NOTE: COMMENTS ARE APPENDED TO THIS PAPER

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Arctic lemmings, *Lemmus* spp. and *Dicrostonyx* spp.: integrating ecological and evolutionary perspectives

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ABSTRACT

Question: What do the evolution and the fluctuation patterns of arctic lemmings – *Lemmus* spp. and *Dicrostonyx* spp. – tell us about their population dynamics and the influence of lemmings on the ecology and evolution of arctic plants?

Methods: We reviewed the literature concerning the evolution of arctic lemmings and analysed their current fluctuation patterns with a focus on the following aspects: (1) changes in morphology related to feeding ecology; (2) *per capita* rate of population growth during the year preceding the peak (r_p), predicted to be high for arvicoline rodents interacting with the winter forage plants and low for arvicoline rodents interacting with specialized predators; (3) the skew of logarithmically transformed density data (sk_d), predicted to be zero for arvicolines interacting with their winter forage plants, negative for arvicolines interacting with specialized predators, and positive for arvicolines interacting with both seasonally renewed and depletable winter forage plants (the 'Barrow model' of Turchin and Batzli, 2001). Moreover, we conducted spectral analysis of those density records, which were at least 15 years long. Here predator–arvicoline models predict that similar spectral density profiles, with statistically significant peaks, are obtained with untransformed and logarithmically transformed data, whereas arvicoline–plant models predict that such profiles are only obtained using logarithmically transformed data.

Key insights: Arctic lemmings differ from other microtine rodents by having several features which increase their foraging efficiency under harsh conditions at the cost of reduced agility. These features were acquired rapidly at the dawn of the Pleistocene. Density fluctuations of all arctic lemming populations, for which sufficient data are available, correspond to the predictions of the 'Barrow model' and differ from the predictions of predator–arvicoline models. Our interpretation is as follows. When the Polar Sea froze, the primary productivity of northernmost Eurasia and North America was reduced, causing a shift from predation-controlled to food-limited dynamics in microtine rodents. This change in population dynamics triggered an extraordinarily rapid change in the characteristics of lemmings and precipitated an intense, sustained lemming–vegetation interaction, as old as the tundra itself, which has probably played a major role in the evolution of arctic plants.

Predictions: Increasing primary productivity along the southern (lower) boundary of the ranges of arctic lemmings should lead to their elimination by voles via apparent competition.

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Exclusion of lemmings should initiate dramatic changes in the vegetation of those tundra habitats, which have at least moderate snow cover and do not freeze in solid ice in winter. Exclusion of predators should have no impact on dynamics of inland populations of arctic lemmings.

Keywords: Arctic, *Dicrostonyx*, herbivory, *Lemmus*, outbreaks, population cycles, time trajectories, vegetation.

INTRODUCTION

In their review of the history of arctic lemming research, Stenseth and Ims (1993) proposed that current hypotheses concerning the population dynamics of lemmings could be regarded as branches of three major projects. One was launched by Elton (1942) and further developed by Chitty (1957) and Krebs (1964, 1978), with an emphasis on processes within populations and on ecological and evolutionary similarities between all rodents with sustained population cycles (Krebs and Myers, 1974). In contrast, the California school focused on direct and indirect aspects of lemming–vegetation interactions (Schultz, 1964, 1969; Pitelka 1973; Batzli *et al.*, 1980; Turchin and Batzli, 2001; Pitelka and Batzli, 2007). The Fennoscandian School (Kalela, 1949, 1962, 1971) differed from both these projects by regarding the outbreaks of arctic lemmings and the cycles of boreal voles as two fundamentally different phenomena. On the basis of the observations of Norwegian botanists (e.g. Nordhagen, 1928), Kalela (1949) proposed that Norwegian lemmings are in strong, exploitative interaction with the vegetation (see also Lack, 1954; Tihomirov, 1959; Rosenzweig and Abramsky, 1980). Conversely, boreal vole cycles were only accompanied by minor vegetation changes, primarily in the fertility of plants, which Kalela (1962; see also Tast and Kalela, 1971) interpreted as evidence for a central role of changing plant fertility for boreal vole cycles.

More recent research has indicated that these fertility fluctuations are in fact consequences rather than causes of boreal vole cycles (Ericson, 1977; Oksanen and Ericson, 1987). Today, there is growing consensus that boreal vole cycles are generated by exploitative interaction between specialist predators (primarily small mustelids, i.e. weasels and stoats) and their primary prey, the vole guild (Henttonen *et al.*, 1987; Oksanen, 1990; Hanski *et al.*, 1991, 1993, 2001; Korpimäki *et al.*, 1991, 2004, 2005; Turchin and Hanski, 1997; Korpimäki and Norrdahl, 1998; but see Selås, 1997; Oli, 2003; Högstedt *et al.*, 2005; Kent *et al.*, 2005). Predation is also frequently regarded as the main regulatory factor for arctic lemming populations (Wilson *et al.*, 1999; Gilg *et al.*, 2003; Gauthier *et al.*, 2004). On the other hand, Norwegian lemmings have a profound impact on the tundra vegetation, which provides support for Kalela's (1949) idea of a fundamental difference between the dynamics of boreal voles and arctic lemmings (Kalela, 1971; Kalela and Koponen, 1971; Oksanen and Oksanen, 1981; Oksanen, 1983; Moen *et al.*, 1993; Oksanen and Moen, 1994; Virtanen *et al.*, 1997a; Moen and Oksanen, 1998; Virtanen, 2000; Olofsson *et al.*, 2002).

Further insights into the lemming enigma can be obtained from the evolution of the two arctic lemming genera, *Dicrostonyx* spp. and *Lemmus* spp., referred to as collared and brown lemmings, respectively (during discussion at the genus level). Both the arctic lemmings and the tundra developed in the dawn of the Pleistocene, when Eurasia and North America moved to such high latitudes that the now land-locked Arctic Ocean froze, creating frigid conditions along the northern edges of the surrounding continents (Hoffmann and Taber, 1968). The arvicoline rodents that began to adapt to this new, harsh environment belonged to the same subsection (Lemmini) but were not closely related. The first ones resembled current grey-sided voles [*Myodes rufocanus* (Pall.)], without specialized digging claws and with body dimensions comparable to *Microtus* spp. but with rooted molars (Guthrie and Matthews, 1971). They rapidly evolved to collared lemmings, indicating dramatic changes in selective pressures. Their skulls became robust, providing points of attachment for powerful jaw muscles. The complexity of their molars increased, allowing them to grind hard food items, and their claws became adapted to dig the hard tundra snow (Hoffmann and Taber, 1968; Guthrie and Matthews, 1971; Chaline *et al.*, 1999). Due to the phylogenetic constraint imposed by their molar structure, collared lemmings remained dependent on dicotyledons, leaving the niche of arctic graminoid eaters available (Batzli, 1993; Jarrell and Fredga, 1993). The bog lemmings (*Synaptomys* spp.) of boreal and temperate wetlands had continuously growing, rootless molars (Jarrell and Fredga, 1993; Chaline *et al.*, 1999), and were therefore prepared to invade this empty niche. They rapidly obtained the distinctive characteristics of modern brown lemmings, which, by and large, correspond to the distinctive characteristics of collared lemmings (above; see also Chaline *et al.*, 1999). The evolution of these two lemming genera was thus a convergent response to the new environment, which called for increasing foraging efficiency and where co-existence required different feeding niches and habitat preferences (Morris *et al.*, 2000).

