Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change

ROLF A. IMS AND EVA FUGLEI

While population cycles are geographically widespread, it is on arctic tundra that such cycles appear to be most influential for the functioning of the whole ecosystem. We give an overview of tundra species that exhibit population cycles and describe what are currently believed to be the causal mechanisms. Population cycles most likely originate from trophic interactions within the plant-based tundra food web, where lemmings, either as prey for carnivores or as consumers of plants, play the key role. The predominance of trophic interaction cycles at northern latitudes is ultimately related to climate, and such cycles should therefore be vulnerable to climate change. Recent evidence indicates that changes have already taken place in the dynamics of some key herbivores and their predators, consistent with the expected impacts of climate change. There is a strong need for large-scale integrated monitoring and research efforts to further document such changes and their ecosystem consequences.

Keywords: arctic tundra, climate change, ecosystem functioning, food web dynamics, lemmings

Life on the arctic tundra is subject to dramatic year-to-year variation in terms of bioproduction. In some years wildlife populations flourish, while in others the tundra appears remarkably devoid of wildlife. Although indigenous people and early explorers have always been aware of the violent booms and busts in arctic wildlife, it was not until the English ecologist Charles Elton (1924) started to examine statistics on fur-bearing animals that these multiannual fluctuations were found to follow a cyclic pattern. Elton recognized that there were conspicuous peaks in the number of arctic fox skins exported from arctic Canada every 4 years, and he found a similar cyclicity in the Norwegian zoologist Robert Collett's compilation of records on "lemming years" in Norway (Lindström et al. 2001). Today, the literature is considerably broader: Many thousands of scientific papers on population cycles have been published in the 80 years after Elton's discovery. The phenomenon is not restricted to arctic species, although it is definitely most common in northern areas (Kendall et al. 1998). Moreover, it is on the arctic tundra that population cycles seem to be most intertwined with the functioning of the whole ecosystem. The important ecosystem consequences of population cycles were highlighted three decades ago during the International Biological Program (e.g., Batzli et al. 1980), but in recent years this perspective has drawn less attention. The recent realization that climate change will affect arctic ecosystems severely, and that altered cyclic dynamics in tundra species are likely to be involved (Callaghan et al. 2004), calls for a renewed focus on the role of such cycles in the Arctic.

In this article we provide an overview of what is known about cyclic dynamics in terrestrial arctic ecosystems (i.e., tundra). First, we take a species-oriented view and describe tundra species exhibiting population cycles. Second, we place these species in an ecosystem context by outlining the basic architecture of the plant-based tundra food web and the types of interactions taking place within this web. We then show how cycles can be a product of trophic interactions by reviewing the most plausible theories and recent empirical evidence. Finally, we examine the role of arctic climate in these interaction cycles and end with a discussion of how climate change may act to alter them and what the wider consequences of such changes may be.

Arctic species with cyclic population dynamics

For laypeople, population cycles are perhaps most conspicuous in the two species treated in Elton (1924): the arctic fox and the lemming. The cycles in the population of the arctic fox—the most valuable furbearer on the tundra—were, and to some extent still are, influential in the economy of arctic communities. The lemming cycle, on the other hand, represents the most pronounced fluctuations in terms of biomass.

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Multiannual population cycles, however, are not limited to these two species; they can be observed in many tundra organisms.

Plants. Vascular tundra plants (sedges, forbs, and dwarf shrubs) exhibit pronounced between-year differences in production measures such as the number of vegetative shoots and flowers, with apparent peak production at intervals of approximately 4 years (Laine and Henttonen 1983). However, time series of plant production indices from the arctic region are generally shorter than population time series for many animals, and for this reason, formal statistical evidence for multiannual plant cycles is currently missing. We will return to plant production cycles when discussing food web dynamics and how cycles may be generated.

