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Impact of marine-subsidized predators on lemming–plant oscillations

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ABSTRACT

Questions: Assuming that arctic lemming oscillations are generated by interactions between lemmings and depletable plants, how should these oscillations change in response to varying densities of marine-subsidized predators and differences in the production of herbaceous forage? Are the patterns thus generated consistent with existing data?

Features of the model: Rosenzweig-type predator–prey model, with lemmings interacting with depletable plants and herbaceous plants. The impact of marine-subsidized predators is included as an extra mortality factor, influencing lemmings in summer.

Ranges of parameters: We set the carrying capacity of depletable plants at 2000 $\text{kg}\cdot\text{ha}^{-1}$. We used carrying capacities for herbaceous plants of 1000 $\text{kg}\cdot\text{ha}^{-1}$ (grassland/meadow) and 100 $\text{kg}\cdot\text{ha}^{-1}$ (heath). In the absence of predation, we assume that the population growth rate of lemmings in summer is zero when their foraging rate is 44% of the saturation rate. In subsequent simulations, we successively increased the foraging rate required for a zero population growth rate to simulate the impact of a successively larger pool of marine-subsidized predators.

Predictions: On grassland/meadow tundra, increasing intensity of summer predation reduces the amplitude and period of lemming and plant oscillations and increases the minimum and average density of lemmings and depletable plants. The predicted predator–lemming relationship is thus mutualistic rather than exploitative. In heath-type tundra, the predicted positive impact of summer predation on lemmings is even stronger because, without intense summer predation, the predicted oscillations are violent enough to lead to local extinctions. In tundra areas with such dynamics, natural selection should favour lemmings that react to high population densities by emigrating.

Keywords: arctic, herbivory, lemming, oscillations, population cycles, predation, tundra, vegetation.

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INTRODUCTION

Brown lemmings and collared lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) form the dominating component of many arctic food webs (Wielgolaski, 1975; Batzli *et al.*, 1980; Černjavskij and Tkačev, 1982). The low primary productivity typical for arctic ecosystems increases the likelihood of food limitation in herbivores, and resource-consumer models predict that such systems often have a cyclic or chaotic attractor, leading to sustained, violent density oscillations (Oksanen *et al.*, 1981; Oksanen and Oksanen, 2000; Turchin *et al.*, 2000; Turchin and Batzli, 2001). Most long-term records of arctic lemmings display oscillations with sharp, short-lived peaks and extended low phases (Oksanen *et al.*, 2008), corresponding to the predictions of the Barrow model of Turchin and Batzli (2001). The model is also supported by observational and experimental studies, demonstrating the existence of a strong rodent–plant interaction at Barrow, Alaska (Schultz, 1964; Pitelka, 1973; Batzli, 1975; Batzli *et al.*, 1980; Pitelka and Batzli, 2007; Johnson *et al.*, 2012) and in many parts of the Eurasian tundra (Tihomirov, 1959; Oksanen and Oksanen, 1981; Černjavskij and Tkačev, 1982; Andersson and Jonasson, 1986; Kirjušenko, 1985; Moen *et al.*, 1993; Oksanen and Moen, 1994; Virtanen *et al.*, 1997a, 1997b, 2002; Virtanen, 1998, 2000; Černjavskij, 2002; Olofsson *et al.*, 2002, 2004a, 2009, 2012; Aunapuu *et al.*, 2008; Ravolainen *et al.*, 2011; Hoset *et al.*, 2013).

Like the models of Oksanen *et al.* (1981), Oksanen (1990a), and Turchin *et al.* (2000), the Barrow model treats, intentionally, unproductive tundra areas as closed systems, where predators do not play any dynamic role. The Barrow model is intended to be an exploration of dynamics generated by lemming–plant interactions, not an accurate representation of population dynamics of lemmings at Barrow (Turchin and Batzli, 2001). However, the food webs of the tundra are more or less linked to marine food webs (Oksanen *et al.*, 2008; Gauthier *et al.*, 2011; Legagneux *et al.*, 2012), at least via jaegers [*Stercorarius* spp. (see Sittler *et al.*, 2011)], which breed even on the inland tundra (Krebs, 1964; Andersson, 1976a; Oksanen *et al.*, 1997; Aunapuu *et al.*, 2008). The relatively productive arctic marine environments (Slagstad *et al.*, 2011) also subsidize (*sensu* Polis and Hurd, 1997) other predators preying on lemmings during peak years, such as arctic foxes (e.g. Roth, 2002, 2003) – primarily red foxes in Fennoscandia (see Elmhagen *et al.*, 2002; Killengreen *et al.*, 2011) – and, as recently revealed, even snowy owls (Therrien *et al.*, 2011). All these predators prey on coastal lemming populations during summers of high lemming density, often consuming a significant proportion of their production (Pitelka, 1973; Černjavskij and Tkačev, 1982; Wilson *et al.*, 1999; Krebs *et al.*, 2003; Gilg *et al.*, 2003, 2006; Pitelka and Batzli, 2007; Gauthier *et al.*, 2011; Legagneux *et al.*, 2012).

The periodic presence of predators need not, however, imply predation-driven dynamics. Outbreaks generated by herbivore–plant systems with cyclic or chaotic attractors can be profitably exploited by marine-subsidized predators. This was highlighted by Oksanen *et al.* (1981) and Oksanen and Oksanen (2000), but they did not analyse the dynamic consequences of such 'outbreak cropping' that likely depend on the regional pool of marine-subsidized predators and distance to the sea. The impact of these predators may also depend on the production of herbaceous forage, because it potentially influences lemming–vegetation dynamics (Turchin and Batzli, 2001). Spatial variation in the production of herbaceous forage and variation in the size of the predator pool can be included in the Barrow model (Turchin and Batzli, 2001) without structural changes, by adjusting parameter values. The logic of the Barrow model also applies to collared lemmings (*Dicrostonyx* spp.), which interact with dwarf shrubs and herbaceous dicots (Batzli, 1993). Like mosses, dwarf shrubs grow slowly and retain most of their energy and nutrient reserves in their shoots in winter (Kjelvik and Kärenlampi, 1975) and are therefore vulnerable to winter herbivory (Dahlgren *et al.*, 2009).

We will study the dynamics of such a system with simulations, where we treat the size of the marine-subsidized predator pool as a continuous variable. The production of herbaceous forage will be treated as a step function, obtaining only two values. Most plant communities of the tundra are namely either heaths, dominated by lichens, mosses, and/or dwarf shrubs, or grasslands/meadows, dominated by herbaceous plants, due to positive feedbacks (Zimov *et al.*, 1995; Hobbie, 1996; Nilsson *et al.*, 1998, 2000; Gallet *et al.*, 1999; Olofsson *et al.*, 2004b; van der Wal and Brooker, 2004). For each of these two tundra types, we will compare the predictions generated by our simulations to the predictions of the model of Gilg *et al.* (2003), in which lemming dynamics are driven by winter predation by stoats, whereas summer predation by jaegers, snowy owls, and arctic foxes plays a stabilizing role, limiting lemming outbreaks. Thereafter, we will compare the dynamics generated by these two models to documented oscillation patterns of arctic lemmings. Based on our results, we will infer how differences in oscillation patterns influence survival strategies of lemmings and plants and how this influences the relation between dynamics and energy flow in arctic ecosystems. Conforming to the theoretical discoveries of Abrams (1992a, 1992b), we show that the outcomes of such interactions can be counterintuitive: predator–prey relations can be mutualistic; predators exploiting herbivores can have negative impacts on plants; and strong herbivore–plant interactions may result in a low ratio of consumption to primary production.