Paleobiological evidence does not reveal whether these rapid changes were directly dictated by the rigours of the physical environment or whether they were consequences of changes in population dynamics. Current distribution patterns of arctic lemmings and voles in space and time support the latter alternative. In Fennoscandia, where collared lemmings are absent, the otherwise forest-dwelling grey-sided voles prevail even on tundra heaths (Henttonen and Viitala, 1982; Oksanen *et al.*, 1999; Ekerholm *et al.*, 2001). Elsewhere, such habitats are dominated by collared lemmings (Morris *et al.*, 2000). Moreover, *Microtus* voles abound in graminoid-rich Fennoscandian mountain tundra habitats during years with low numbers of Norwegian lemmings but are absent or uncommon in these habitats during lemming outbreaks (Henttonen *et al.*, 1977; Framstad *et al.*, 1993). Applying the principle of temporal uniformity (i.e. assuming that the relationship between patterns and processes was the same in the past as it is in the present), we regard these changes as an indication of a shift from a predation-controlled arvicoline guild, structured by apparent competition (Holt, 1977), to a food-limited guild, structured by resource competition, favouring individuals capable of exploiting depleted resources (MacArthur, 1972; Tilman, 1982, 1988).

The principle of temporal uniformity also implies that we can test the hypothesis outlined above by comparing current fluctuation patterns of arctic lemmings and boreal voles to predictions of different parameterized models of small rodent dynamics. We focus on four models, which have been at least preliminarily tested with promising results. The first is the *specialist predator model* (Hanski *et al.*, 1991, 1993, 2001; Turchin and Hanski, 1997; Klemola *et al.*, 2003), where predation is assumed to drive the small arvicoline cycles but social factors are regarded as vital in slowing down the per capita rate of population growth of arvicolines (see Stenseth, 1986). This creates the characteristic peak phase with high arvicoline density and a low per capita rate of density change (Krebs and Myers, 1974). Predator populations, the small mustelids, are predicted to grow exponentially and to crash precipitously when arvicoline populations are depleted (Turchin *et al.*, 2000; Ekerholm *et al.*, 2001; Hanski *et al.*, 2001). Also in the *Traill Island model* of Gilg *et al.* (2003), which focuses on collared lemmings, the final winter decline is caused by small mustelids (stoats) but no social regulation of lemmings is assumed in the model. Instead, the per capita rate of population growth of lemmings is assumed to be strongly reduced by generalist and nomadic predators, which have different switching or invasion thresholds and can therefore respond to rising densities of lemmings, maintaining high predation pressure even during the increase phase of the cycle.

In the *simple arvicoline–plant model* of Turchin *et al.* (2000), the only population dynamically significant interaction is between arvicolines and perennial winter food plants – that is, arvicoline populations behave as predators of plants, growing exponentially at maximal per capita rate and crashing when winter resource plants are depleted. The *Barrow model* of Turchin and Batzli (2001), which focuses on brown lemmings, differs from the simple arvicoline–plant model by assuming that lemmings also have annually renewed resources, uninfluenced by past herbivory (e.g. graminoids, sprouting from subterranean rhizomes). In this model, the crashes of arvicolines are followed by low-level seasonal fluctuations. Outbreaks ensue when the perennial resources have increased to a level where they alone suffice to support the growth of lemming populations.

The above four models, focusing on arvicoline–plant and predator–arvicoline interactions, thus predict vastly different rates of realized per capita population growth rate of arvicolines during the year when arvicolines are approaching their population peak, to be abbreviated r_p. This contrast between the two model types emerges from a shared assumption of the specialist predator and Traill Island models. In both models, specialist, resident predators account for the final decline of arvicolines. This requires that some other factor reduces the rate of population growth of arvicolines, which would otherwise be several times higher than the maximum rate of population growth of specialist predators, leading to a rapid decrease in the numerical predator–prey ratio.

Another central diagnostic prediction concerns the skew of logarithmically transformed density data, to be abbreviated sk_d. On a logarithmic scale, exponential growth at constant per capita growth rate translates to a linear increase, where every data point is equally far from the preceding one. The distribution of such a data set about its mean is skew-free (Turchin *et al.*, 2000). Both the simple arvicoline–plant model and the Traill Island model predict exponential dynamics for arvicolines, though with very different rates of population growth. Therefore, both models predict a skew-free distribution of logarithmically transformed density data. The density-dependent reduction of per capita rates, predicted by the specialist predator model, generates time-series where logarithmically transformed density indices have negative skew (Turchin *et al.*, 2000). Conversely, positive skew is generated by the Barrow model, where realized per capita rates are low during the low phase, when the arvicolines fluctuate seasonally, interacting almost exclusively with annually renewable resources.

Fourier analysis provides a further tool to help distinguish between the central predictions of the models discussed above. It matches time-series data against sinus curves with different periods (Turchin, 2003). Therefore, the goodness of fit, reflected as the sharpness of the peak in the spectral density profile, depends both on the regularity of the cycle and the shape of the fluctuation pattern. Due to the importance of direct density-dependence, rodent cycles generated by the specialist predator model are predicted to have the approximate shape of a sinus curve (Hanski *et al.*, 1991, 1993, 2001; Turchin and Hanski, 1997). Moreover, in cycles driven by specialized predators, arvicolines should hit the ‘hard ceiling’ provided by social regulation. Hence, absolute peak densities should remain constant from cycle to cycle. These factors generate spectral density profiles with sharp peaks even when using raw data, reflecting changes in absolute numbers. Predator-type cycles of food-limited rodents consist of exponential growth curves, and absolute heights of peaks should vary, due to the impact of seasonality on resource supply (Turchin *et al.*, 2000). Therefore, the match between data and any sinus curve should be poor. Rodent–plant interactions should thus generate fluctuations, where spectral density peaks are only obtained with logarithmically transformed data, which render exponential curves to a 'saw tooth' pattern and shift the emphasis from absolute numbers to per capita rates. The predictions are summarized in Table 1.

Equipped with the two diagnostic parameters described above, Turchin *et al.* (2000) showed that the fluctuation patterns of Norwegian lemmings could be better accounted for by the simple arvicoline–plant model than by the specialist predator model. Using the same two diagnostic parameters and Fourier analysis, we will now explore how the fluctuation patterns of all arctic lemmings match the predictions of all four models discussed above. We will analyse brown and collared lemmings separately, because their feeding ecology is different (Batzli, 1993) and collared lemmings are claimed to be more vulnerable to predation (Gilg *et al.*, 2003). With the results of our analyses as our point of departure, we will explore the implications of lemming dynamics for the evolution and ecology of arctic plants, threatened by global warming.

MATERIALS AND METHODS

We compiled all time-series records known to us on population dynamics of brown and collared lemmings, covering at least 10 consecutive years with annual density indices or at least 5 years with semi-annual data. The locations of all included lemming populations are shown in Fig. 1; the density records are provided in the Appendix. The taxonomy of lemmings is based on Fredga *et al.* (1999). We have focused on records from treeless tundra areas, where the rodent guild is dominated by lemmings. The only exception to this rule is the record from the birch woodlands at Kilpisjärvi (Turchin *et al.*, 2000). [These woodlands are summer habitats of Norwegian lemmings, wintering on the tundra (see Kalela, 1971).] Species with a density sum of less than a third of the most abundant species were omitted to avoid confounding the analyses with data from suboptimal habitats, where rates of population growth might be inflated by immigration from optimal habitats. The material thus obtained consists of nine density records of brown lemmings, five records of collared lemmings, and one record of collective lemming densities, expressed on a subjective density scale of 0–4. (This record has only been used in Fourier analysis.) As points of reference, following Turchin *et al.* (2000), we have used three cyclic and predation-controlled North

Table 1. Summary of the predictions of the four models concerning the per capita rate of population growth during the year preceding the peak (r_p), the skew of logarithmically transformed density data (sk_d), and the spectral density profiles yielded by the Fourier analysis

Model	r_p	sk_d	Spectral density profiles
Specialist predator	<0.7	<0	Equally clear peaks with log transformed and non-transformed data
Traill Island	<1.5	≈ 0	Equally clear peaks with log transformed and non-transformed data
Simple rodent–plant	>3.0	≈ 0	Clear peaks with log transformed data only
Barrow	>3.0	>0	Clear peaks with log transformed data only

Note: The clarity and the statistical significance of the peaks of spectral density profiles are strongly dependent on the number of data points; the relevant thing to do is thus to compare the peaks yielded by non-transformed and logarithmically transformed data to each other within each data set.

