduced voles and each of the five “vole-free” ones, and four at sites on the mainland shores of the lake. All of the islands were separated from each other by at least 300 m of water and the mainland sites were spaced more than 1 km apart. Vole populations at the different sites can thus be regarded as independent, especially since no migration of voles between sites has been recorded.

Vole densities were estimated twice a year, in spring (i.e. the end of June) and fall (i.e. the end of August), using Ugglan Special multiple capture vole traps. The vole densities are presented as total numbers of captured individuals per unit area (hectare). The only micro-rodents captured on the islands were gray-sided voles, but several other species of voles, and a few lemmings were trapped at the mainland sites. Dispersal of

voles into and out of the mainland sites from the surroundings may confound direct comparisons between mainland and island sites. However, since voles do not generally disperse over long distances, the effects of such movements are likely to be minor. The traps were placed in grids at 10-m intervals, baited with crushed oats and checked at 8-h intervals over a 48-h period on the predator-free islands and a 96-h period at the mainland sites. The mean percentages of voles captured at least twice during the same trapping session were 76% (range 68–84%) for mainland reference grids and 78% (range 71–85%) for predator-free islands, indicating that vole censuses were equally efficient, or at least nearly identical, in all of the grids. Between trapping occasions, traps were left open in the terrain.

The effects of voles on bilberries were studied using individually marked ramets in 12 permanent plots at each of the 13 study sites. Twenty bilberry ramets were marked at each permanent plot in the summer of 2000. The numbers of live, dead and missing ramets were then recorded annually in the middle of the summer and all dead or missing ramets were replaced by marking the nearest living ramets, so there were 20 marked, living ramets at the beginning of every year. Since previous studies from these islands have shown that almost all bilberry ramets cut by voles are cut during the winter (Hambäck and Ekerholm 1997), all cuttings of ramets recorded each year were attributed to winter herbivory.

At the end of August 2003, we recorded the population structure of bilberry ramets at each site. An additional vole-free island, with no permanent bilberry plots, was included in this part of the study. We sampled 40 random plots (0.25 m × 0.25 m) at all 14 sites. All bilberry ramets within the plot were counted, then cut at ground level and collected. If there were less than five ramets in a plot, the ramets closest to the plots were collected to obtain a total of five ramets. These additional ramets were used only for estimating the age structure of bilberries, not for estimating population density. The age of each ramet was determined by the retrospective aging method published by Tolvanen (1995), and the ramets were then dried at 40°C for 48 h and weighed.

The effects of voles on the quality of bilberry twigs were investigated in preference trials with caged voles. At the beginning of September 2001, when bilberry twigs had started to become dormant, aboveground parts were harvested from three sites: one predator-free island, one vole-free island and one mainland site. The harvested ramets were kept in a freezer (3–4 weeks) until the start of the preference test. The gray-sided voles were collected from the Iešjávri area in the same

period as the bilberry twigs and 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. Eleven immature (post-juvenile or pre-adult) voles were used in the preference trial, six male and five female, with weights ranging from 18 to 27 g. In the preference trials, 26 ramets from each of the three areas were offered to each vole for 10 h, in 35 × 57-cm cages, along with rabbit pellets as a less preferred food source. The ramets were fixed in foam designed to hold flower arrangements in place (Oasis), and were thus standing in a natural upright position. Ramets were picked randomly from the total sample of ramets collected in the field and the age-distribution of the ramets in the preference trial should thus have been similar to the age distribution in the field. The positions of shoots from each treatment were randomized within each cage. Since voles generally cut ramets at the base before starting to forage on them, the preference of voles could be quantified simply by counting the number of shoots cut in each cage during each trial.

Latin nomenclature is based on Lid (1987), Mitchell-Jones et al. (1999), and DelHoyo et al. (1992). The densities of bilberry ramets (new and total) at the vole-free islands, predator-free islands and mainland sites and density of new bilberry ramets were compared using generalized linear models (GLM) with quasi Poisson errors, to adjust for over-dispersion. The treatments were considered as fixed categorical factors. The frequency of bilberry ramets eaten by voles in the preference trial as well as on the different island and mainland sites was tested using generalized linear models using binomial errors. All analyses were performed with the GLM function in the R statistical package (R development Core Team 2006).