THE MODEL AND THE SIMULATION PROCEDURE

Starting with the Barrow model of Turchin and Batzli (2001), we assume that the vegetation consists of herbaceous plants (V) and depletable plants (mosses and dwarf shrubs, M), thus generalizing the vegetation groups explicitly assumed by Turchin and Batzli (2001). We model the summer growth of depletable plants with a Rosenzweig-type prey equation (see Oksanen *et al.*, 1981), consisting of a logistic growth term (with carrying capacity $K_M = 2000$ $\mathrm{kg \cdot ha^{-1}}$ of dry, edible biomass) and a Lotka-Volterra type exploitation term, where the exploiter has a type-II functional response. We model the dynamics of herbaceous plants with a regrowth equation in which growth rate in summer is highest when above-ground biomass is zero and decreases linearly when above-ground biomass approaches carrying capacity. The Barrow model – focused on the graminoid rich lowland tundra of Alaska – assumed that $K_V = 1000$ $\mathrm{kg \cdot ha^{-1}}$. It also assumed no competition between depletable plants and herbaceous plants. Its other assumptions included zero growth terms for all plants during and at the onset of winter, as well as that 90% of the herbaceous plant biomass is unavailable in winter due to withering and/or translocation of soluble materials to inaccessible roots and rhizomes. For depletable plants, we thus obtain a seasonally modified logistic equation with growth in summer only. Note that the carrying capacity of herbaceous plants reflects the maximum biomass reached within one growing season, thus being equivalent to productivity. By contrast, the carrying capacity of depletable plants is achieved when the rate of addition of edible biomass is balanced by the rate of dieback of mosses (Turchin and Batzli, 2001) and the rate of lignification of dwarf shrub shoots.

The lemming (H) equation is a Lotka-Volterra-type predator equation following the structure of Rosenzweig and MacArthur (1963). In it, the amount of food consumed directly affects the growth/decline rate. We rearranged the equation so that it explicitly includes the seasonal foraging rate $G(\tau)$ required for a zero growth rate of the lemming population. Lemming density is measured in individuals per hectare. Our equations come from Turchin and Batzli (2001):

$$\frac{dV}{dt} = U(\tau)\left(1 - \frac{V}{K_V}\right) - \frac{AVH}{V + \alpha M + B} \tag{1}$$

$$\frac{dM}{dt} = u(\tau)M\left(1 - \frac{M}{K_M}\right) - \frac{\alpha AMH}{V + \alpha M + B} \tag{2}$$

$$\frac{dH}{dt} = RH\left[\frac{A(V + \alpha M)}{V + \alpha M + B} - G(\tau)\right] \tag{3}$$

where $U(\tau)$ is the seasonal maximum growth rate of herbaceous plants; K_V is their carrying capacity; A is the maximum per capita consumption rate of lemmings; B is their half-saturation constant; α is the discounting parameter relating the consumption rate of depletable plants to the consumption rate of herbaceous plants; $u(\tau)$ is the seasonal maximum growth rate of depletable plants per biomass unit; K_M is their carrying capacity; R is the conversion rate of plant biomass to lemming population growth; and $G(\tau)$ is the seasonal per capita forage-consumption rate of lemmings at which their rate of population growth is zero. Seasonality is denoted in the model by the parameter τ, which takes on one of two values: w (winter) and s (summer) ($\tau = s$ for summer during 1/6 of the year; $\tau = w$ for winter during 5/6 of the year).

Based on the energy needs of lemmings during summer and winter (Batzli and Cole, 1979; Batzli *et al.*, 1980), Turchin and Batzli (2001) inferred that $G(s) = 0.44A$ and $G(w) = 0.63A$, where A is the largest physiologically possible rate of forage consumption. On the basis of Melchior (1972), Batzli and Cole (1979), and Kirjušenko (1985), Turchin and Batzli (2001) estimated that the maximum consumption rate of brown lemmings is 12 kg per lemming per year. Including the mechanical damage associated with grazing, they assumed that $A = 15$ kg per lemming per year. Thus in their model, $G(s) = 6.6$ kg per lemming per year and $G(w) = 9.45$ kg per lemming per year.

We conducted one set of simulations using the plant parameters of the original Barrow model (which is focused on places in the tundra where herbaceous plants abound and which we refer to as grassland/meadow tundra) and another set where we assumed considerably lower production of herbaceous forage, expressed as $K_V = 100\ \text{kg} \cdot \text{ha}^{-1}$, which is typical for heath-type tundra. Each set began with a simulation in which lemming parameters were identical to the original Barrow model. In subsequent simulations, we gradually increased the maximum summer mortality parameter ($G(s)_{\max}$) to simulate the impact of summer predation. Like Gilg *et al.* (2003, 2006), we assumed that predators are regionally present in constant numbers (which we refer to as the regional, marine-subsidized, predator pool). We assume as well that these predators respond to increasing lemming density by moving into lemming habitats and/or by starting to prey on lemmings when their density at snow-melt exceeds some threshold. Once they have made their decision, we assume they stay for the summer and leave at the beginning of the winter. In terms of Turchin (2003), summer predation thus represents a fast dynamic variable. We assume that there is no winter predation.

We assume that predators are absent or use other resources when lemming density at snow-melt, H_s, is less than 10 lemmings per ha of optimal lemming habitat. Thus $G(s) = 0.44A = 6.6$ kg per lemming per year, as assumed by Turchin and Batzli (2001). At higher lemming densities, predators are present and do exploit lemmings. Hence, the value of $G(s)$ must also include the foraging rate required for lemmings to reproduce at a rate that equals the losses imposed by predators. We assume that $G(s)$ increases linearly from $0.44A$ *to* $G(s)_{\mathbf{max}}$, as lemming density at snow-melt increases from 10 to 20 lemmings per hectare. $G(s)_{\mathbf{max}}$ is a system-specific parameter that reflects the regional size of the marine-subsidized predator pool. For $H_s > 20$, we assume that $G(s) = G(s)_{\mathbf{max}}$. Our assumptions are based on the result of Gilg *et al.* (2003), i.e. that per capita predation risk is density dependent for low lemming densities, whereas the total response of predators at moderate to high lemming densities matches the increase in lemming production (so that the per capita mortality imposed by predators remains constant). Our thresholds are an order of magnitude higher than the corresponding values inferred by Gilg *et al.* (2003, 2006) because the Barrow model was parameterized for patches of optimal lemming habitat whereas the model of Gilg *et al.* (2003, 2006) was parameterized for high arctic landscapes in which optimal lemming habitats cover only a small fraction of the total area. (For details of the simulation process and the complete set of parameter values, see evolutionary-ecology.com/data/2809Appendix.pdf).

