

Winter grazing by the Norwegian lemming (*Lemmus lemmus*) at Kilpisjärvi (NW Finnish Lapland) during a moderate population peak

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Winter grazing of the Norwegian lemming (*Lemmus lemmus*) was studied at Kilpisjärvi at the edge of the Scandinavian mountain chain during a moderate population peak and the year after. Signs of lemming grazing were recorded soon after snow melted along elevational and topographic gradients on three mountains. On all mountains in both winters, grazing peaked at the lower part of the alpine zone and then declined both in the forest zone and on the highest summits. Grazing was most intense in snow-protected depressions and slopes, whereas hillocks with thin snow were very little grazed. In the first winter, grazing was most intense in the mountains juxtaposed to the Scandes. In the following winter, grazing had clearly declined on these mountains, but remained unchanged at the most distant mountain from the Scandes. Topography and snow conditions played a key role for over-wintering of lemmings, but no clear link between annual variation in snow conditions and grazing patterns could be detected. The spatio-temporal pattern of lemming grazing conformed to a travelling wave type population dynamics.

Introduction

Population fluctuations are characteristic for the Norwegian lemming, *Lemmus lemmus*, in northern Fennoscandia. In the alpine zone, low amplitude fluctuations occur synchronously with other microtine rodents (Virtanen *et al.*

1997, Ekerholm *et al.* 2001), but large-scale population outbreaks are infrequent, and the onset of migratory periods seems to occur at 25–35 year intervals (Kalela 1961, Henttonen & Kaikusalo 1993). During peak years lemmings devastate vegetation (Kalela 1961, 1971, Kalela & Koponen 1971, Oksanen & Oksanen 1981,

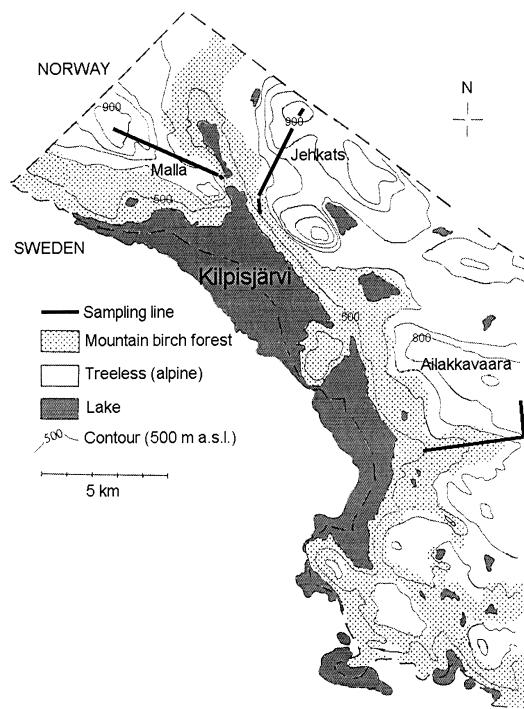


Fig. 1. A map of the study area in NW Finland. The sampling was carried out from highest parts of each mountain along sampling lines towards lowland areas.

Eurola *et al.* 1984, Moen *et al.* 1993), but even at low densities the Norwegian lemmings have a strong impact on vegetation structure and biomass in mountain snowbed habitats (Virtanen *et al.* 1997, Virtanen 2000).

According to Kalela (1961, 1971) winter grazing of Norway lemmings in mountain habitats depends on snow conditions, with grazing being most intense in the sites with deep snow. His studies also showed that lemmings over-winter mainly in areas above the treeline. However, the sampling schemes used by Kalela (1961, 1971) provide only limited documentation of the spatio-temporal pattern of lemming's winter grazing. Snow conditions, both snow depth and spatial distribution, are decisive for the availability of winter food resources (Henttonen & Kaikusalo 1993, Reid & Krebs 1996), and lemming winter breeding succeeds only when snow cover is deep enough (Kaikusalo & Tast 1984). Depending on snow fall and wind conditions, there can be drastic differences in the

spatial distribution of snow cover among years. Moreover, occasional warm spells (especially in the early winter) may result in an ice layer on the ground, which prevents access by lemmings to ground layer bryophytes.