Invertebrates. Population cycles of herbivorous insects are commonplace and ecologically important in forest ecosystems (Berryman 1996). This contrasts with the situation on arctic tundra, where herbivorous insects are relatively unimportant in terms of abundance and ecosystem impact (MacLean 1981). The bulk of terrestrial arctic invertebrates are found in the soil, where they play a crucial role as decomposers (detrivores) of dead organic material (detritus). To our knowledge, there are no population time series of sufficient length to examine whether there are multiannual population cycles present in arctic soil invertebrates. We suspect, however, that such population cycles exist, because cyclic lemmings' burrowing activity, disposal of dead plant material, and excreta have a great impact on soils.

Small rodents: Lemmings and voles. Lemmings and voles are disproportionally common on the tundra relative to other ecosystems. Voles are represented mainly by species of the genus *Microtus* in the low-arctic tundra subzone. Two genera, *Lemmus* and *Dicrostonyx,* represent the lemmings, with five and two species, respectively. There is never more than one lemming species of each genus present at the same location (Stenseth and Ims 1993). *Lemmus* species are distributed mainly in the low- to middle-arctic tundra subzones, whereas *Dicrostonyx* can be found all over the tundra and as far north as vascular plants exist.

Voles and lemmings are small herbivores (the adult body size is 40 to 120 grams) that subsist on a diet of grasses, sedges, and herbs (*Microtus*); sedges and mosses (*Lemmus*); or herbs and dwarf shrubs (*Dicrostonyx*) (Batzli et al. 1980). Their digestive efficiency is generally low, ranging from 30% of ingested food for *Lemmus* to 50% for *Dicrostonyx* (Batzli et al. 1980). Arctic lemmings and voles are active year-round (under the snow in winter) and have a very high metabolic rate (Batzli et al. 1980). The combination of high metabolic rate and low digestive efficiency requires a high rate of food intake. A Norwegian lemming (*Lemmus lemmus*) may consume eight times its own body weight per day (Stenseth and Ims 1993).

The maximum reproductive rate of voles and lemmings is impressive: A female Norwegian lemming can become pregnant as soon as she is weaned (16 days old). Pregnancy lasts 20 days, and each litter normally contains 5 to 7 young (with a maximum of 16). Only a few hours after a female has delivered a litter, she often mates again. The breeding season can commence under the snow in the middle of the winter and last until the next fall. It is thus conceivable that a lemming population could increase from less than one individual to several hundred individuals per hectare (ha) in 2 years (Stenseth and Ims 1993). The maximum reproductive potential is rarely attained in the field, however, and there are large differences in the realized reproductive rate between seasons, years, and species.

Lemming cycles usually exhibit a statistical periodicity (mean interval between peak years) of around 4 years (figure 1; Stenseth 1999). However, the cycle period can be shorter (3 years for Siberian lemmings at Taymyr Peninsula; Summers and Underhill 1987) or longer (more than 4 years for Norwegian lemmings in northern Norway; Angerbjörn et al. 2001). At locations with more than one species of lemming or vole, the different species cycle in synchrony (Stenseth and Ims 1993). Within the same species, population cycles can be synchronized over large areas (Krebs et al. 2002). Vole species with a wide geographic distribution tend to exhibit their most pronounced population cycles at northern latitudes (boreal forest, northern alpine areas, and tundra) (Hansson and Henttonen 1988). To our knowledge, noncyclic lemming populations in the Arctic have so far been found at only one location, in arctic Canada (Reid et al. 1995).

Predatory mammals: Arctic foxes, weasels, and ermine. Three circumpolar predatory mammals exhibit cyclic population dynamics on arctic tundra: the arctic fox (*Alopex lagopus*), the ermine (*Mustela erminea*), and the weasel (*Mustela nivalis*). The arctic fox is among the vertebrates that are best adapted to a life at high latitudes (Fuglei and Øritsland 1999). In inland tundra regions, the arctic fox belongs to the terrestrial ecosystem, preying mainly on lemmings (Elton 1924). In lemming peak years, the arctic fox responds with high pregnancy rates and large litter sizes. Consequently, populations of "lemming foxes" exhibit cycles of approximately 4 years (figure 2). This contrasts with the populations of "coastal foxes" on arctic islands without lemmings, which are more stable and exhibit no signs of cyclicity (Fuglei et al. 2003). In coastal habitats, arctic foxes prey opportunistically on the much more stable components of the marine ecosystem, such as seabirds and carrion from sea mammals. Coastal foxes have lower pregnancy rates, and smaller and less variable litter sizes, than inland lemming foxes, which leads to more stable population dynamics. In coastal habitats with cyclic lemming populations, arctic foxes are "ecosystem switchers" that alternate between exploiting mainly terrestrial productivity in lemming peak years and marine productivity in lemming low years (Roth 2003).