To simulate the impacts of a successively larger pool of marine-subsidized predators, we increased the value of $G(s)_{\mathbf{max}}$ – with $0.001A$ between subsequent simulations – until we reached $G(s)_{\mathbf{max}} = 1.44A$. The latter is so intense a rate of summer predation that lemmings decrease rapidly if their spring density exceeds 20 per hectare. We ran 1000 simulations. In each, the first step was to run the system for several centuries to allow the oscillation patterns to settle into their attractors. Thereafter, we continued the run for 200 more years. From these latter 200 years of each simulation, we computed average densities of lemmings and average biomasses of depletable and herbaceous plants, and averages of their minima and maxima. We also identified the extreme values for the entire period of 200 years. For each 200-year run, we also computed average periods of the lemming oscillations and identified the extreme values (shortest and longest peak-to-peak period in each simulation).

RESULTS, DIAGNOSTIC PREDICTIONS AND IMPLICATIONS

Results for grassland/meadow tundra with $K_V = 1000\ \mathrm{kg \cdot ha^{-1}}$

For predator-free grassland/meadow tundra (leftmost points of Fig. 1, Fig. 2A; uppermost left panel of 2809Appendix, Fig. A1), the dynamics generated in our simulation reproduce the results of Turchin and Batzli (2001). The oscillations are chaotic, with a pseudoperiod of slightly more than 5 years (extremes 5.7 and 4.4 years). The amplitude is between two and three orders of magnitude (left sides of Figs. 1A and 1D, Fig. 2A). The increase phase is rapid in all seasons, but fastest in summer. The peak is in autumn. In the next winter, the vegetation is depleted (2809Appendix, Fig. A1, left column, top panel) and lemmings crash. The crash is followed by an extended low phase, during which lemmings are supported primarily by herbaceous forage. The biomass of depletable plants oscillates even more violently, with minimum values below $1\ \mathrm{kg \cdot ha^{-1}}$ and maxima close to carrying capacity, $2000\ \mathrm{kg \cdot ha^{-1}}$. Above-ground biomass of herbaceous plants is depleted in lemming years, but these plants sprout back from inaccessible rhizomes, reaching carrying capacity each summer (leftmost points of Figs. 1B and 1C, 2809Appendix, Fig. A1, uppermost left panel). In summer, herbaceous plants grow so fast that lemmings never have a detectable impact on their maximum biomass (see 2809Appendix, Fig. A1).

Moving rightwards in each of the four panels A, B, C and D of Fig. 1, we move from the predator-free system of the original Barrow model, with $G(s) = 0.44A$ to cases with successively larger pools of marine-subsidized predators per unit land area. Within the

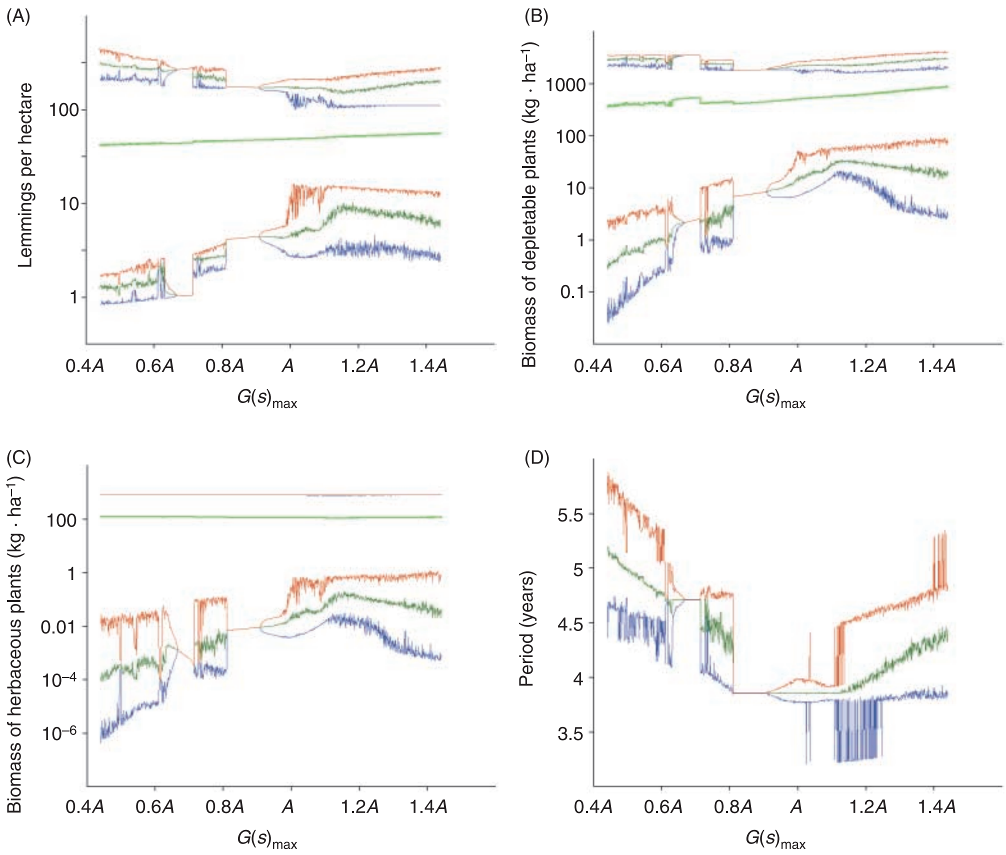

Fig. 1. Impact of increasing summer predation pressure on lemming–plant dynamics in a meadow/grassland tundra where the carrying capacity of herbaceous plants is 1000 kg·ha^{-1}. The *x*-axis, $G(s)_{\mathbf{max}}$, translates predation pressure into the relative foraging rate required for a zero growth rate of the lemming population during a summer when lemming density exceeds 20 individuals per hectare. Relative foraging rate is the proportion of A, the maximum per capita rate at which lemmings consume their resources. $G(s)_{\mathbf{max}}$ grows with increased predation pressure. At values of $A > 1$, there is so much predation pressure that lemmings cannot eat fast enough in the summer to sustain their population. The *y*-axes: **A** (log lemming individuals per hectare): the three highest lines show the highest (red), the mean (green), and the lowest (blue) maxima obtained in each simulation. The three lowest lines show the highest (red), the mean (green), and the lowest (blue) minima obtained in each simulation. **B** (biomass of depletable plants, log kg·ha^{-1}): coding as in **A**. **C** (biomass of herbaceous plants, kg·ha^{-1}): coding as in **A** but maximum values of all simulations in **C** are very similar to each other. **D** (years): peak-to-peak periods of the longest (red), average (green), and shortest (blue) oscillation periods obtained in each simulation. The figure is based on 1000 simulations, each lasting for 200 years. The thick bright green line between the maxima and minima in **A**, **B**, and **C** represents the mean density (lemmings) or mean biomass (plants) averaged over the entire period of 200 years.