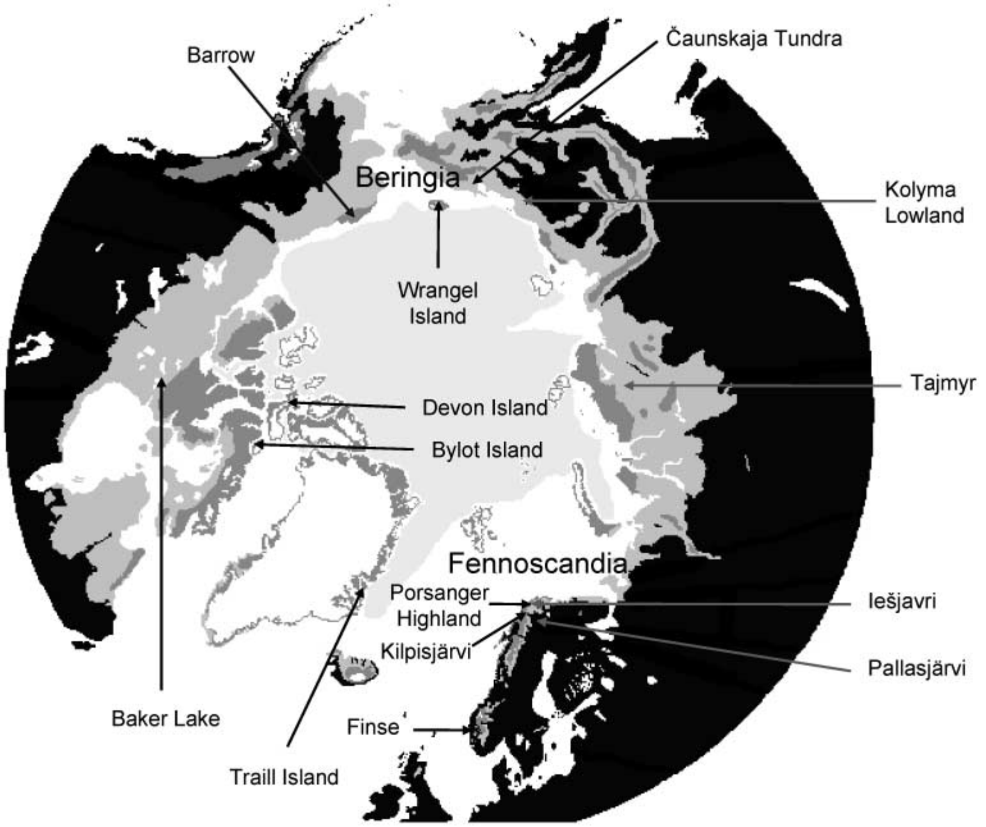

Fig. 1. Locations of the study sites from where the data used in the present study were obtained. Light grey: low arctic tundra and its altitudinal counterparts on boreal mountains. Dark grey: high arctic tundra and its altitudinal counterparts on low arctic and boreal mountains. Black: boreal forests and temperate areas. White: ice and water. Pale grey: permanently frozen sea. Redrawn based on the UNEP/GRID-Arendal Arctic Environmental Atlas (http://maps.grida.no/arctic/); boundaries between sub-zones adjusted following Richter (2001).

Fennoscandian vole guilds from the taiga-tundra ecotone (see Fig. 1), called 'reference voles' (Hanski *et al.*, 1991, 1993, 2001; Oksanen *et al.*, 1992, 1999; Hanski and Henttonen, 1996; Oksanen and Henttonen, 1996; Ekerholm *et al.*, 2001; Hambäck *et al.*, 2004).

In Table 2, we summarize the life zones and main habitats in each area from where density indices have been obtained, their mean July temperatures, mean annual precipitation rates, and the dominating rodent species of the area. We define population peaks operationally as the seasonal maxima in years when the average density is higher than that in the previous and the subsequent year and at least one-tenth of the highest value represented in the record. The latter criterion, not used by Turchin *et al.* (2000), has been introduced because the seasonal fluctuations, generated by the Barrow model, could otherwise create spurious peaks. Having identified the peaks in each density record, we computed the per capita rates of population growth during the year preceding the peak (r_p) as follows: $r_p = \Sigma(\ln(N_p) - \ln(N_{p-1}))/n$, where N_p is the density index for the seasonal maximum in the

Table 2. Characteristics of the areas represented in Fig. 1: their dominating habitats, mean July temperatures ($\check{T}_{\text{Jul}}$, in °C), mean annual precipitation (Pre, in mm), and their numerically dominating arvicoline species

Area	Main habitat	$\check{T}_{\text{Jul}}$	Pre	Dominating rodent species	Source of data
1. Pallasjärvi	Dark taiga	13	560	*Myodes glareolus*	Turchin *et al.* (2000)
2. Kilpisjärvi	Birch brushwood	11	450	*Myodes rufocanus*	Turchin *et al.* (2000)
3. Iešjávri	Forest tundra	11	345	*Myodes rufocanus*	Our data
4. Kolyma Lowlands	Forest tundra	11	170	*Lemmus bungei*	Černjavskij (2002)
5. Baker Lake	Low arctic tundra	10	170	*Lemmus chrysogaster*	Krebs (1964)
6. Porsanger Highland	Low alpine tundra	9	345	*Lemmus lemmus*	Our data
7. Finse	Low alpine tundra	8	1100	*Lemmus lemmus*	Framstad *et al.* (1997)
8. Čaunskaja Tundra	Low arctic tundra	8	140	*Lemmus chrysogaster*	Černjavskij (2002)
9. Tajmyr	Low arctic tundra	8	100	*Lemmus sibiricus*	Kokorev and Kuksov (2002)
10. Bylot Island	High arctic tundra	6	160	*Lemmus chrysogaster*	Gauthier *et al.* (2004)
11. Traill Island	High arctic tundra	5	300	*Dicrostonyx groenlandicus*	Gilg *et al.* (2003)
12. Devon Island	High arctic tundra	5	120	*Dicrostonyx groenlandicus*	Fuller *et al.* (1997)
13. Barrow	High arctic tundra	4	120	*Lemmus chrysogaster*	Batzli *et al.* (1980)
14. Wrangel Island	High arctic tundra	2	100	*D. groenl. & L. bungei*	Černjavskij (2002)

Note: Climate data are based on the records of the nearest weather station, corrected for altitudinal differences by −0.6°C per 100 m. Forest tundra refers to transitional areas, where tundra prevails, but patches of taiga or brushwood occur in sites with favourable local conditions.

peak year, N_{p-1} is the density index one year ahead of the peak, and n is the number of population peaks included in the time-series in question. If no lemmings were trapped one year before a given peak, we used half of the smallest non-zero value as a proxy for N_{p-1}. If only a part of the record is regularly semi-annual, only this part has been used in computations of r_p. When computing the skew of the logarithmically transformed density estimates (sk_d; zeroes excluded), we have excluded density records with less than 15 data points, because estimates of skew depend on extreme values, seldom present in small data sets.