In 1997–1999, the population of the Norwegian lemmings reached a moderate peak at the Kilpisjärvi region (H. Henttonen & J. Niemimaa, unpubl.). We analysed the winter grazing patterns of lemmings in 1998 and 1999 to study the use of winter habitats in relation to the advance of the lemming peak (west–east), in relation to elevational zones (forest–middle oroboreoarctic), and in relation to topography (hillock–slope–depression). We also studied how the variable snow conditions in these years affected the grazing patterns, because this modest population peak of lemmings did not advance farther to Lapland. Our hypothesis was that the snow conditions in winters 1997–1999 were unfavourable to lemmings and this could be reflected in the grazing patterns.

Material and methods

Sampling along elevational gradients

The data were collected soon after snow melt in June 1998 and 1999 from three mountains near Kilpisjärvi (Mt. Malla, Mt. Jehkats, and Mt. Ailakkavaara) (Fig. 1). In each area the sampling was started from the highest parts of the mountain. At intervals of 30 m, a metal quadrat (20×20 cm) was thrown and let fall into random place. In each quadrat, the percentage of grazed or destructed vegetation (moss vegetation consumed, dwarf shrubs or graminoids cut) was estimated. In addition, topography (hillock, slope, depression or level ground) of the quadrat site was recorded. The total elevational range sampled for Mt. Malla was 480–920 m, for Mt. Jehkats 500–960 m, and for Mt. Ailakkavaara 480–920. However, for Mt. Ailakkavaara, the range in 1998 was 480–840 m. These gradients comprise following elevational zones: 480–600 m the northern oroboreal and forested parts of the orohemiartic zone (mountain birch zone), 600–800 m the lower oroboreoarctic (including treeless orohemiartic heaths) zone, 800–960 m

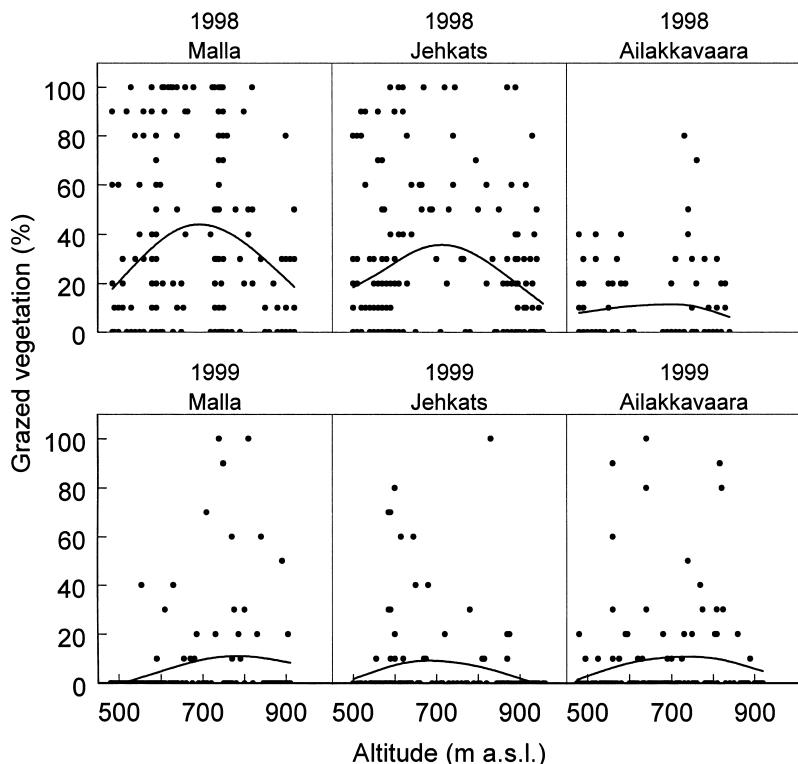


Fig. 2. Percentage of vegetation grazed by the Norwegian lemming on three mountains in relation to altitude during 1997–1998 and 1998–1999. The fitted lines after cubic spline smoothing.

the middle orctic zone (Oksanen & Virtanen 1995). The habitats sampled represent dwarf shrub heaths, alpine grasslands and heath forest types and snowbeds. Wet habitats, such as mires, and meadows, i.e. preferred habitats of the root vole (*Microtus oeconomus*), were discarded. The quadrats that fell onto stones or boulders were also omitted from the analysis. It should be emphasised that the grazing signs and especially faeces of lemmings cannot be confused with those of other rodents in the area.