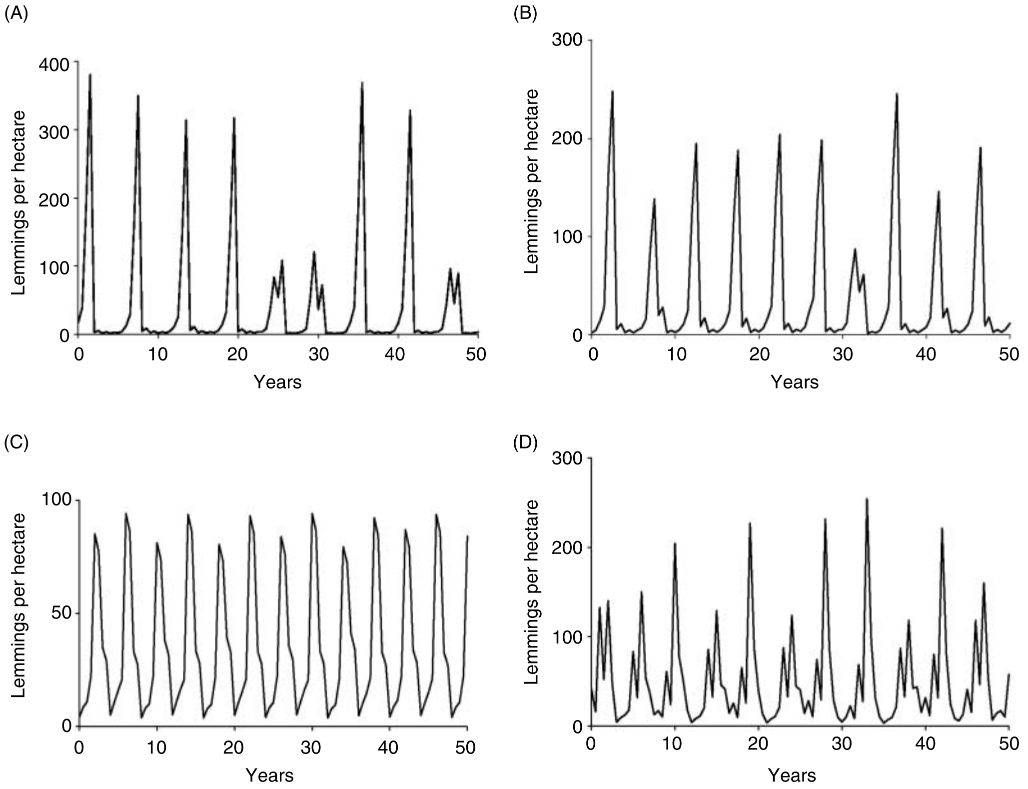

Fig. 2. Simulations of density fluctuations of lemmings in the four focal cases. The carrying capacity of herbaceous plants is assumed to be 1000 $\text{kg} \cdot \text{ha}^{-1}$. **A**: Simulations produced by the original Barrow model of Turchin and Batzli (2001) in which the summer mortality parameter $G(s) = 0.44A$. Simulations **B**, **C**, and **D** report the results of our modification of the Barrow model. The modification allows $G(s)$ to rise linearly from $0.44A$ to $G(s)_{\text{max}}$ when lemming density at snow-melt increases from 10 to 20 lemmings per hectare. In **B**, $G(s)_{\text{max}} = 0.64A$. In **C**, $G(s)_{\text{max}} = 0.94A$. In **D**, $G(s)_{\text{max}} = 1.44A$. The graphs show the last data points of winter and summer, which makes them comparable to the semi-annual trapping records typical for long-term studies of small rodents.

interval $0.44A < G(s)_{\text{max}} < 0.8A$, peak densities of lemmings and peak biomasses of depletable plants decrease, whereas their minima increase. The amplitude of the oscillations of lemmings and depletable plants is thus reduced (Figs. 1A and 1B). The average densities of lemmings and the average biomass of depletable plants both increase. Except for a small window of cyclic dynamics at $G(s)_{\text{max}} \approx 0.7A$, lemming oscillations remain chaotic in spite of increasing predation intensity, and outbreaks retain the same shape as they had in predator-free areas, with sharp rises and population peaks in autumn (Fig. 2B). Oscillations of herbaceous plants remain unchanged (Fig. 1C).

Within the interval $0.8A < G(s)_{\text{max}} < 1.1A$, the oscillation period is reduced to 4 years and the oscillation becomes cyclic or is so close to a regular cycle that its chaotic features could hardly be detected empirically. The amplitude of the lemming oscillation is now slightly less than two orders of magnitude (Figs. 1, 2C). Lemming populations still increase by an order of magnitude in the year preceding the peak, but now the peak is in spring.

Moreover, the decline phase is gradual, lasting for 2 years, during which the consumption and destruction of depletable forage plants is sufficiently heavy to result in relatively high winter mortality but not in sudden mass starvation. Lemming minima are immediately followed by new increase phases.

When $G(s)_{\max} > 1.1A$, chaos returns. Sequences of seemingly regular 4-year oscillations are common but at times they give way to oscillations with longer periods (Fig. 1D, right side; Fig. 2D). Nevertheless, the amplitude of the lemming oscillation remains moderate. The same applies to depletable plants (Figs. 1A and 1B, rightmost parts). The predicted average density of lemmings and biomass of depletable plants still increases with increasing intensity of summer predation but now the increases stem from increasing maxima (Figs. 1A and 1B, right sides, and Fig. 2D).

Two counterintuitive results emerge from the above simulations. First, predation increases the minimum numbers of lemmings and the minimum biomass of depletable plants, thus speeding up the recovery of lemmings. This positive impact is especially strong in cases where predation pressure is high and the production of the lemming population is consumed by predators in peak summers. The predicted relationship between marine-subsidized predators and lemmings is thus mutualistic rather than exploitative (cf. Abrams, 1992b). Second, lemmings are predicted to deplete almost all available forage in peak winters, but averaged over the cycle, the predicted ratio of consumption to primary production is low. In summer, lemmings cannot track the rapid growth of herbaceous plants and in fall, herbaceous plants wither and relocate mobile energy supplies to inaccessible roots and rhizomes.

Results for heath tundra with $K_V = 100\ \mathrm{kg \cdot ha^{-1}}$

In systems with low production of herbaceous forage, pure lemming–plant interactions generate chaotic oscillations with a pseudoperiod of 12 years (leftmost points of Figs. 3A, 3B, 3C and 3D; uppermost panel in the right column of 2809Appendix, Fig. A1). The average amplitude of lemming oscillations is eight orders of magnitude (Fig. 3A). Lemmings stay below a trapability threshold for years (Fig. 4A), but unlike in the extended lows generated on the grassland/meadow tundra, lemmings decline or increase exponentially in all phases of the oscillation (compare the uppermost panels in the right and left columns of 2809Appendix, Fig. A1). For depletable plants, the amplitude is five orders of magnitude (Fig. 3B). Depletable plants reach their carrying capacity several years before lemmings start to be present in detectable numbers.

Adding summer predation in this system and increasing its intensity increases the minimum density of lemmings and the minimum biomass of depletable plants (Figs. 3A and 3B, central and right sides). Lemming oscillations remain chaotic but their pseudoperiod decreases to 6 years (Fig. 3D, central and right side). With a larger size of the predator pool, average lemming density increases, whereas the average biomass of depletable plants decreases (Figs. 3A, 3B and 3D, Figs. 4B, 4C and 4D; 2809Appendix, Fig. A1, right column). Increasing intensity of summer predation also increases the minimum biomass of herbaceous plants (Fig. 3C). On the heath tundra, the predator–lemming mutualism is thus even stronger than on the grassland/meadow tundra, because in the absence of predators, lemming lows of the heath tundra are so deep that they would likely result in local extinctions. Moreover, in contrast to the predictions of classical food chain models (Oksanen *et al.*, 1981; Terborgh and Feeley, 2010), the relationship between predators and depletable plants is negative.