The statistical significance of the differences in the above diagnostic parameters between reference voles, brown lemmings, and collared lemmings were tested by analysis of variance (ANOVA), using Tukey's *post hoc* test for pair-wise comparisons. Statistical tests of diagnostic parameters were conducted using the SPSS 12.0.1 for Windows program package.

In the Fourier analysis (window: Hamming), we only included density records that were at least 15 years in length, because we have found that using analyses based on shorter density records yield flat spectral density profiles even if the entire record provides clear evidence for periodicity. We tested the statistical significance of spectral density peaks against the null hypothesis of white noise using the S-plus test (Venables and Ripley, 1994).

RESULTS

The values of the two diagnostic parameters, r_p and sk_d, differ significantly between arctic lemmings and reference voles but not between brown and collared lemmings (Tables 3 and 4). The mean r_p value for all arctic lemmings is 4.0, which corresponds to a 55-fold increase in population density, whereas the reference voles increase less than two-fold during the year preceding the peak.

Furthermore, the skew values of the logarithmically transformed density data, sk_d, for arctic lemmings are outside the confidence limits obtained for the reference voles. The sk_d values for the reference voles are significantly negative (zero not included in the 95% confidence interval), whereas all sk_d values of arctic lemmings are positive.

The spectral density profiles obtained from raw and logarithmically transformed density records of reference voles are similar, showing a sharp peak corresponding to a period of 4–5 years (Fig. 2, top panels). For lemmings, evidence for regular periodicity is only obtained using logarithmically transformed data (Fig. 2, middle and bottom panels) and from the subjective Tajmyr record (not shown in Fig. 2; $P < 0.0001$ for this time-series).

DISCUSSION

Interpreting the results

The contrast between fluctuation patterns of arctic lemmings and reference voles, detected by Turchin *et al.* (2000; see also Oksanen, 1990) for Fennoscandia, appears to apply throughout the circumpolar tundra. Our analyses support the conclusion that the shift from vole-dominated areas at the transition from boreal to arctic life zones to lemming-dominated areas deeper in the arctic is accompanied by a change from predation-controlled to resource-limited dynamics in microtine rodents, as found by Turchin *et al.* (2000) for Fennoscandia. Lima *et al.* (2006) criticized this approach, pointing out that the shapes of fluctuation patterns are not robust consequences of the animals' trophic position but depend on the values of interaction parameters. True, but the interaction parameters depend on the characteristics of interacting organisms, and the parameter values used in the models are based on the characteristics of arvicolines, their predators, and on arctic winter forage plants, such as mosses (Hanski *et al.*, 1991, 1993, 2001; Turchin and Hanski, 1997; Turchin *et al.*, 2000; Turchin and Batzli, 2001; Gilg *et al.*, 2003; Klemola *et al.*, 2003).

With respect to the realized per capita rate of rodent population growth in the year preceding the peak (r_p), the divergence between predator–small rodent and small rodent–plant models is unambiguous. If any population of arvicoline rodents grows at a per capita rate anywhere near its capacity, the population will inevitably escape the control by resident, specialized predators and grow until winter forage is depleted. This problem is especially severe in the high arctic where weasels are absent and the specialist predator guild is only represented by stoats, which have delayed implantation (only one litter per year) and can

Table 3. The diagnostic parameters: per capita rates of population growth during the years before the peak (r_p) and the skew of logarithmically transformed density data, zero values excluded (sk_d) (the latter only for records with at least 15 positive data points)

Area and rodent genus	r_p	sk_d
Pallasjärvi, *Myodes*	0.36	−0.56
Kilpisjärvi, *Myodes*	0.59	−0.50
Iešjávri, *Myodes*	0.73	−0.96
Reference voles: mean ± standard error	0.56 ± 0.11	−0.68 ± 0.14
Kilpisjärvi, *Lemmus*	3.45	–
Porsanger Highlands, *Lemmus*	3.88	0.93
Finse, *Lemmus*	4.25	0.40
Čaunskaja Tundra, *Lemmus*	2.60	0.08
Kolyma Lowlands, *Lemmus*	3.59	–
Wrangel Island, *Lemmus*	6.81	–
Barrow, *Lemmus*	4.09	0.32
Baker Lake, *Lemmus*	5.36	–
Bylot Island, *Lemmus*	3.91	–
Lemmus spp.: mean ± standard error	4.21 ± 0.41	+0.43 ± 0.18
Kolyma Lowlands, *Dicrostonyx*	3.91	–
Baker Lake, *Dicrostonyx*	2.90	–
Wrangel Island, *Dicrostonyx*	6.36	–
Devon Island, *Dicrostonyx*	1.99	0.40
Traill Island, *Dicrostonyx*	2.97	0.44
Dicrostonyx spp.: mean ± standard error	3.62 ± 0.75	+0.42 ± 0.18

Note: Computations for Wrangel Island are based on the period 1978–1982, when trapping was conducted in spring and autumn.

Table 4. *P*-values of the null hypothesis of no difference [ANOVAs and pair-wise comparisons (Tukey's *post hoc* test)] between arctic lemmings and reference voles and between brown (*Lemmus*) and collared (*Dicrostonyx*) lemmings for per capita rates of population growth during the years before the peak (r_p) and for the skew of logarithmically transformed density data (sk_d)

	r_p	sk_d
ANOVA	0.003	0.005
Lemmus spp. vs. reference voles	0.002	0.006
Dicrostonyx spp. vs. reference voles	0.015	0.015
Lemmus spp. vs. *Dicrostonyx* spp.	0.697	0.998