Results

Vole densities were higher on predator-free islands than on mainland sites with predators throughout the whole study period from 2000 to 2003, except in spring 2002 (Fig. 1). Gray-sided voles accounted for all of the micro-rodents trapped on the islands, and most (75.4%) of those trapped on the mainland; the other species being red voles (*C. rutilus* 1.2%), root voles (*Microtus oeconomus*, 22.8%) and Norwegian lemmings (*Lemmus lemmus*, 0.6%). These other microrodents are not as dependent on bilberries as gray-sided voles, but they do forage on bilberry ramets sometimes. Since we were unable to determine which microrodents had cut given ramets, pooled frequencies are presented, although this

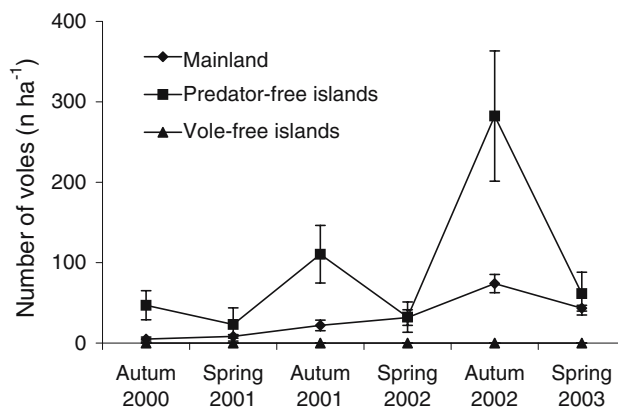


Fig. 1 Estimates of the abundance of gray-sided voles (mean ± SE) on predator-free islands ($n = 4$), mainland sites ($n = 4$) and vole-free islands ($n = 5$)

results in a slight overestimation of the potential gray-sided vole grazing pressure on bilberry ramets. With this caveat, the frequency of bilberry ramets that were cut by gray-sided voles was higher on the predator-free islands than on the mainland (2001, $z = -20.8$; 2002, $z = -34.6$; 2003, $z = -38.1$; $P < 0.001$ for all years), and lowest on the vole-free islands throughout the study period (2001, $z = 15.7$; 2002, $z = 8.9$; 2003, $z = 7.7$; $P < 0.001$ for all years) (Fig. 2).

The few missing ramets on vole-free islands had probably been cut by hares, grouse or broken by the snow pack during the winter. On the predator-free islands, between 50 and 80% of bilberry ramets were cut every year. By 2003, the intense herbivory on bilberry twigs by the dense populations of gray-sided

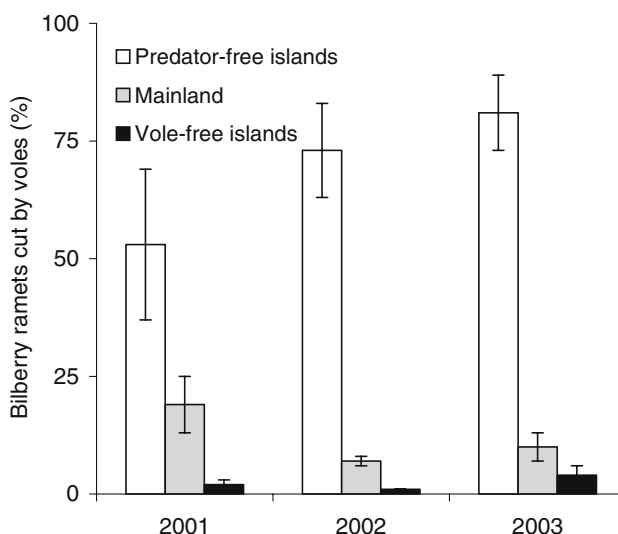


Fig. 2 Proportion of bilberry ramets cut by voles during the winter (mean ± SE) on predator-free islands ($n = 4$), mainland sites ($n = 4$) and vole-free islands ($n = 5$)

voles had reduced the biomass of bilberry twigs by almost 90% on the predator-free islands, and by more than 50% on the mainland sites where predators were present, compared to the vole-free islands (Fig. 3, $F_{2, 11} = 13.2$, $P < 0.001$). Moreover, the density of bilberry ramets was lower on the predator-free islands than on the mainland ($z = 3.7$, $P = 0.003$). However, there was no significant difference in the density of bilberry ramets between mainland sites and vole-free islands ($z = 0.3$, $P = 0.789$). Bilberry plants compensated for the vole damage by producing more new ramets; the density of which was twice as high on the intensively grazed predator-free islands as on the mainland ($z = 2.7$, $P = 0.020$, Fig. 4), although their densities did

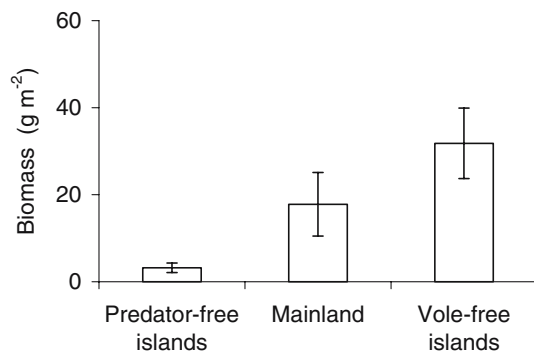


Fig. 3 Aboveground biomass of bilberries (mean ± SE) on predator-free islands ($n = 4$), mainland sites ($n = 4$) and vole-free islands ($n = 5$) in the summer 2003. Bilberry biomass was significantly lower on predator-free islands than on mainland sites and vole-free islands, but there was no significant difference between mainland sites and vole-free islands