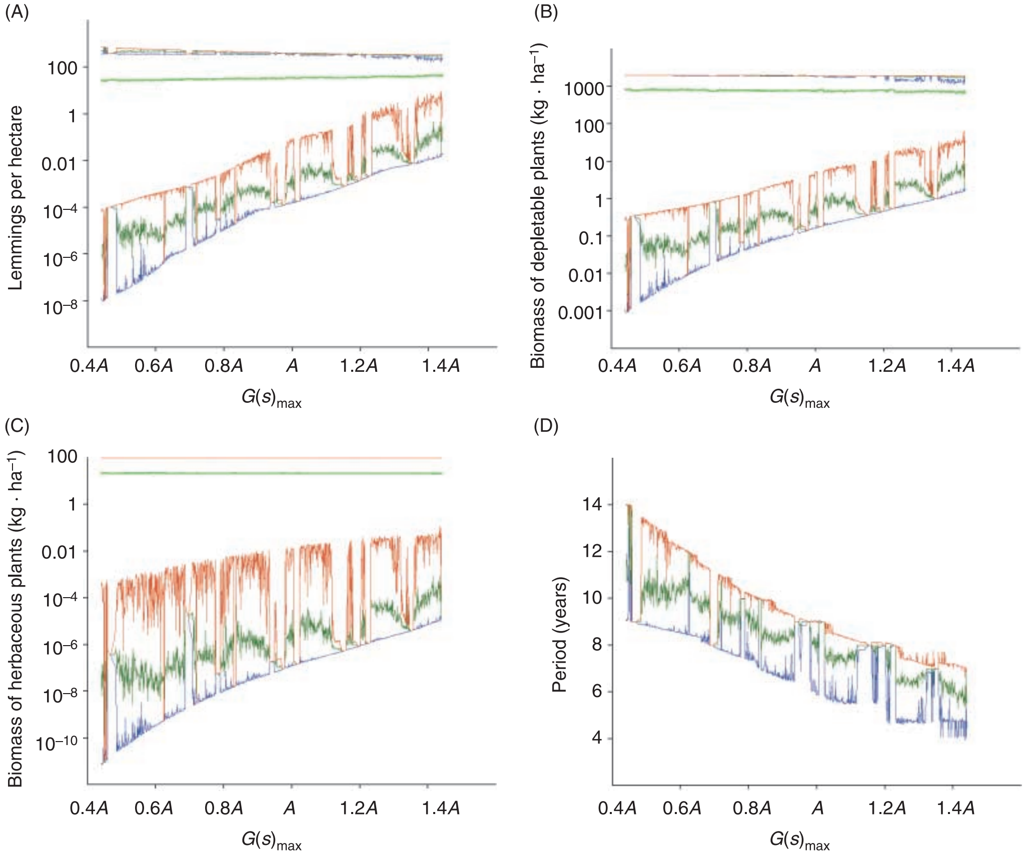

Fig. 3. Impact of increasing summer predation pressure on lemming–plant dynamics on a heath tundra where the carrying capacity of herbaceous plants is 100 kg · ha^{-1}. All axes and coding as in Fig. 1. The figure is based on 1000 simulations, each lasting for 200 years. Maximum values of all simulations in **A**, **B**, and especially **C** are very similar to each other.

Diagnostic predictions

For both grassland/meadow and heath tundra, our simulations predict that lemmings approach the peak with a constant or accelerating per capita rate and increase at least by an order of magnitude during the year preceding the peak. The underlying reason is that the biomass of depletable plants increases as a function of time elapsed from the previous peak (see 2809Appendix, Fig. A1). Hence, lemmings are predicted to forage and to produce offspring at the highest *per capita* rate during the last year of population increase. Conversely, in models where specialized mammalian predators drive rodent oscillations (Hanski *et al.*, 1991, 2001; Oksanen, 1990a; Hanski and Korpimäki, 1995; Gilg *et al.*, 2003; Korpimäki *et al.*, 2005), either social factors or generalist predators slow down the per capita rates of rodent population growth in pre-peak years. If lemmings increase more than by a factor of four during pre-peak years, they would be multiplying at a rate that their predators cannot match.

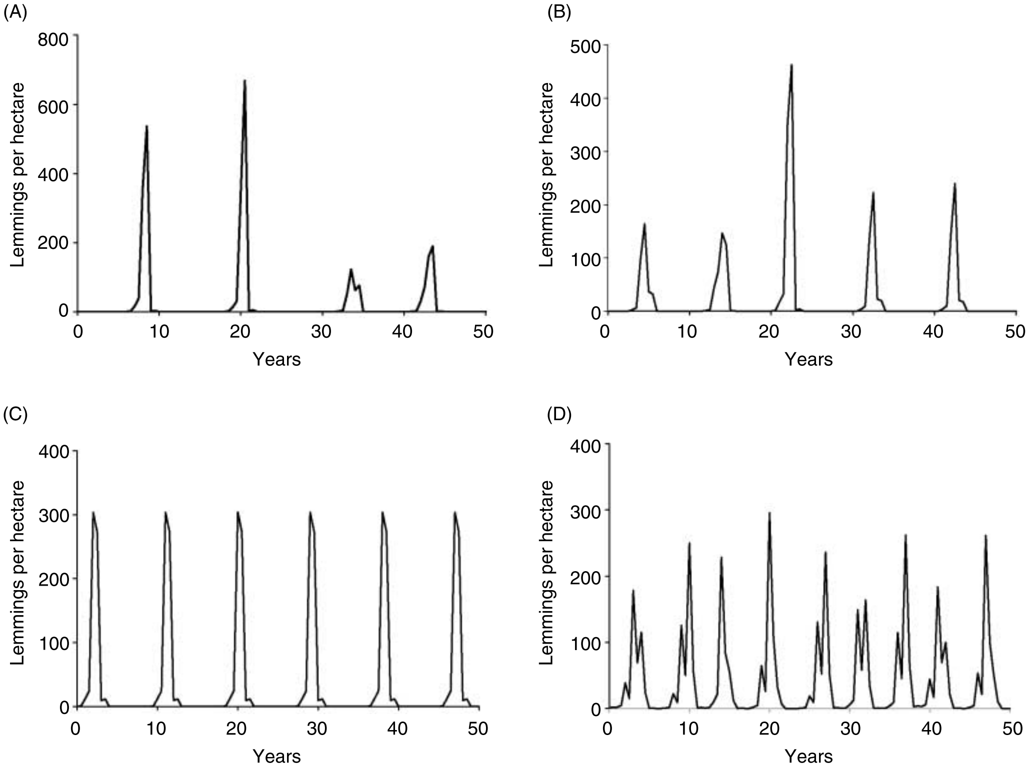

Fig. 4. Simulations of density fluctuations of lemmings in the four focal cases. The carrying capacity of herbaceous plants is assumed to be 100 kg·ha^{-1}. Except for the reduction of carry capacity, these simulations are like those in Fig. 2.