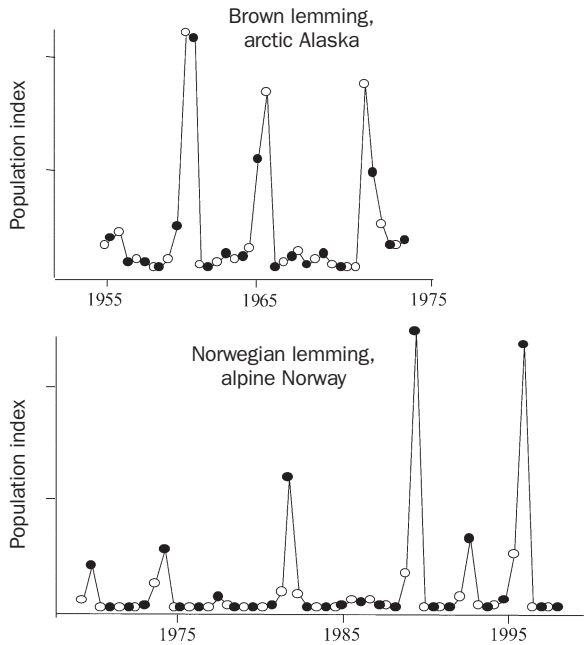

Figure 1. Time series of population indices of brown lemmings in arctic Alaska (top) and Norwegian lemmings in alpine Norway (bottom), based on the number caught in snap traps. Open circles represent spring samples; filled circles represent fall samples. Note that peak densities are reached during different seasons in the series (cf. figure 10). Modified from Stenseth (1999).

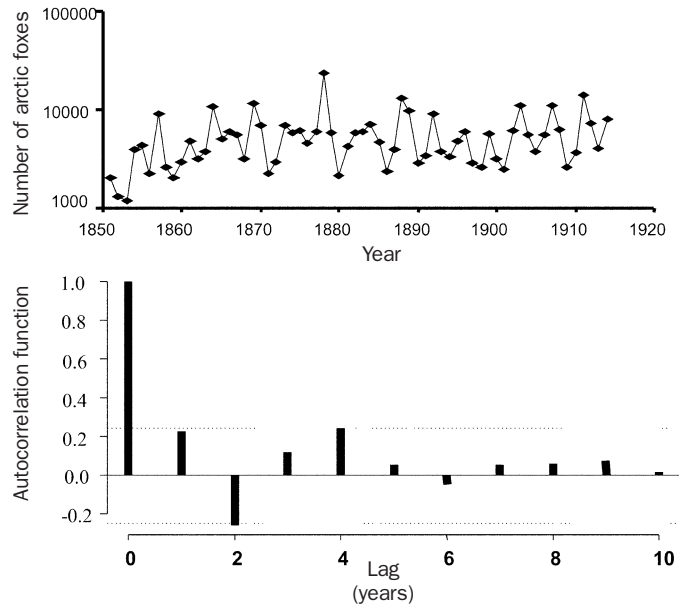

Figure 2. Upper panel: Population fluctuations for the arctic fox in arctic Canada, reflected in the number of fox skins obtained annually by the Hudson Bay Company. Data were obtained from Elton (1924). Lower panel: Autocorrelation function based on log-transformed data, indicating significant positive autocorrelation ($p < 0.05$, indicated by bars that meet or cross the broken horizontal line) with a lag of 4 years, thus indicating a 4-year cycle.