Statistical analyses

The amount of lemming grazing was measured as % of vegetation grazed in small quadrats. In practice, these % values were classes ranging at 5% intervals between 0% and 100%. A large proportion of quadrats had no grazing resulting in a high proportion of zeroes in the data. Therefore, an assumption of normally distributed errors was not met, and instead, in the modelling Poisson error structure was used. Gener-

alised additive models (Hastie & Tibshirani 1990) were employed to examine the variation in grazing intensity along elevational gradients. In these models run by S-plus (S-PLUS 2000), spline smoothers with three degrees of freedom were used. A model with variables and their interactions was constructed and then the significance of terms was tested by deletion (*F*-tests). Another model was constructed to test the grazing pattern in relation to topography. In this analysis, the factor 'altitudinal zones' (forest, lower orctic, middle orctic) replaced 'altitude'. The response variables were over-dispersed (McCullagh & Nelder 1989) and thus corrected dispersion parameters were used. The significance of the explanatory variables and their interactions was tested as above.

Results

The amount of grazing in relation to mountain region, altitude, and topography in the two consecutive winters is shown in Fig. 2. The model

for % grazed vegetation as response variable contained the following explanatory variables: spline(altitude) + region + year + spline(altitude) × year + spline(altitude) × region + region × year. The null deviance of the response variable was 36 723 (df = 955), and the residual deviance after fitting the model with all significant terms was 26 608 (df = 946). Significant region × year term ($F_{2,948} = 9.9, p = 0.00005$) suggested marked differences in grazing between years and regions. In winter 1997–1998, grazing was intense on Mts. Malla and Jehkats but low on Mt. Ailakkavaara. On Mts. Malla and Jehkats grazing clearly was less intense in 1998–1999 than in the previous winter, whereas on Mt. Ailakkavaara grazing remained at the same level in 1998–1999 (Fig. 2).

As shown by the hump-curved trend-lines, grazing intensity varied clearly in relation to altitude. The trend-lines conformed to a unimodal pattern with greatest grazing intensity in the lower oroarctic zone (ca. 600–750 m a.s.l.) and less intense in the high altitudes (> 800 m) and in the low altitudes (< 600 m). The altitudinal trends of grazing were more or less similar for winters 1997–1998 and 1998–1999 (spline(altitude) × year, $F_{1,945} = 3.3, p = 0.07$), and for the mountains (spline(altitude) × region, $F_{1,946} = 0.5, p = 0.59$).

The variation in grazing in relation to topography is summarised in Fig. 3. The initial model contained the following explanatory terms: altitude zone + region + year + topography + topography × year + topography × altitude zone + topography × region. The main trends in grazing were similar in all altitudinal zones (topography × altitude zone, $F_{6,932} = 1.9, p = 0.07$) and on all mountains (topography × region, $F_{6,938} = 1.4, p = 0.22$). A significant interaction suggested that grazing in relation to topography was not uniform in both winters (year × topography, $F_{3,944} = 3.2, p = 0.02$). This interaction reflected the overall decline of grazing from winter 1997–1998 to 1998–1999 (Fig. 3).

Discussion

Winter grazing by lemmings in relation to elevation showed a regular unimodal pattern with the

peak at altitudes of 650–750 m, in a relatively narrow zone above the timberline. The detected elevational pattern is compatible with Kalela's (1961, 1971) studies showing that in winter Norway lemmings clearly prefer areas above the tree-line (see also Kalela & Koponen 1971). The preference of these areas has been attributed to the presence of deep snow patches and the higher availability of winter food, especially mosses (Kalela 1971). Less intense grazing in low altitudes show that relatively few lemmings over-winter at the level of mountain birch forests. Both suboptimal snow conditions and food availability (Kalela 1961, 1971), and/or predation risk is higher at lower elevations (Oksanen 1993, Henttonen & Kaikusalo 1993, Steen *et al.* 1997, C. Gower & H. Henttonen unpubl., H. Henttonen & J. Niemimaa unpubl.) may account for the reduced winter grazing at low altitudes. Less intense grazing at the highest altitudes is probably caused by lower average snow depth, lack of snowbeds (snow accumulation sites) and discontinuous plant cover (Eurola *et al.* 1986).