On grassland/meadow tundra with high summer predation pressure, where the predictions of our simulations concerning the amplitude and period of the oscillation converge with the predictions of Gilg *et al.* (2003), the predicted patterns are nevertheless different. According to our simulations, such oscillations should consist of two years of increase and two years of decline, whereas Gilg *et al.* (2003) predict that the increase should occur during three successive years and the decline should be completed during the fourth.

A further diagnostic prediction concerns depletable forage plants. In all our simulations, including the original Barrow model, their biomass is predicted to vary by more than an order of magnitude during the time between the lowest point of the lemming oscillation and the subsequent lemming peak. In contrast, Gilg *et al.* (2003, 2006) predict that plant biomass remains so high in all phases of the oscillation that lemmings can forage and reproduce at the rate determined by their physiological capacity.

Evolutionary and community ecological implications

The steep decline phases of lemming oscillations represent phases of strong natural selection, where only the fittest have a chance to survive. Our results imply that the behavioural strategy maximizing the chances to survive a lemming decline depend on the composition of the vegetation and on the intensity of summer predation. Hence the evolution of lemming behaviour should have taken different directions in different arctic landscapes. The lemming declines predicted for grassland/meadow tundra with high summer predation pressure have amplitudes similar to the predation-driven vole cycles of the taiga (Henttonen *et al.*, 1987). In such areas, mobility in peak summers would likely reduce survival chances by increasing exposure to predators. In contrast, on heath tundra with low summer predation pressure, the predicted lemming crashes are so extreme that staying in a crowded area would be suicidal. A tendency to emigrate from densely populated areas should therefore be favoured by natural selection. Emigration should be especially rewarding in areas where a large part of the tundra occurs as isolated patches because, in such landscapes, the violent dynamics predicted by our simulations create a high risk of local extinction. Consequently, many patches of suitable lemming habitat should be lemming-free due to past extinctions. A chance to colonize such an area increases the fitness rewards of emigration behaviour.

The periodic destruction of depletable plants, predicted by our model, should favour herbaceous plants, because they allocate their resources to inaccessible below-ground organs (Pjastolova, 1972; Batzli, 1975; Zimov *et al.*, 1995; Norrdahl *et al.*, 2002; Hambäck *et al.*, 2004; Dahlgren *et al.*, 2009; see also Stebbins, 1981; Olofsson *et al.*, 2004a), unless the area is very nutrient-poor (Grime, 1979; Oksanen, 1990b). Among depletable plants, periodic devastation should favour species with good colonization ability or the ability to re-grow from surviving basal parts. On the other hand, species that have photosynthetic organs elevated by a single stem or comparable structure should suffer. For such plants, a single bite at the base destroys the entire shoot/thallus. Because plants of the latter type are more competitive than the colonizers and grazing-tolerant species (Oksanen and Virtanen, 1997), the changes in biomass predicted by our simulations should therefore be accompanied by changes in species composition, too. For woody plants, our model implies that lemming oscillations should be accompanied by changes in fertility because damaged dwarf shrubs prioritize reconstruction of their shoot systems and reduce their resource allocation to reproduction (Ericson, 1977; Oksanen and Ericson, 1987).

DISCUSSION

Geographic patterns related to parameter values

As a biome, the Arctic is heterogeneous. The Eurasian–Alaskan tundra is characterized by high NDVI-values, indicating a predominance of habitats with continuous vegetation, whereas in the Canadian–Greenlandic sector, the NDVI-values obtained in large-scale surveys imply that the vegetation is sparse and discontinuous (Walker *et al.*, 2005; see also Krebs *et al.*, 2011). In the Eurasian–Alaskan sector, the impact of mobile, marine-subsidized predators is thus likely to be diluted over vast areas. In contrast, in the Canadian–Greenlandic sector, where habitats comparable to the Eurasian–Alaskan tundra are restricted to coastal plains and valleys (Bliss *et al.*, 1973; Bliss, 1977; Bay, 1998), marine-subsidized predators are likely to aggregate to smaller areas, which will amplify their impact. In eastern and central Canada, arctic predators are also, to a large degree, subsidized by agricultural practices in the temperate zone whose inputs are carried north by the dramatically increased snow goose populations (Jeffries *et al.*, 2004; Legagneux *et al.*, 2012).

Within the Eurasian–Alaskan sector, the Urals form a boundary between different types of tundra vegetation (Virtanen *et al.*, 1999a). The European tundra has been heavily impacted by the Ice Ages and therefore has nutrient-poor soils that favour mosses, lichens, and dwarf shrubs even if grazing intensity were high (Grime, 1979; Oksanen, 1990b; Oksanen and Virtanen, 1998). Habitats dominated by graminoids and herbs are thus restricted to sites where deep snow creates ideal grazing conditions for lemmings and melt waters draining from more elevated habitats increase nutrient supply (Nordhagen, 1928; Dahl, 1957; Gjærevoll, 1956; Oksanen and Virtanen, 1995; Virtanen *et al.*, 1999b). In contrast, the Siberian–Alaskan tundra is underlain by nutrient-rich organic soils, hence large areas are grasslands and meadows (Aleksandrova, 1970; Brown *et al.*, 1980; Virtanen *et al.*, 1999a).

With respect to the predator pool, the Fennoscandian tundra differs from the rest of the circumpolar arctic. Jaegers and snowy owls are common in coastal tundra areas from the White Sea eastwards across Russia (Wiklund *et al.*, 1998; Černjavskij, 2002; Menyushina *et al.*, 2012), Alaska (Batzli *et al.*, 1980; Pitelka and Batzli, 2007), Canada (Krebs *et al.*, 2003; Gauthier *et al.*, 2011; Legagneux *et al.*, 2012; but see Pattie, 1977), and Greenland (Gilg *et al.*, 2006). But on the Fennoscandian tundra, snowy owls are rare visitors and the abundance of all avian predators is low (Andersson, 1976a; Oksanen *et al.*, 1997; Aunapuu *et al.*, 2008). Moreover, the only moderately abundant avian predator, the long-tailed jaeger, has limited ability to prey upon Norwegian lemmings (Andersson, 1976b).

We thus propose that from the standpoint of arctic lemming dynamics, the circumpolar tundra consists of four different landscape types: the Fennoscandian tundra, where heaths prevail and summer predation pressure is low; the tundra of European Russia, where vegetation is similar to the Fennoscandian tundra but marine-subsidized predators are more abundant; the Siberian–Alaskan tundra, consisting primarily of grasslands and meadows and having relatively large pools of marine-based predators (Batzli *et al.*, 1980; Wiklund *et al.*, 1998); and the Canadian–Greenlandic tundra, where habitats with continuous vegetation are similar to their Siberian and Alaskan counterparts but are sandwiched between ice caps and/or polar deserts and the coast, creating conditions where the impact of marine-subsidized predators is likely to be maximal (Gilg *et al.*, 2003, 2006; Krebs *et al.*, 2003, 2011; Gauthier *et al.*, 2011; Legagneux *et al.*, 2012). In the following section, we relate the predictions and implications outlined above to this geographic set-up. We focus on areas where relevant data are available and proceed from the Fennoscandian tundra eastwards.