The small mustelids of the tundra, the ermine and the weasel, are not much larger than their rodent prey. In fact, least weasels in Fennoscandia are considerably smaller than adult Norwegian lemmings. As a result of their small size, weasels and ermines can hunt in the burrows of small rodents year-round, and for that reason they are supposed to be the most efficient of all predators on lemmings and voles (Oksanen et al. 1985). Owing to a high reproductive rate, the population levels of weasels and ermine—more than any other predators of lemming—follow those of their prey, although with a time delay due to a less rapid growth and decline phase than that of the prey population (Korpimäki and Krebs 1996). A weakness of our present knowledge of the role of small mustelids in arctic ecosystems is that no quantitative population data (e.g., population density and demographic rates) are available.

Predatory birds: Owls, raptors, and jaegers. A species-rich guild of arctic avian predators preys on lemmings and voles (Wiklund et al. 1999). The guild includes two owls, the snowy owl (*Nyctea scandiaca*) and the short-eared owl (*Asio flammeus*), and one raptor, the rough-legged buzzard (*Buteo lagopus*); all three species depend heavily on small rodents. The diet is more flexible in the jaegers, which are represented by three species: the long-tailed jaeger (*Stercorarius longicaudus*), the parasitic jaeger (*Stercorarius parasiticus*), and the pomarine jaeger (*Stercorarius pomarinus*). The jaegers live a dual life. In the winter they are marine birds at more southern latitudes, whereas in spring they migrate north to become a part of the tundra food web during the summer breeding season. The owls and the rough-legged buzzard prey on small mammals year-round, but only the snowy owl may stay in the Arctic during the winter.

The lemming cycle is reflected in the breeding density and success of these birds. During the low phase of the lemming cycle, very few predatory birds appear on their breeding ground. Snowy owls, short-eared owls, and rough-legged buzzards may not appear at all (Batzli et al. 1980). However, in lemming peak years, breeding pairs of predatory birds with large clutches abound on the tundra. Thus, the numerical response is to some extent due to high production of young. However, the main reason for the rapid numerical response (e.g., in the snowy owl) is that the birds are nomadic; they may move over vast areas in search of regions with peak-phase lemming populations (Gauthier et al. 2003).

Ptarmigan, geese, and shorebirds. Ptarmigan (*Lagopus* spp.) are among the species with best documented and most thoroughly studied population cycles (Moss and Watson 2001). The cycle period and amplitude for ptarmigan vary widely between geographic regions. Most studies of ptarmigan population cycles are from alpine areas and moorlands south of the

Arctic, and unfortunately, long time series of ptarmigan abundances are missing for the tundra region. In northern Fennoscandia, populations of willow ptarmigan cycle with a period of approximately 4 years, apparently linked to the cycles of voles and lemmings in this region (Moss and Watson 2001). An intimate link to the arctic lemming cycle has also been documented for arctic waders and geese, which exhibit "demographic cycles" due to a recurrent high proportion of juveniles in the wintering flock every 3 to 4 years (figure 3).

Reindeer and caribou. The long generation time of ungulates requires longer time series for proper statistical detection of population cycles than are presently available from census data. However, midden deposits from the Thule culture in western Greenland seem to reflect periodic fluctuations in caribou population peak size every 60 to 100 years (Born and Böcher 2001). Dendrochronological analyses of damage caused by caribou trampling on tree roots also indicate long-term fluctuations in arctic Canada (Morneau and Payette 2000). However, the empirical evidence for true population cycles in caribou and reindeer is too weak to warrant a discussion of their causes and consequences.