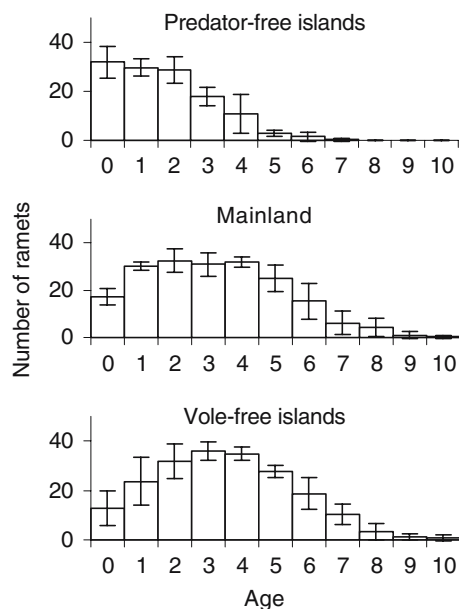


Fig. 4 Age structure of the bilberry ramets on predator-free islands, mainland sites and vole-free islands

not significantly between mainland sites and the vole-free islands ($z = 1.2$, $P = 0.247$). Moreover, voles had a pronounced effect on the age structure of bilberry ramets. The mean age of bilberry ramets was lower on the predator-free islands than on both the mainland and the vole-free islands ($F_{2, 11} = 31.2$, $P < 0.001$). The predator-free islands were dominated by ramets that were less than 3 years old, while up to 6-year-old ramets were abundant on the mainland and the vole-free islands. No ramets more than 7 years old were found on the predator-free islands, but 10-year-old ramets were found on both the mainland and vole-free islands.

The greenhouse preference trial revealed that the voles preferred bilberry ramets from predator-free islands more than ramets from mainland sites ($z = 2.0$, $P = 0.048$) and ramets from mainland sites more than ramets from vole-free islands ($z = 3.8$, $P < 0.001$, Fig. 5).

Discussion

During several subsequent years, vole densities on predator-free islands exceeded normal peak densities on the mainland (Hambäck and Ekerholm 1997; Hambäck et al. 2004; Dahlgren 2006). The lack of predation is probably the main reason why the vole densities are higher on the islands than on the mainland. The lack of opportunities for voles to disperse may also be a contributory factor, although voles can disperse from the islands during the winter, when the lake is covered by ice. The high densities of voles reduced the abundance of bilberry ramets, their main winter food plant. Similar effects of voles have been reported from other boreal and arctic ecosystems (Ericson 1977; Andersson

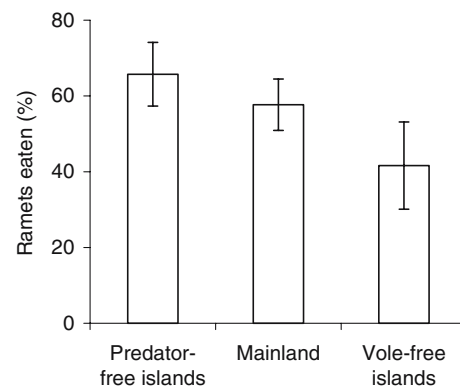


Fig. 5 Vole preferences measured as the percentage of ramets (mean ± SE) from predator-free islands, mainland sites and vole-free islands cut by voles. All treatment means are significantly different from each other

and Jonasson 1986; Ericson and Oksanen 1987; Tolvanen 1994; Grellmann 2002; Olofsson et al. 2004). However, this study shows that the effect is more pronounced in the absence of predators. Gray-sided voles reduced the abundance of bilberry by less than 50% on mainland sites and by more than 90% on the predator-free islands. Moreover, our study reveals that the grazing resistance of bilberry stabilizes the plant–herbivore interaction. Although up to 80% of the bilberry ramets were eaten repeatedly over many years on the predator-free islands, the species persisted, and bilberry plants compensated for lost tissue by producing new ramets. After more than 10 years of heavy grazing, bilberry still produced twice as many ramets on predator-free islands as on vole-free islands and these new ramets were of high quality as food for the gray-sided voles.