The Fennoscandian tundra

Our model predicts that maximally violent lemming oscillations should be observed on the Fennoscandian tundra, where the stabilizing impacts of herbaceous forage and marine-subsidized predators are weakest due to the geographic patterns summarized above. The recorded oscillations of Norwegian lemmings match these predictions: Their outbreaks are especially violent, and their peaks are short-lived, separated by long periods when lemmings are not trapped (Framstad *et al.*, 1997; Turchin *et al.*, 2000; Ekerholm *et al.*, 2001; Kausrud *et al.*, 2008; Olofsson *et al.*, 2012; see also Oksanen *et al.*, 2008). Such periods can emerge as consequences of the internal dynamics of the system, as indicated by the recent return of lemming peaks to northernmost Norway (Ekerholm *et al.*, 2001; Ims *et al.*, 2011; Olofsson *et al.*, 2012).

Also, the strong impacts of Norwegian lemmings on the Fennoscandian tundra vegetation (Kalela, 1971; Oksanen and Oksanen, 1981; Oksanen, 1983; Moen *et al.*, 1993; Oksanen and Moen, 1994; Virtanen *et al.*, 1997a, 1997b, 2002; Virtanen, 1998, 2000; Aunapuu *et al.*, 2008; Olofsson *et al.*, 2012; Hoset *et al.*, 2013), which can be observed as changed NDVI-values in satellite images (Olofsson *et al.*, 2012), and the lack of predator activity in typical lemming habitats (Oksanen *et al.*, 1992, 1997; Aunapuu and Oksanen, 2003; Aunapuu *et al.*, 2008) further support the conjecture that the oscillations of Norwegian lemmings are driven by lemming–plant interactions. However, all Fennoscandian tundra habitats are not dynamically alike. Experimental results (Ekerholm *et al.*, 2004; Hambäck *et al.*, 2004; Dahlgren *et al.*, 2009) imply that rodent oscillations in productive scrublands are driven by predation; but in these habitats, voles dominate the rodent guild.

The tundra of Siberia and Alaska

For the Siberian–Alaskan sector, our simulations predict lemming dynamics that are less violent than that of Fennoscandia. Summer predation during peaks is pronounced (Pitelka, 1973; Batzli *et al.*, 1980; Černjavskij, 2002; Pitelka and Batzli, 2007) but so is the impact of lemmings on the vegetation (Tihomirov, 1959; Černjavskij and Tkačev, 1982; Pitelka and Batzli, 2007). Available winter forage is, by and large, depleted during lemming peak winters (Batzli, 1975; Černjavskij and Tkačev, 1982), although the consumption to production ratio is only about 10%, due to the prevalence of herbaceous plants (Bunnell *et al.*, 1975). Also, long-term exclusion of lemmings triggers dramatic changes in the vegetation (Johnson *et al.*, 2012). Oscillations of brown and collared lemmings, which coexist in this sector, are violent but, unlike the Fennoscandian case, a few individuals are usually trapped even at the lowest point of the oscillation (Batzli *et al.*, 1980; Černjavskij, 2002). These data are consistent with our predictions. Stoats and weasels are present on the Siberian mainland (Broekhuizen *et al.*, 2007) but not on Wrangel Island, where lemmings oscillate violently (Černjavskij and Tkačev, 1982; Menyushina *et al.*, 2012). The presence of specialized predatory mammals is therefore not a necessary condition for these lemming oscillations.

The Canadian–Greenlandic sector

For these areas, where marine-subsidized predators aggregate in relatively limited pieces of tundra with primarily grassland/meadow type vegetation (Bliss, 1977; Bay, 1998), our simulations predict 4-year cycles with moderate amplitude (two orders of magnitude), with two years of increase followed by two years of decrease. The oscillation pattern documented on Traill Island, northeast Greenland on the basis of winter nest counts (Gilg *et al.*, 2006) is consistent with this prediction but not with the predictions of Gilg *et al.* (2003). Also, the high per capita rate of lemming population increase in pre-peak years (Oksanen *et al.*, 2008) is consistent with the predictions of our simulations but not those of Gilg *et al.* (2003). The response of stoats to lemmings is time delayed but the observed stoat predation indices are low (always <15% of winter nests fur lined) compared with those of Barrow (MacLean *et al.*, 1974), Banks Island (Maher, 1967), and Siberia (Broekhuizen *et al.*, 2007). At Zackenberg, northeast Greenland (Schmidt *et al.*, 2008), there is no statistical correlation between the stoat density index and lemming density in the previous year ($r = +0.102$, $P = 0.793$). Instead, there is a significant positive correlation between lemming density and the stoat density index in the same year ($r = +0.725$, $P = 0.018$), indicating that in this area, stoat density behaves as a fast dynamical variable, which cannot drive oscillatory dynamics (Turchin, 2003). The outbreak year was followed by a year of low fertility of mountain avens, *Dryas* spp. (Berg *et al.*, 2008). On Devon Island, the trapping record of Fuller *et al.* (1977) documents violent oscillations of collared lemmings but there is no statistically significant multi-annual variation in the stoat predation index (Fuller *et al.*, 1977). To date, the evidence from Greenland and Devon Island is thus consistent with our hypotheses that the dynamics of arctic lemmings is driven by lemming–plant interactions and modified by the impacts of marine-subsidized predators.

The above conclusions do not seem to apply to Bylot Island (Gauthier *et al.*, 2011; Legagneux *et al.*, 2012) or to the arctic coasts of Canada (Reid *et al.*, 1995; Wilson *et al.*, 1999; Krebs *et al.*, 2011). The evidence available to date indicates that in these areas, collared lemmings – at least – are controlled by marine-subsidized predators and the systems have locally stable point equilibria. These areas seem thus to resemble coastal deserts, where marine-subsidized predators keep herbivores at stable and very low densities (Polis and Hurd, 1997). Wilson *et al.* (1999) regarded their system as cyclic but the record is too short for such conclusions and the documented density variation is only one order of magnitude. On Bylot Island, where brown lemmings are also present, their densities are more variable but their density variation is irregular. Legagneux *et al.* (2012, p. 1713) interpret these brown lemming density variations as follows: 'under some conditions, they appear to be able to escape predation, leading to outbreaks'. The predator–lemming system of Bylot Island thus seems to have a locally stable point equilibrium but its stabilizing forces can occasionally be too weak to control brown lemmings.

Survival strategies of lemmings

Several pieces of circumstantial evidence, such as sequential observations of moving lemmings, road kills, crossings of major watercourses, and appearance of lemmings in unusual places (Salkio, 1958; Myllymäki *et al.*, 1962; Aho and Kalela, 1966; Kalela, 1971; Oksanen and Oksanen, 1981; Henttonen and Kaikusalo, 1993; Østbye *et al.*, 1993; Ekerholm *et al.*, 2001) indicate that Norwegian lemmings differ from their congeners by having a strong tendency to emigrate during outbreak years. Also, the wave-like spreading of lemming outbreaks from the main mountain range to isolated highlands (Kalela, 1949; Henttonen and Kaikusalo, 1993) is easiest to explain as a consequence of long-range emigrations. Such emigration behaviour conforms to the predicted evolutionary response of lemmings to lemming–plant oscillations under the conditions of the Fennoscandian tundra. Krebs (1993) argued that the indications of emigration behaviour in Norwegian lemmings could be interpreted as local movements or seasonal habitat changes. But why, then, should such observations pertain almost exclusively to Norwegian lemmings – even in the timberline region and in forested areas where the local rodent community is dominated by voles? The sudden occurrence of large numbers of lemmings in places where other small mammals are not seen or trapped, such as small islands in the middle of Lake Iešjávri (8 × 12 km; our observations), indicates that the concept of 'local movement' must be interpreted broadly to be applicable to Norwegian lemmings. In North America and Siberia, where avian predators are more abundant and lemming outbreaks are synchronous over large areas (Danell *et al.*, 1999; Krebs *et al.*, 2003), indications of such emigration behaviour have not been observed.