Food webs, types of interaction, and key species

Food chains describe how matter and energy is passed on between trophic levels in the ecosystems, from plants (the producers) at the bottom of the chain to apex predators (consumers) at the top. In between these two ends of the food chain, there may be consumers at various intermediate trophic levels (herbivores and intermediate predators). The length of food chains (i.e., the numbers of trophic levels or links) varies widely among ecosystems. The plant-based food chain in tundra ecosystems is relatively short, usually consisting of three trophic levels (plants, herbivores, and carnivores), a number that has been theoretically predicted in terrestrial ecosystems that are dominated by mammals (Post 2002). However, describing ecosystems as linear food chains by lumping species into trophic levels is a gross simplification that conceals how the ecosystem is actually functioning. There are crucial interactions among individual species, both within and between trophic levels, that may determine the structure and dynamics of the entire ecosystem (Paine 1980). The web of pathways that outline the flow of energy and matter between species at different trophic levels represents the food web. Food webs are complex constructs, although the plant-based food web on arctic tundra is simple (figure 4) compared with the equivalent food web in a forest ecosystem. Moreover, outlines of food webs, such as the one in figure 4, depict only interactions that involve consumption (i.e., plant–herbivore and predator–prey interactions) and not other types of interactions, such as competition or facilitation, that can take place within each trophic level (figure 5). The interplay among different types of interactions may lead to unexpected indirect effects that influence the dynamics and structure of the entire web (Abrams et al. 1998).

There have been many attempts to establish general principles for food web structure and dynamics, but there are few that seem to hold. In particular, there has been considerable controversy over whether terrestrial food webs are under top-down or bottom-up control (e.g., Meserve et al. 2003). Top-down control implies that predators indirectly control the abundance and dynamics of plants through regulation of their herbivore prey, while bottom-up control means that primary productivity by plants controls the dynamics and structure of the food web. The question of how population cycles in the tundra ecosystem are generated revolves around this dichotomy of bottom-up versus top-down control of ecosystem functioning (Oksanen and Oksanen 2000). However, it does not have to be one or the other exclusively, as cycles may result jointly from both bottom-up and top-down processes (Gauthier et al. 2003).

Untangling determinants of food web dynamics benefits from identification of key species and key interactions among species (Murdoch et al. 2002). It is clear that lem-

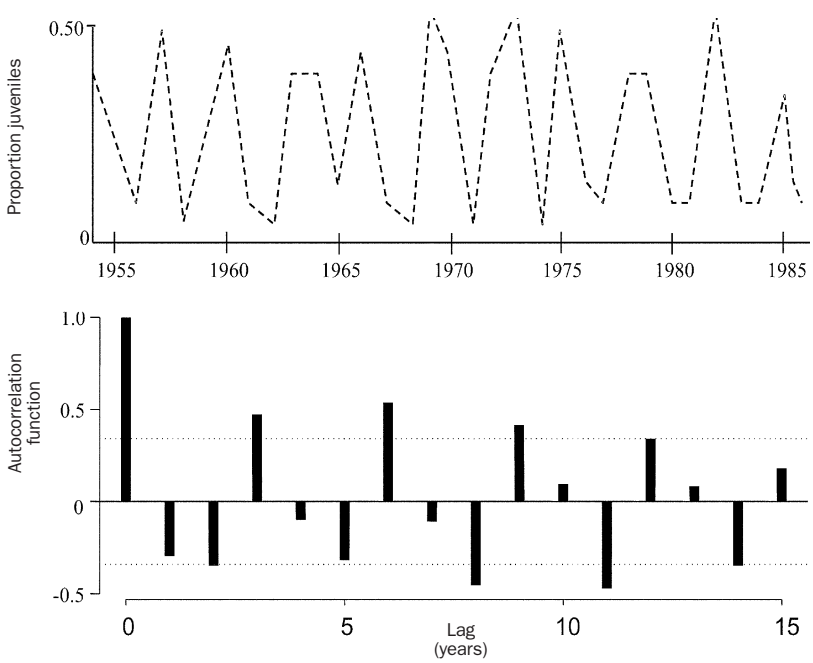

Figure 3. Upper panel: Demographic 3-year cycles in brent geese (*Branta bernicla*) breeding at the Taymyr Peninsula in Siberia, expressed as the proportion of juveniles (first-year birds) in populations at wintering sites in Europe. Data were obtained from Summers and Underhill (1987). Lower panel: Autocorrelation function based on logit-transformed data indicating significant positive autocorrelation ($p < 0.05$, indicated by bars that meet or cross the broken horizontal line) with a lag of 3 years, thus indicating a 3-year cycle.