Lemming grazing showed a clear pattern in relation to topographic positions in areas above the tree-line. In agreement with Kalela (1961, 1971), Henttonen and Järvinen (1981), Oksanen and Oksanen (1981), Eurola *et al.* (1984), grazing was most intense in snow protected depressions and sheltered slopes. In depressions bryophyte-dominated (e.g., *Polytrichum* spp.) snowbeds and in sheltered slopes *Vaccinium myrtillus* heaths with bryophyte-rich ground layer prevail. On sites with shallow snow cover, supporting mainly lichen-rich dwarf shrubs heaths, the frequency of winter grazing was much lower than on snow protected sites. An exception was Mt. Malla where some grazing occurred on hillocks during winter 1997–1998. It is possible that the overall snow conditions in this region (the area close to high Norwegian mountains) were favourable even on elevated hillocks.

Contrary to our expectations, grazing pattern in relation to topography was fairly similar during the two winters. In winter 1997–1998 snow cover was shallow, only 20 cm, until the end of January. Indeed, during an exceptional warm spell in January (up to 7 °C) snow even melted a bit in places. As a result, ice layers were formed in depressions particularly in areas

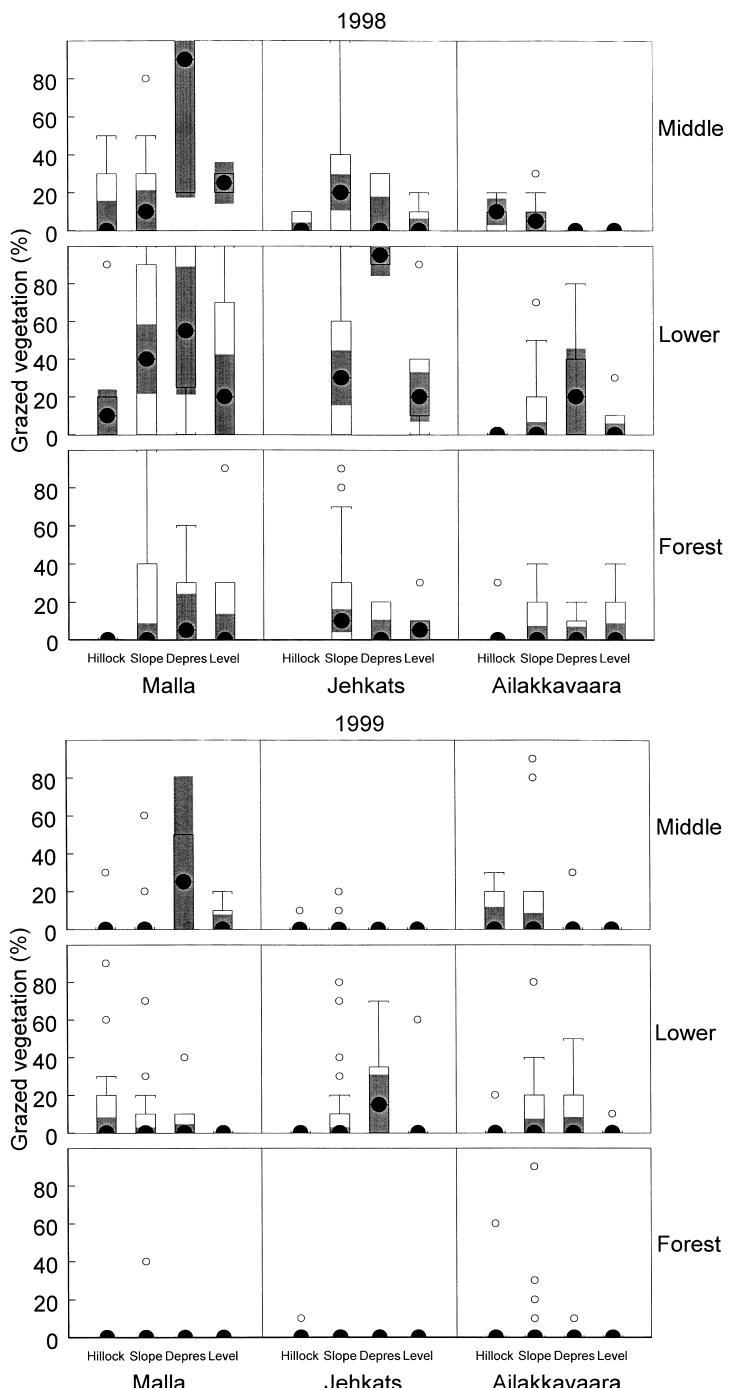


Fig. 3. Vegetation grazed by the Norwegian lemming at different topographic positions during winters 1997–1998 (above) and 1998–1999 (below) in forest (mountain birch) zone, lower oroarctic zone and middle oroarctic zone (Depres = depression). In the plots the median, the upper and lower quartiles, the extent of data points beyond the quartiles (fences), the outliers (open circles). The grey shadings indicate the 95% confidence interval of the median values. Owing to the sampling method used the number of samples (N) in each case varied between 2–59 being typically 11–29 in the data from the lower oroarctic zone.

above the treeline. These ice layers were still visible at time of snowmelt in June 1998, and they had presumably affected the build up of tunnels by lemmings (own observations). However, no systematic deviations in grazing among the topographic levels, and between the two winters, were seen. This suggests that annual variations are not necessarily reflected in the topographic pattern of winter grazing of lemmings. Nevertheless, we maintain that snow conditions may strongly affect the availability of winter food and hence winter survival (Henttonen *et al.* 1983). According to Henttonen and Kaikusalo (1993), the unpredictable snow conditions and small snowbed areas in the subcontinental areas of northern Fennoscandia limit lemming densities in comparison to the high mountains of Norway and Sweden where snow cover is more predictable and the coverage of snowbed areas in the landscape is much larger.