Dynamics and survival strategies of depletable plants

According to the traditional view, the shortness of the growing season in snow-beds accounts for the replacement of woody plants by graminoids and forbs (Nordhagen, 1928; Gjærevoll, 1956), and the harshness of the environment accounts for the weakness of competitive interactions between plants growing in such sites (Grime, 1979; see also Callaway *et al.*, 2002; Sammul *et al.*, 2006). However, woody plants transplanted to such sites survive well if lemmings are excluded (Moen and Oksanen, 1998; Virtanen, 1998; Eskelinen, 2007), and in such exclosures, plant–plant competition is as intense as in more productive habitats (Olofsson *et al.*, 2002). In Fennoscandia, lemming outbreaks can also be observed from space as reductions of NDVI-values (Olofsson *et al.*, 2012). At least on the Fennoscandian tundra, the lemming–plant interaction is thus strong enough to shape the vegetation at a large spatial scale and to have a major impact on interactions between plants. As wintering Norwegian lemmings mow down the vegetation, even woody plants, which these lemmings cannot eat, are influenced (Olofsson *et al.*, 2012).

The strongest impact of Norwegian lemmings is on mosses (Moen *et al.*, 1993). These increased at Kilpisjärvi by an order of magnitude during seven successive lemming-free years (Kyllönen and Laine, 1980; Oksanen, 1983) and have increased equally dramatically in long-term lemming exclosures (Virtanen *et al.*, 1997a; Virtanen, 2000; Olofsson *et al.*, 2012). The increase in moss biomass has been accompanied by changes in the composition of the moss community. Colonizing species (*Pohlia* spp.), small hepatics and small mosses were replaced by robust haircap mosses (Polytrichaceae) and/or by layering mosses (e.g. *Hylocomnium splendens*). Also, at Barrow, mosses increased in lemming exclosures at the cost of graminoids (Johnson *et al.*, 2012) but no changes in the composition of the moss community were reported.

CONCLUDING REMARKS

The tundra is one of earth's major biomes, covering over eight million square kilometres (Walker *et al.*, 1995; Körner *et al.*, 2011). Today, arctic ecologists agree about the importance of lemmings in arctic food webs but disagree about the mechanisms regulating the populations of these important herbivores. To preserve the arctic biota in a changing climate, it is of utmost importance to understand their dynamics. Arctic plants and animals are threatened by global warming, which has triggered an expansion of shrubs and trees (Sturm *et al.*, 2001; Tape *et al.*, 2006; Forbes *et al.*, 2010). These changes generate positive feedbacks because an increasing abundance of woody vegetation accelerates global warming (Chapin *et al.*, 2005; Swann *et al.*, 2010). It seems, however, that all plants can be controlled by food-limited herbivores (Oksanen *et al.*, 2010; Oksanen and Olofsson, 2010). Moreover, a basic rule in predator–prey interactions is that an increasing resource supply for the prey may be absorbed by an increasing predator population (Rosenzweig, 1971). If herbivores play a predator's role in the dynamics (Turchin *et al.*, 2000; Oksanen *et al.*, 2008), they should thus be able to prevent or at least to slow down the expansion of woody plants (Dahlgren *et al.*, 2009; Olofsson *et al.*, 2009, 2012). If, in contrast, lemmings are regulated by their predators and do not have detectable impacts on the vegetation, as argued by Gilg *et al.* (2003, 2006, 2009), then the plants of lemming habitats would respond directly to global warming.

Difficulties with conducting long-term experiments in the arctic can contribute to the divergence of opinion on arctic lemming dynamics. But the field studies of recent years provide us with the pieces of the puzzle. A way to tackle this uncertainty and the challenging logistics of the arctic is to proceed sequentially when pursuing the applicability of contesting hypotheses. First, formalize the hypotheses and compare the fit of contrasting models using data sets from different systems. Then, second, conduct experiments designed to test contrasting predictions from the models in different systems. The first step helps us in planning more powerful tests by helping us to identify the most critical predictions (Power, 2001).

The present modelling exercise represents the first step in this scheme. Our simulations predicted the observed geographic differences in lemming oscillations. Violent, chaotic oscillations are observed in Fennoscandia where the simulations predict just such dynamics due to the combination of prevalent heath-type vegetation and low predator density. We also have direct evidence for strong lemming–plant interactions, ranging from experiments to changes observed from space (Olofsson *et al.*, 2012). In this area, lemmings also respond to crowding by emigration, as is typical for all animal populations that frequently face a discrepancy between numbers and resources (Kalela, 1949). In areas with pronounced outbreak cropping, lemming oscillations are regular and their amplitude is moderate, as predicted by our model. The shapes of these oscillations are more consistent with the predictions of our simulations than the predictions of Gilg *et al.* (2003), implying that food depletion remains a plausible cause of lemming population collapses in these parts of the arctic, too (see also Berg *et al.*, 2008). Alternative explanations for oscillation shapes have been proposed (Gauthier *et al.*, 2009; Ims *et al.*, 2011; but see Oksanen *et al.*, 2009). But at least for Fennoscandia, the overwhelming direct evidence concerning the strength of the lemming–plant interaction has clarified the issue.

It follows also that the fitness of these lemmings should be determined primarily by their efficiency in food utilization. The pronounced division of feeding niches between collared and brown lemmings (Batzli, 1993) and the evidence for competition between these lemmings (Morris *et al.*, 2000; Ale *et al.*, 2011; Morris and Dupuch, 2012) further supports the inference of food limitation, which normally results in divergence of feeding niches and in habitat segregation between coexisting competitors (MacArthur, 1972).

Population dynamics and evolution interact because organisms are unlikely to be successful in areas where population dynamics diverge from the dynamics to which they are adapted (Oksanen *et al.*, 2008). Due to the trade-off between elusiveness and the ability to exploit low-quality forage (Oksanen, 1992), purely predation-driven dynamics are more likely to exclude arctic lemmings than to drive their density oscillations, provided that voles are also present in the area. Strong impacts of specialized predators may therefore be more relevant in the context of range limitation of arctic lemmings (Oksanen, 1993; see also Holt and Barfield, 2009) than in their population regulation.

The natural next step consists of experiments integrated with long-term surveys. Instructive experiments would include predator removal (Korpimäki and Norrdahl, 1998), island experiments (Hambäck *et al.*, 2004; Dahlgren *et al.*, 2009), and combined exclosure and transplantation experiments (Virtanen, 1998; Moen and Oksanen, 1998). Also, remote sensing (Olofsson *et al.*, 2012) and descriptive studies on changes in the vegetation and plant biomass should provide relevant information. Such studies should provide critical tests because of the divergent predictions generated by food-centred and predation-centred hypotheses.

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