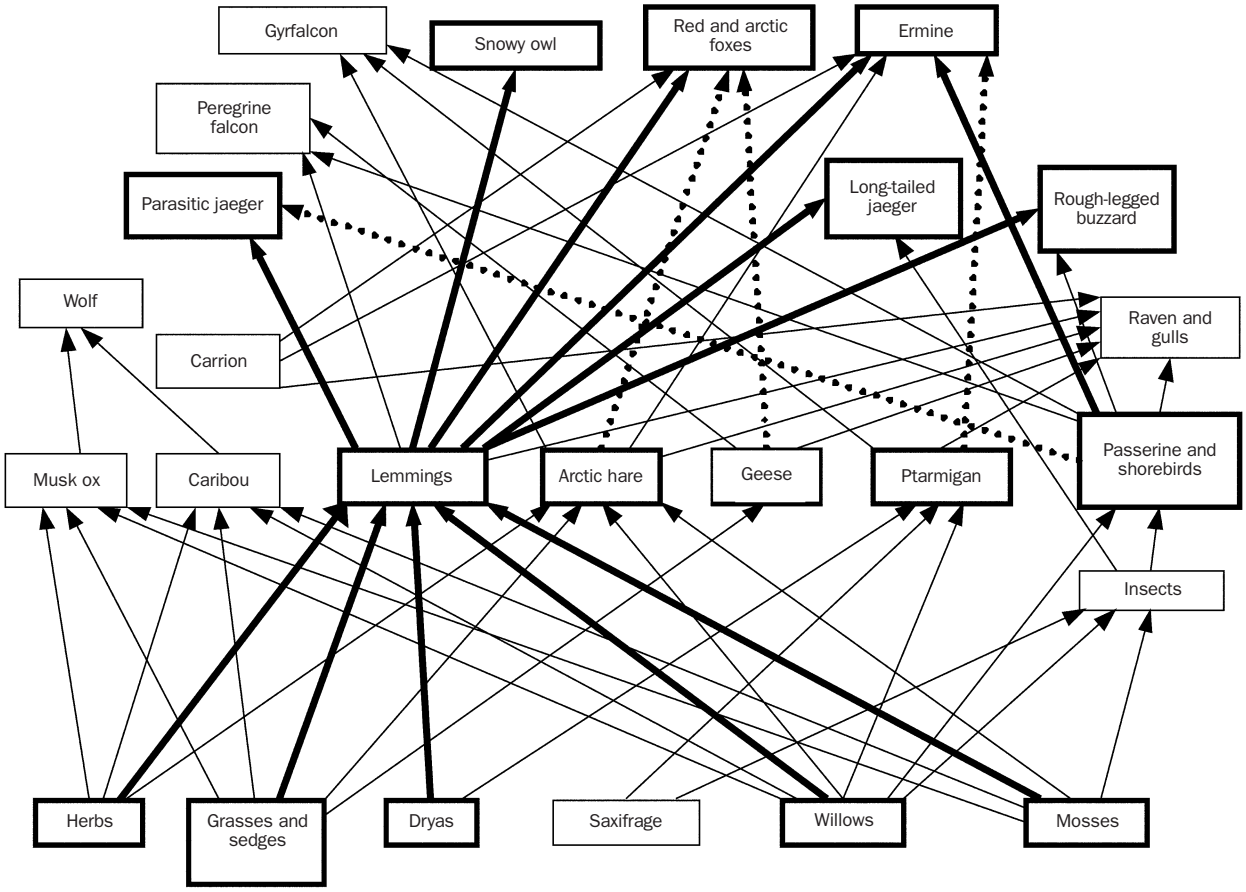

Figure 4. Outline of a typical high-arctic plant-based food web. Components of the food web involved in lemming population or production cycles are in bold frames and linked with thick arrows. Thick, solid lines indicate direct relationships with lemming cycles, while dashed lines indicate indirect relationships (i.e., alternative prey mechanisms). Modified from Krebs and colleagues (2003).

mings possess key species attributes (i.e., they are likely to interact strongly and dynamically with many components of the food web; figure 4). For this reason, we center our discussion of possible cycle-generating mechanisms on lemmings and their trophic interactions with plants and predators.