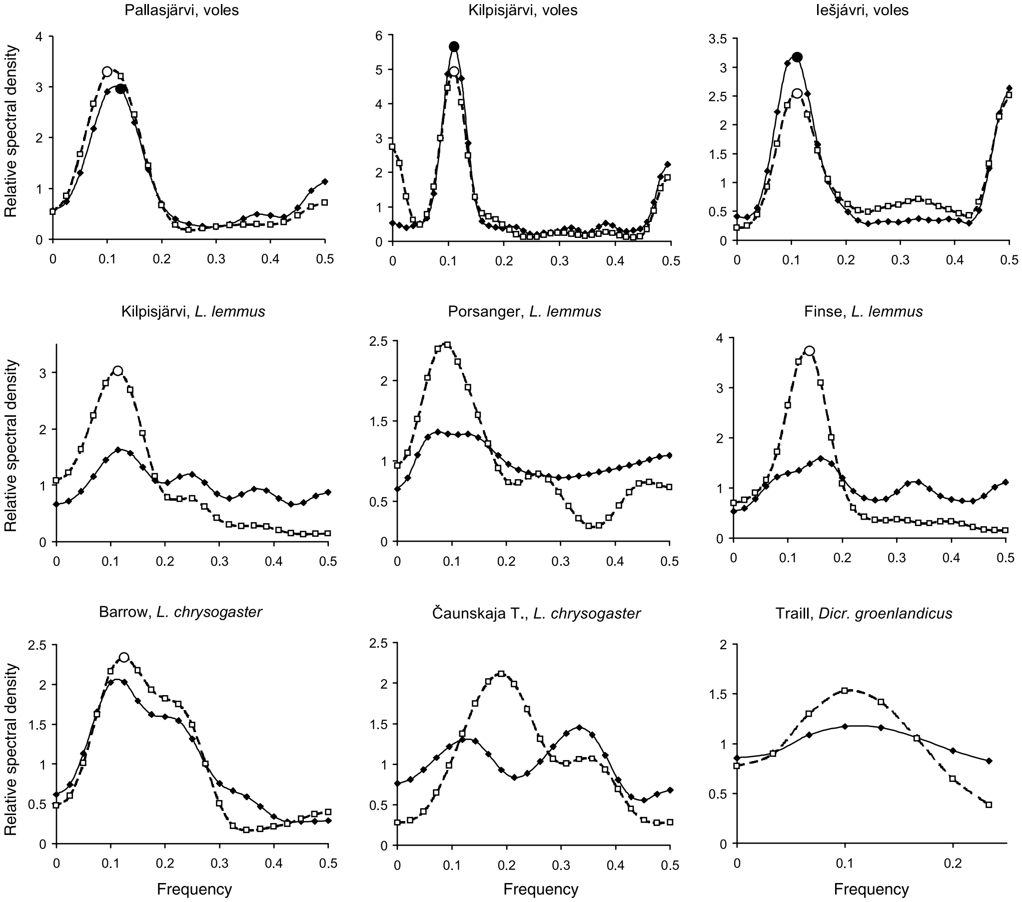

Fig. 2. Spectral density profiles (relative values; i.e. values divided by their mean) yielded by Fourier analyses of unbroken density records of at least 15 years in length of arctic lemming populations and of the three reference vole guilds from Pallasjärvi, Kilpisjärvi, and Iešjávri. The black diamonds represent analyses based on raw density indices, the white squares analyses based on logarithmically transformed data. Statistically significant peaks ($P < 0.05$ for the null hypothesis of white noise) in the spectral density profile are denoted by large dots. The time step in each data set is half a year; i.e. a frequency of 0.1 represents a 5-year cycle, a frequency of 0.17 represents a 3-year cycle, and a frequency of 0.5 represents seasonal density variation. For the Traill Island data set, only frequencies from 0.25 and below could be tested, because density indices are provided on an annual basis.

thus maximally increase by a factor of 4 per year. Not even surplus killing (Oksanen *et al.*, 1985; Jedrzejewska and Jedrzejewski, 1998) is likely to compensate for an order of magnitude difference between the population growth rates of the prey and the predator. The high per capita growth rates of arctic lemming populations in the year preceding the peak thus argue against both the specialist predator model (Hanski *et al.*, 1991, 1993, 2001; Turchin and Hanski, 1997) and the Traill Island model (Gilg *et al.*, 2003).

The mismatch between the spectral density profiles yielded by raw and logarithmically transformed lemming data is a further argument against the relevance of the specialist predator model for arctic lemmings. The case of Tajmyr fits to this pattern: subjective records are closer to a logarithmic than a linear scale, because only order-of-magnitude differences can be thus detected.

The positive skew of logarithmically transformed density records (sk_d), found in all lemming records long enough to test this parameter, is only consistent with the predictions of the Barrow model of Turchin and Batzli (2001). Moreover, the positive skew in logarithmically transformed density data is greatest in northern Fennoscandia, where the cycles of Norwegian lemmings are characterized by long periods of low-level seasonal fluctuations, punctuated by violent outbreaks (see Appendix). Conversely, the low phases of lemmings at Barrow and in southern Norway (Finse) are shorter. The contrast between northern Fennoscandia and Barrow probably depend on different growth rates of mosses. Turchin and Batzli (2001) assumed that the mosses recover completely within 2 years, in accordance with data from the wet tundra at Barrow (Tieszen *et al.*, 1980). In the winter habitats of North Fennoscandian lemmings, the recovery of a depleted moss cover takes at minimum a decade (Oksanen, 1983), prolonging the period when lemmings are dependent on winter-green graminoids. At Finse, higher precipitation probably speeds up the recovery of mosses (see Table 2).

Diagnostic parameters for the supposedly predation-controlled lemming populations of Traill Island and Bylot Island are within one standard error from the means for collared and brown lemmings, respectively, indicating that the Barrow model applies to these populations, too. As noted also by Gilg *et al.* (2003), there is a discrepancy between the predictions of the Traill Island model and the fluctuation patterns of lemmings on this island. The model predicts a gradual population rise, lasting for 3 years, lemmings increasing annually by a factor of three to four. According to the data, however, lemming densities have risen from very low values (0.14 and 0.36 individuals per ha respectively) to the peak within a single year. Unless the stoats (no weasels present), supposedly responsible for the decline, are present in large numbers already in the low phase of the lemming cycle (e.g. using marine-based prey), it is not plausible to assign the subsequent declines to stoat predation. Moreover, the maximum reported level of winter nest predation by stoats is only 14%, and during the decline phase of the second cycle only 3% of winter nests have been subject to predation (Gilg *et al.*, 2006). These data do not rule out alternative explanations.

Gauthier *et al.* (2004) propose that predation accounts for the lemming cycles of Bylot Island. However, their study focuses on geese. No data on specialized predators of lemmings are presented. Their lemming exclosures have not been quantitatively studied, and their focal habitat, an arctic fen, freezes in solid ice in winter. In Fennoscandia, the strong impacts of lemmings are found in winter habitats – on moist but not waterlogged sites with deep snow (Nordhagen, 1928; Kalela, 1971; Oksanen and Oksanen, 1981; Moen *et al.*, 1993; Virtanen, 2000; Virtanen *et al.*, 2002).

These cases of supposedly predation-controlled populations of arctic lemmings might reflect the momentum created by the excellent experimental studies supporting the conjecture of predation-driven vole cycles in the boreal zone (Korpimäki *et al.*, 1991; Norrdahl, 1995; Korpimäki and Norrdahl, 1998; Klemola *et al.*, 2000, 2002; Norrdahl *et al.*, 2002), and by the common perception that all cycles of arvicoline rodents share the same causal background. Indeed, there is good evidence for the role of avian predation in causing the temporary summer declines, typical for coastal lemming populations (Pitelka, 1973; Fuller *et al.*, 1977; Wilson *et al.*, 1999; Gilg *et al.*, 2003; Krebs *et al.*, 2003) (see also the Appendix), but at least at Barrow and on Wrangel Island, this does not prevent lemmings from having a strong impact on the vegetation (Pitelka, 1973; Batzli *et al.*, 1980; Černjavskij and Tkačev, 1982; Virtanen *et al.*, 2006; Pitelka and Batzli, 2007). Given the impact of the ‘marine energy shunt’ on terrestrial food webs in coastal deserts (Polis and Hurd, 1996; Barrett *et al.*, 2005) and the high productivity of northern seas (Koblentz-Mishke *et al.*, 1970), it is likely that a corresponding ‘marine energy shunt’ supports dense predator populations along many arctic coasts and that lemmings are constantly kept at low density (see Reid *et al.*, 1995). However, such predators with alternative resources in another habitat should have stabilizing functional response (Oksanen *et al.*, 2001), making it unlikely that they would drive population cycles.

The lemmings and the tundra – not one without the other?

In the Introduction, we summarize evidence for the rapid evolution of collared and brown lemmings when the tundra was formed (Hoffmann and Taber, 1968; Guthrie and Matthews, 1971; Chaline *et al.*, 1999) and interpret this as a consequence of a shift from predation-controlled to food-limited dynamics. The results of our analysis of density fluctuations in arctic lemmings corroborate this conjecture. A likely reason behind this dramatic change in population dynamics is the northwards shift of Eurasia and North America, resulting in reduced actual evapotranspiration and, therefore, reduced primary productivity (Rosenzweig, 1968). In the unproductive environment thus created, winter resources could no longer sustain arvicoline densities high enough to support predatory endotherms (Oksanen and Oksanen, 2000; Aunapuu *et al.*, 2008). Consequently, natural selection began to favour individuals capable of exploiting a depleted resource supply at any cost. The main cost was reduced agility and, therefore, inferiority to voles in apparent competition (Holt, 1977), restricting brown and collared lemmings to the Arctic where food limitation rules (Oksanen, 1992; Oksanen, 1993). The population dynamical dichotomy between boreal voles and arctic lemmings outlined above is thus in line with the Exploitation Ecosystems Hypothesis (Oksanen *et al.*, 1981, see also Rosenzweig, 1971).