Food resources have been hypothesised to be crucial for the population dynamics of *Lemmus* in tundra and alpine habitats (Tihomirov 1959, Batzli *et al.* 1980, Kalela & Koponen 1971, Oksanen *et al.* 1981, Stenseth & Ims 1993, Henttonen & Kaikusalo 1993, Krebs *et al.* 1995, Turchin *et al.* 2000). Grazing was intense particularly in the westernmost area, with 40%–50% of vegetation grazed. This suggests that winter food resources were considerably consumed during this low to moderate peak. It remains unclear, however, whether these levels of consumption led to food limitation during the lemming peak. To resolve this would require detailed quantitative studies on the temporal and spatial patterns of the availability and use of winter resources.

The temporal patterns in winter grazing were consistent with the geographic trend in lemming dynamics in 1997–1999 (H. Henttonen & J. Niemimaa unpubl.). Lemming populations had increased first in the mountain areas of Norway and Sweden immediately W and NW of our study area. Correspondingly, winter grazing in 1997–1998 was most intense in the NW part of our study region on Mt. Malla and Mt. Jehkats, but not as intense on Mt. Ailakkavaara. During the winter 1998–1999, there was much less grazing than in the previous winter, particularly in the mountain birch forest zone. The decline of grazing intensity reflects clearly the decline of

lemming populations by winter 1998–1999. On Mt. Ailakkavaara, however, no clear reduction in grazing took place between the two winters. As with the trapping data of H. Henttonen and J. Niemimaa (unpubl.), the signs of winter grazing show that the lemming peak advanced and declined in a wave-like manner and may thus reflect a “travelling-wave” (Ranta *et al.* 1997, Ranta & Kaitala 1997, Blasius *et al.* 1999) of lemming population dynamics. During the great migratory of years the lemming distribution can spread 200 km into the taiga (Henttonen & Kaikusalo 1993), but in 1997–1998 the advance of the peak was depressed, and the travelling-wave covered only some tens of kilometres (H. Henttonen & J. Niemimaa unpubl.).

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