How are interaction cycles generated?

The origin of lemming and vole population cycles has been sought ever since Elton's 1924 paper, and some 30 to 40 hypotheses have been put forward. Several general overviews of this research on population cycles in small mammals are available (e.g., Stenseth and Ims 1993, Korpimäki and Krebs 1996, Turchin 2003, Korpimäki et al. 2004). Here we restrict our focus to mechanisms that may underlie lemming and vole cycles in the context of arctic food webs. Indeed, the current view is that such population cycles cannot be understood unless they are viewed as an integral part of the food web (Berryman 2002, Turchin 2003).

Plant production cycles and plant–herbivore interactions. There are three ways by which plants may be involved in the generation of interaction cycles. There may be an internally driven plant production cycle, which is simply converted into herbivore population cycles. Alternatively, the cycles may be the outcome of plant–herbivore interactions involving grazing-induced changes in plant quality, or they may result from changes in plant quantity.

Internally driven plant production cycles. The idea of an internally driven plant production cycle stemmed from the observation that good production years in tundra plants coincided with lemming peak years even when plants were protected within exclosures (and thus were not subject to grazing) (Laine and Henttonen 1983). Production cycles in perennial plants can be generated if energy reserves must be accumulated over several years to attain thresholds for successful seed production. Synchronization within and between different plant species will then be brought about by climatic variation (Laine and Henttonen 1983). This mechanism has been mathematically validated and is now thought to underlie the general phenomenon of mast production in many perennial plants (e.g., Satake and Iwasa 2002). Even though plant production cycles can be expected on theoretical grounds, empirical evidence for them in arctic plants is poor and partly contradictory (e.g., Oksanen and Ericson

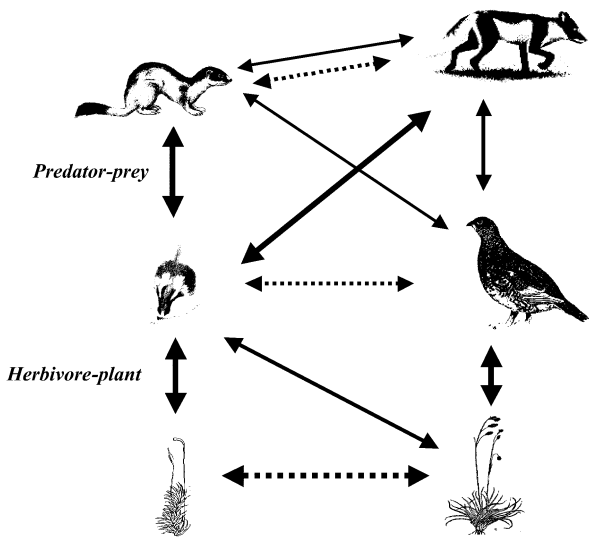

Figure 5. Examples of different types of interaction among tundra species in food webs. Solid lines represent food web interactions that involve consumption between trophic levels (predation or herbivory), while dotted lines depict interactions between species within trophic levels (competition or facilitation).

$$\frac{dP}{dt} = \overbrace{uP\left(1 - \frac{P}{K}\right)}^{\text{Logistic plant growth}} - \overbrace{\frac{APH}{P+B}}^{\text{Herbivore functional response}}$$