When interspecific competition prioritized the ability to exploit depleted vegetation, the impacts of lemmings on plants were re-enforced. On the Fennoscandian tundra, direct and indirect effects of Norwegian lemmings thus appear to account for the sharp shift from ericoid-dominated heaths and tall herb meadows to graminoid-dominated ‘early snow-beds’ along gradients of increasing snow cover. Traditionally, this habitat shift has been interpreted as a result of the supposed inability of ericaceous dwarf shrubs to tolerate deep snow (Gjaerevoll, 1956), but dwarf shrubs and tall forbs planted to these grasslands survive well if protected against herbivorous mammals (Moen and Oksanen, 1998; Virtanen, 1998; Olofsson *et al.*, 2002; Eskelinen, 2007), indicating that this local boundary represents a shift between the ‘steppe’ (grassland) stage and the heath stage of the tundra (Zimov *et al.*, 1995), the grassland stage being created and maintained by recurrent, strong impacts of herbivorous mammals on the vegetation. The role of snow depth is probably indirect. According to our own, unpublished data, the density of snow along the ground is much lower in habitats where snow accumulates, probably because the snow crystals get buried quickly and are therefore not deformed as strongly as they are in upland sites, where they are carried by wind over long distances.

The typical winter habitats of Norwegian and Siberian lemmings are characterized by high plant species diversity and an overwhelming predominance of non-clonal herbaceous plants, dependent on sexual reproduction (Söyrinki, 1938, 1939; Kalliola, 1939; Gjaerevoll, 1956; Oksanen and Virtanen, 1995; Virtanen *et al.*, 1999). This is in striking contrast to the low species diversity of vascular plants and the prevalence of vegetatively reproducing species in wetlands, freezing in solid ice (Söyrinki, 1938, 1939; Kalliola, 1939) and on lemming-free offshore islands, where vast areas are covered by moss bank vegetation with a low abundance of vascular plants (Warren Wilson, 1952; Virtanen *et al.*, 1997b). Even the impacts of grey-sided voles, resembling the ancestors of collared lemmings, can be dramatic. According to the exclosure experiments of Olofsson *et al.* (2004a), the impacts of grey-sided voles surpass the impacts of the dense Fennoscandian reindeer populations even on lichen heaths with thin snow cover and, therefore, poor grazing conditions for arvicoline rodents. In habitats with more suitable snow conditions, food-limited grey-sided voles wreak havoc on woody vegetation, favouring herbaceous plants (Hambäck, 1998; Hambäck *et al.*, 2004; Dahlgren, 2006; Dahlgren *et al.*, 2007; Aunapuu *et al.*, 2008). However, arvicolines interacting with dwarf shrubs remove entire shoots and consume them in their runways, and thus their impact can be difficult to detect without conducting systematic studies.

There are two tundra areas where systematic studies have been conducted, focusing on the impacts of brown lemmings on plant biomass, population dynamics of tundra plants, species composition of the arctic vegetation, and on nutrient circulation: Fennoscandia and Beringia (Fig. 1). In both areas, unquestionable evidence for a strong lemming–vegetation interaction exists (Nordhagen, 1928; Schultz, 1964, 1969; Pitelka, 1973; Batzli *et al.*, 1980; Oksanen and Oksanen, 1981; Černjavskij and Tkačev, 1982; Oksanen, 1983; Moen *et al.*, 1993; Oksanen and Moen, 1994; Virtanen *et al.*, 1997a, 2002; Moen and Oksanen, 1998; Virtanen, 2000; Olofsson *et al.*, 2002; Pitelka and Batzli, 2007; Aunapuu *et al.*, 2008), contributing to the abundance of graminoids and other disturbance-adapted plants. Even ungulates can be important in this context (Olofsson *et al.*, 2004b; Olofsson and Oksanen, 2005; Bråthen *et al.*, 2007). In the Pleistocene, when the arctic herbivore guild had not been impoverished by mass extinctions, graminoid-rich tundra habitats were more widespread than today, probably due to the combined impacts of big grazing mammals and a more continental climate (Kurtén, 1971; Zimov *et al.*, 1995; Sher *et al.*, 2005). However, big grazers cannot exploit winter resources in snowy habitats. It is therefore likely that the distinctive characteristics of arctic lemmings and the characteristics of tundra plants growing in well-drained, snow-rich habitats evolved through intense, reciprocal lemming–plant interaction, and the species thus formed can only flourish as long as this strong interaction prevails.

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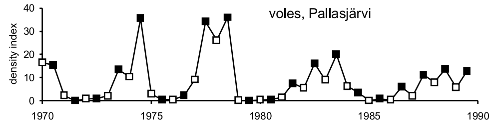
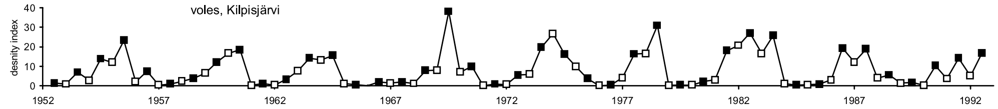
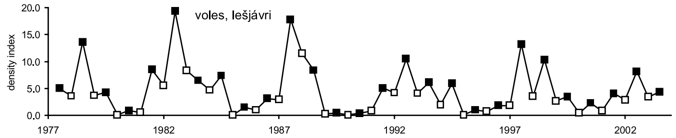
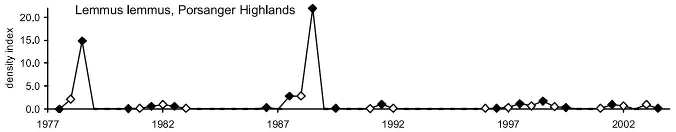
APPENDIX

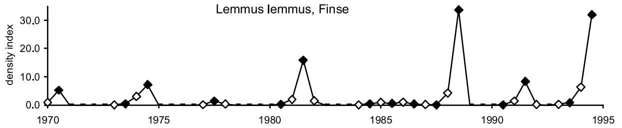
Density indices for the arctic lemming populations and reference voles used in our analyses. Values for Tajmyr represent averages of the indices provided for different parts of the peninsula. To facilitate comparisons, all data sets are presented as semi-annual records by deleting summer records if autumn records were available. White symbols represent spring data, black symbols autumn data. The winter peaks at Barrow (denoted as white triangles) have been treated as spring data in our analyses. The summer records for Wrangel Island during times when autumn trapping was not conducted are denoted by grey symbols.