Previous studies on the resistance of bilberry have shown that the number of ramets recovers rapidly from simulated herbivory events (Tolvanen et al. 1993) and frost damage (Tolvanen 1997), since bilberry plants produce new ramets from dormant buds at the base of removed ramets. After single defoliation events, plants may compensate for the lost tissue by reallocating resources from belowground nutrient and carbon reserves (Chapin et al. 1980). Our results indicate that even though bilberry initially decreases in abundance due to vole grazing the species is grazing-tolerant, since bilberry plants were still compensating for the herbivore damage by producing more new ramets on the predator-free islands than in control plots after more than 10 years of severe depletion of ramets every winter. It is extremely unlikely that the plants were still using resources stored before the voles were introduced to these islands for the compensatory regrowth at the end of this period. The new ramets produced every summer have to store sufficient carbohydrates and nutrients in the rhizomes to provide resources for new ramets in the spring. A contributory factor to the high compensatory ability of bilberry ramets could be reduced competition between plants on the predator-free islands, since the abundance of other dwarf shrubs like *E. nigrum*, *B. nana* and *V. vitis-idaea* has also decreased on these islands (Hambäck et al. 2004; Dahlgren 2006).

Bilberry leaves and ramets contain a wide range of defense substances (Laine and Henttonen 1987; Oksanen et al. 1987; Hambäck et al. 2002; Strengbom et al. 2003) and several authors have postulated that variations in the food quality of bilberry plants may be explanatory factors for the fluctuations in microtine populations (Laine and Henttonen 1987; Selås 1997, 2006). However, these defense substances seem to

have little or no deterrent effect on gray-sided voles, since bilberry twigs are still their most preferred winter food sources (Kalela 1957; Ericson 1977; Tolvanen et al. 1992; Hambäck and Ekerholm 1997; Hambäck et al. 1998, 2002; Strengbom et al. 2003) and up to 80% of bilberry ramets were eaten year after year on the predator-free islands. Many plants have been found to produce defense substances in response to herbivory, thereby reducing their palatability and the fitness of the herbivores (Agrawal 1998). However, most reported examples of induced defenses have been in response to invertebrate herbivory, although several *Carex* species have been shown to induce defense substances in response to grazing by microrodents (Seldal et al. 1994; Bråthen et al. 2004). Furthermore, a large number of studies have found indications that mammalian herbivory generally increases the susceptibility of plants rather than inducing effective defense responses (Nykänen and Koricheva 2004). Accordingly, we found no indications that inducible defenses reduce the palatability of bilberry ramets, since voles preferred the ramets from the heavily grazed predator-free islands more than ramets from the mainland and vole-free islands.

The most likely explanation for the higher palatability of ramets from the predator-free islands is that these ramets were younger and thus more nutritious. Both vole preference/performance (Klemola et al. 2000a, b; Strengbom et al. 2003) and chemical analyses (Laine and Henttonen 1987; Oksanen et al. 1987; Seldal et al. 1994; Strengbom et al. 2003) are frequently used methods for quantifying the palatability of food sources. Both of these approaches have specific advantages and drawbacks. Here, we measured the suitability of available food resources by bioassaying vole preferences, instead of by direct chemical analyses. However, the main finding from this study, that grazing increased the quality of bilberry ramets as food for voles, is in agreement with previous studies using chemical analyses, which have found that simulated or real vole grazing increases the N content and sometimes reduces the concentrations of phenols and tannins in bilberry ramets (Laine and Henttonen 1987; Oksanen et al. 1987; Strengbom et al. 2003).

We thus conclude that bilberry relies on tolerance rather than defense to cope with vole herbivory, and does so well. Therefore, bilberry should be regarded as a fairly grazing-tolerant plant, which compensates for herbivory losses by producing new ramets even after repeated heavy grazing. In the absence of predators, vole populations increased rapidly during summer, and consequently consumed almost all of the bilberry ramets during the following winter. When bilberry

twigs had been depleted, voles switched to less preferred food plants like *B. nana*, *E. nigrum* and *V. vitis-idaea* (Hambäck et al. 2004; Dahlgren 2006). The reduced competition from other dwarf-shrubs may be a contributory factor to the strong regrowth of bilberry ramets on predator-free islands.

In this study of the interactions between herbivores and both their food plants and predators, we found that vole predators can influence the interaction between gray-sided voles and bilberries. Direct food shortages could explain the seasonal decline of vole populations during the winter on predator-free islands. However, bilberries are highly resistant to grazing and produce new, high-quality shoots before the next winter. The resistance and lack of induced, effective defenses in bilberries thus prevents the development of extended periods in which vole densities are low due to severe reductions in food quantity or quality, even in the absence of predators. The studied interaction between gray-sided voles and bilberry twigs thus lacks substantial time delays, which could generate population cycles, supporting the conclusion of Klemola et al. (2000a, b, 2003) that interactions between rodents and vascular plants are unlikely to cause population cycles. In this study of the interactions between herbivores and both their food plants and predators, we found that vole predators can influence the interaction between gray-sided voles and bilberries.

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