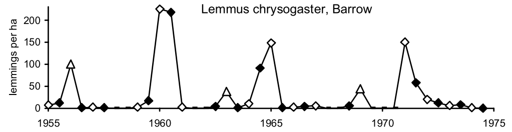


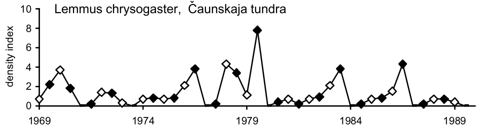


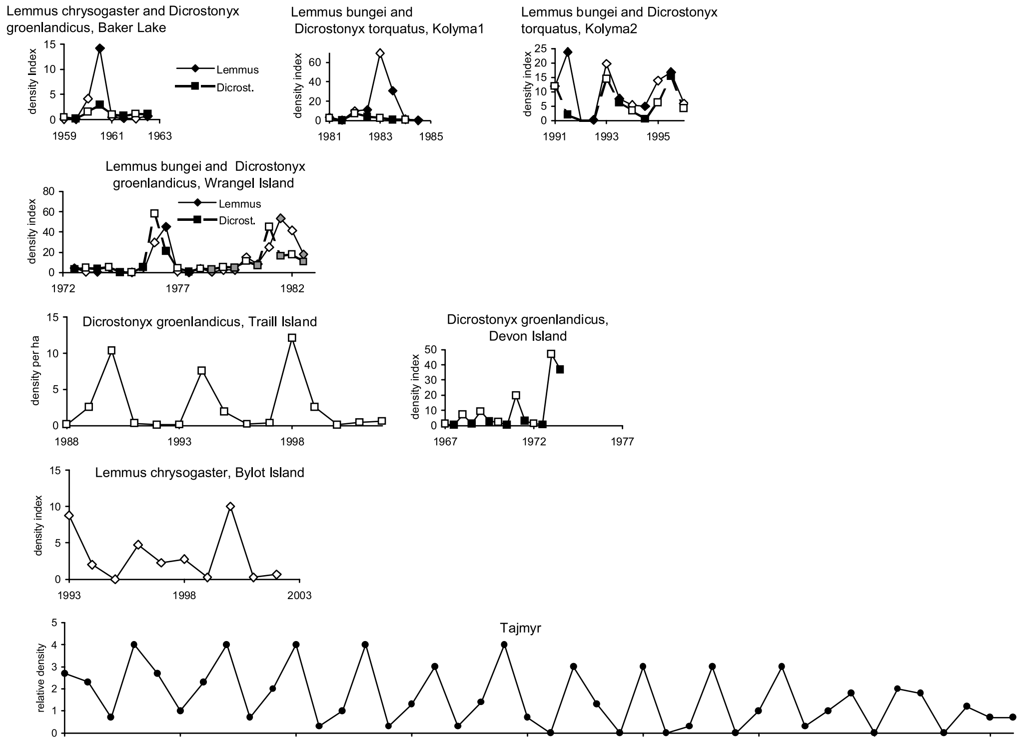











Lemmus chrysogaster and Dicrostonyx groenlandicus, Baker Lake
density Index
15
10
5
0
1959
1961
1963
Lemmus
Dicrost.
Lemmus bungei and Dicrostonyx torquatus, Kolyma1
density index
60
40
20
0
1981
1983
1985
Lemmus bungei and Dicrostonyx torquatus, Kolyma2
density index
25
20
15
10
5
0
1991
1993
1995
Lemmus bungei and Dicrostonyx groenlandicus, Wrangel Island
density index
80
60
40
20
0
1972
1977
1982
Lemmus
Dicrost.
Dicrostonyx groenlandicus, Traill Island
density per ha
15
10
5
0
1988
1993
1998
Dicrostonyx groenlandicus, Devon Island
density index
50
40
30
20
10
0
1967
1972
1977
Lemmus chrysogaster, Bylot Island
density index
15
10
5
0
1993
1998
2003
Tajmyr
relative density
5
4
3
2
1
0
1960
1965
1970
1975
1980
1985
1990
1995
2000

Evolutionary Ecology Research, 2009, **11**: 483–484

Arctic lemmings are not simply food limited – a comment on Oksanen *et al.*

We appreciate the attempt by Oksanen *et al.* (2008: *Evol. Ecol. Res.*, **10**: 415–434; http://evolutionary-ecology.com/issues/v10n03/hhar2304.pdf) to link possible evolutionary changes to the history of colonization of the Arctic by lemmings. However, we do not agree that lemming evolution and colonization history help us to understand current lemming population dynamics.

Oksanen *et al.* (2008) note that field exclosures in Fennoscandia show evidence of moss overgrazing by lemmings. Habitat degradation is clearly visible in peak lemming years, especially in critical wintering habitat such as snowbeds. Based on this evidence and their analysis of lemming populations through time, Oksanen *et al.* reach generalizations about lemming–vegetation interactions across the Arctic. Their food-limitation model generates a time-lag owing to the overuse of mosses by *Lemmus* (during years of peak lemming abundance) followed by the delayed recovery of mosses.

It is true that previous models assumed a recovery time for mosses of 2 years (Turchin and Baltzi, 2001: *Ecology*, **82**: 1521–1534). But recovery time of these plants following severe overgrazing appears much longer in northern Fennoscandia, on the order of 10 years (Oksanen *et al.*, 2008). After overgrazing, recovery of mosses (and even vascular plants) is indeed slow in the Arctic. But the period typical of most lemming cycles is 3–5 years. A 10-year recovery time-lag cannot generate a 3- to 5-year population cycle.

Moreover, the time-series analyses in Oksanen *et al.* have a troubling technical flaw. Of the 15 time-series that they use, 13 are based on index values rather than estimates of population density. Indices may overestimate or underestimate density and the bias may itself depend on density (Anderson, 2003: *Wildlife Soc. Bull.*, **31**: 288–291). So one cannot reliably calculate per capita population growth rates based on indices.

We are convinced that the generalizations of Oksanen *et al.* do not apply in the Arctic regions where we have worked. No study conducted in the Canadian Arctic in the past 40 years has ever noted evidence of widespread habitat degradation, including mosses, after a lemming peak. Recent evidence from lemming exclosures in both wet and mesic tundra sites at Bylot Island (G. Gauthier, unpublished data) also fails to support the overgrazing hypothesis. The food limitation hypothesis for *Lemmus* population cycles may apply in Fennoscandia but not in Canada.

Oksanen *et al.* also generalize their food depletion hypothesis to *Dicrostonyx* populations. However, *Dicrostonyx* eat very little moss, and yet are highly cyclic in several places where *Lemmus* are scarce (Walker Bay) or absent (Greenland). In Canada, we have never seen *Dicrostonyx* food resource depletion after peak populations.

In addition, we do not believe that one can describe population dynamics and evaluate a mechanistic model from census data taken only once or twice a year. By using annual and semi-annual censuses, Oksanen *et al.* ignore seasonality. Yet moss is a dominant part of *Lemmus* diet only in winter. In summer, *Lemmus* eat mostly other plants, especially graminoids. If the food-limitation hypothesis were true, the most difficult period for lemmings in peak years would be the end of winter, when mosses become increasingly depleted. Therefore, the end of winter and early spring would be the time when *Lemmus* should experience decreased reproduction and a population decline. After the snow melts and new food supplies are renewed, *Lemmus* populations should grow rapidly. However, in peak lemming years, the strongest reproductive output often occurs under the snow in late winter and spring. Populations of lemmings peak shortly after snow melt and then decline or even crash during the summer (Millar, 2001: *Ecoscience*, **2**: 145–150).

The summer decline is often associated with increased predation mortality. In previous research, we found evidence for a strong role of predators in lemming cycles at some Canadian sites (Reid *et al.*, 1995: *Oikos*, **73**: 387–398; Wilson *et al.*, 1999: *Oikos*, **87**: 382–398). Nonetheless, Oksanen *et al.* reject the predator hypothesis either by pointing out weaknesses in these studies or by arguing that they were conducted at coastal sites where predators may benefit from allochthonous exchanges with the marine environment. We do not dispute some of these weaknesses, but we believe that the food-limitation hypothesis has at least as many.

To reach convincing conclusions, one needs detailed seasonal data on changes in actual numbers. But there are hardly any winter data on lemming and northern vole populations. We also need data on how predation, parasitism, food shortages, and social processes affect population changes. Empirical field studies that might provide such data are still scarce for lemmings and limited to a few sites in the circumpolar world for too short a period to rely on at this point. Therefore, we conclude that the jury is still out on what factors drive the lemming cycles in many parts of the Arctic and that the conclusions of Oksanen *et al.* are premature.

We thank Tarja and Lauri Oksanen for a fruitful exchange and also Erkki Korpimäki for his comments.

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On the implications of currently available data on population fluctuations of arctic lemmings – reply to Gauthier *et al.*

Gauthier *et al.* (2009: *Evol. Ecol. Res.*, **11**: 483–484) raise two major questions about our recent paper (Oksanen *et al.*, 2008: *Evol. Ecol. Res.*, **10**: 415–434). Can the evolutionary background of a species provide clues for its current population dynamics? And can patterns revealed by imperfect data be used for testing population dynamical hypotheses?

We interpreted the evolution of arctic lemmings as an indication of a shift from predator control to resource limitation. This shift provides clues for population dynamical hypotheses if adaptations carry a cost. Predator-controlled herbivore guilds are structured by apparent competition, where success depends on the r/a ratio (Holt, 1977: *Theor. Popul. Biol.*, **12**: 276–290), i.e. the ratio of reproductive capacity to vulnerability. Conversely, food-limited herbivore guilds are structured by resource competition, where the outcome depends on R^*, i.e. the lowest resource density at which the organism can still survive (Tilman, 1982: *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press). If there is a trade-off between properties minimizing a (speed and agility) and R^* [the ability to exploit depleted resources (Oksanen, 1992: *Evol. Ecol.*, **6**: 15–33)] and the more agile voles are present, regulation by predators should lead to exclusion of arctic lemmings (Oksanen, 1993: *Linn. Soc. Symp. Ser.*, **15**: 425–437; K. Kyrö, L. Oksanen, and T. Oksanen, unpublished data).

In their second major point, Gauthier *et al.* (2009) argue that snap trapping indices are too inaccurate to be used for testing population dynamical conjectures. Inaccuracies in the database can reduce the likelihood of detecting differences between the objects of study but cannot account for the statistically significant contrasts between arctic lemmings and reference voles. Moreover, we have focused on robust predictions. According to the predation-based models (Hanski *et al.*, 2001: *Ecology*, **82**: 1505–1520; Gilg *et al.*, 2003: *Science*, **302**: 866–868), rodent densities must not increase more than four-fold during the year preceding the peak, while a more than 20-fold increase is predicted by the food-based models (Turchin *et al.*, 2000: *Nature*, **405**: 562–565; Turchin and Batzli, 2001: *Ecology*, **82**: 1521–1534). During the year preceding the peak, the density indices for *Lemmus* spp. increased, on average, by 67-fold and those for *Dicrostonyx* spp. by 37-fold, whereas the indices for the reference voles increased less than two-fold. Due to trap saturation at high densities, all these estimates are downward biased. But this bias only strengthens the point that just before the peak, arctic lemmings are increasing at a rate that resident specialized predators cannot match.

As for the other points, the Barrow model is taxonomically neutral and requires only that lemmings exploit both depletable and annually renewed forage plants. The model can be applied to *Dicrostonyx* spp. if we assume that woody plants form the depletable part of the diet. With original parameter values, the Barrow model generates the 3- to 5-year cycles discussed by Gauthier *et al.* (2009). To reconcile this model with the longer periods of Fennoscandian cycles, we must assume lower growth rates for depletable forage plants. Studies on plant growth rates can thus be used to test the model.

Gauthier *et al.* (2009) claim that 'no study conducted in the Canadian Arctic in the past 40 years has ever noted evidence of widespread habitat degradation, including mosses, after a lemming peak'. The visibility of herbivore impacts depends on the frequency of the disturbance. During a decade with low lemming densities, the species composition of Fennoscandian snowbed vegetation changes profoundly, making the impacts of lemming outbreaks obvious. In cycles with a shorter period, there is less time for the vegetation to change qualitatively, and biomass changes may not be easily observed. The detailed plant population studies of Berg *et al.* (2008: *Adv. Ecol. Res.*, **40**: 275–298) reveal strong lemming impacts on dwarf shrubs in northeast Greenland, and lemmings also seem to regulate the moss cover at Barrow, Alaska (Oksanen, 1983: *Am. Nat.*, **122**: 45–52; Pitelka and Batzli, 2007: *Acta Theriol.*, **52**: 323–336). Moreover, depletion of woody plants can be difficult to detect. We did not detect the impacts of grey-sided voles on dwarf shrubs visually, but by marking shoots and by experimentally introducing and excluding voles (Oksanen and Oksanen, 1981: *Rep. Kevo Subarctic Res. Stat.*, **17**: 7–31; Hambäck and Ekerholm, 1997: *Oikos*, **80**: 276–288; Hambäck *et al.*, 2004: *Oikos*, **106**: 85–92; Olofsson *et al.*, 2004: *Oikos*, **106**: 324–334).

As pointed out by Gauthier *et al.* (2009), the food-based models predict that lemming populations crash in the post-peak winter, whereas according to them lemming densities peak right after the snow melt and decline or crash during the summer. They cite Millar (2001: *Ecoscience*, **8**: 145–150), but that study focuses on reproductive biology and does not discuss the timing of crashes. The data compiled by us include one summer crash (at Barrow 1965); all other documented crashes have occurred in winter. Moderate summer declines, attributable to avian predation, occur often in coastal areas. According to the indices, all studied inland populations, including the one studied by Krebs (1964: *Arct. Inst. N. Am., Tech. Paper*, **15**: 1–104) at Baker Lake, Canada, peaked in late summer and crashed in winter.

We see the coast versus inland contrast as part of a broader question concerning the impact of marine-based subsidies on food web dynamics in unproductive terrestrial systems (Polis and Hurd, 1996: *Food Webs: Integration of Patterns and Dynamics*, pp. 275–285. New York: Chapman & Hall). The experiments demonstrating the impact of predation on lemmings (Reid *et al.*, 1994: *Oikos*, **73**: 387–398; Wilson *et al.*, 1999: *Oikos*, **87**: 382–398) were conducted at the coast, and refer to populations which we do not regard as cyclic. [The densities of the lemmings of Wilson *et al.* (1999) varied only within the range 1 to 10 individuals per hectare.] Moreover, coastal predators do use marine-based prey (Sitter *et al.*, 2000: *Arctic*, **53**: 53–60). Studies conducted on the coastal tundra make an important contribution to our understanding of the arctic. The arctic coastline is long and a substantial part of the tundra is coastal, especially in the high arctic where much of the inland area is made up of ice caps and polar deserts. Nevertheless, results obtained from coastal areas need not be representative of the inland tundra.

While the available time trajectory data do corroborate the Barrow model, other ideas, which have not yet been rigorously modelled, could also account for their patterns. We are currently analysing an idea in the context of the low arctic tundra where productive willow scrublands still occur, which we call the 'pacemaker hypothesis'. It presupposes that the period of the cycle is set by predator–vole–lemming interactions in small patches of productive pacemaker habitat. The dramatic increase in the pre-peak year happens primarily in the widespread unproductive habitats; there lemmings crash due to starvation in the post-peak winter.

We agree with Gauthier *et al.* (2009) that the enigma of arctic lemming cycles is far from solved. Experimental results and long-term records are few. Thus, large geographical and/or interspecific differences in population dynamics of arctic lemmings might remain to be detected. To date, however, the only clear difference detected between the dynamics of different populations of arctic lemmings is the greater frequency of summer declines in coastal areas, which fits the food-based hypotheses.

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