$$\frac{dH}{dt} = RH\left(\frac{AP}{P+B}\right) - G$$

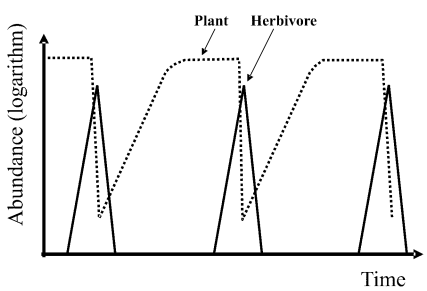

Figure 6. Cyclic dynamics in a simple trophic system consisting of plants and herbivores, according to the classical model of Rosenzweig and MacArthur (see Turchin and Batzli 2001). The graph depicts the biomass dynamics on a logarithmic scale (thus, linear sections of the curves represent exponential increase). The herbivore biomass is too small to be shown in the low phase of the cycle. Parameters in the model are as follows: A, *maximum consumption rate by herbivores;* B, *half-saturation constant of herbivore functional response;* G, *death rate of herbivores;* H, *herbivore density;* K, *carrying capacity of plants (maximum plant biomass in the absence of predators);* P, *plant biomass;* R, *reproductive rate of herbivores;* u, *growth rate of plants.*

1987). Long time series of plant production data from the Arctic and their relation to the lemming cycle would be very welcome.

Grazing-induced plant quality cycles. Grazing-induced plant quality cycles may involve changed levels of nutrients and chemical defense compounds (Karban and Baldwin 1997). Both types of compounds, at least in theory, can create multiannual population cycles in herbivore populations, if the induced response in plants operates with a time delay (Turchin and Batzli 2001). However, experimental evidence to date contradicts this hypothesis for arctic voles (Ekerholm et al. 2005). Similar experiments remain to be done on arctic lemmings.

Grazing-induced plant quantity cycles. The existence of plant quantity cycles due to periodical overgrazing is one of the oldest hypotheses to explain lemming cycles (Lindström et al. 2001). This idea was fueled by observations of severely damaged vegetation after peak years in *Lemmus* species. *Lemmus* may remove or destroy as much as 90% to 100% of the aboveground biomass in their winter habitats (Stenseth and Ims 1993). Their winter food consists mainly of mosses, which recover very slowly after grazing (Turchin and Batzli 2001). This induces a delay in the trophic interaction, which is necessary to create cycles. Mathematical models developed to mimic a simple bitrophic system, with an interaction between a fast-growing consumer population (lemmings) and a slowly recovering resource (plants) (figure 6), easily give rise to cycles in which the lemmings exert a top-down control on the plants. A characteristic feature of some of these models is that they generate cycles with different shapes for the consumer and the resource. The consumer typically has sharp, angular peaks, while the resource has rounded peaks (figure 6). Consequently, Turchin and colleagues (2000) claimed that the "saw-shaped" dynamics of Norwegian lemmings in alpine and low-arctic habitats in Norway (figure 1) was consistent with lemmings as a consumer in a cyclic consumer–resource interaction. There are, however, some caveats to this interpretation. First, population time series of the Norwegian lemming are based on the number of animals trapped in ordinary snap mousetraps. Such a population index probably overestimates peaks, because peak-year animals show increased movement activity. Second, the trapping series may be dominated by captures in nonoptimal habitats, which are ruled by invasion–extinction dynamics. This suspicion arises because no Norwegian lemmings are usually trapped during the low years of the cycle. *Lemmus* time series from optimal habitats in Alaska (Batzli et al. 1980) seem to be characterized by less erratic dynamics. It may be that the Norwegian lemming is a special case, being a species at the climatic border of the Arctic and probably having a different migration pattern than other lemming species (Stenseth and Ims 1993). Also, the seasonal aspect of the population dynamics seems to differ between the Norwegian lemming and more arctic lemming species (see below).

A few more words of caution are warranted with respect to the practice of comparing expectations from theoretical

models with data. Models are crude simplifications, which may or may not capture the essential aspects of reality. An endless array of models can be constructed that vary in their degree of realism, ranging from the simple one depicted in figure 6 to much more complex models. For example, Klemola and collegues (2003) have recently developed a fairly complex and realistic model incorporating details such as three-level trophic interactions (i.e., plant–lemming–predator), several resource types (e.g., mosses and vascular plants), different predator types, varying season length, and the age structure of the lemming population. Their model did not produce the saw-shaped dynamics predicted by much simpler models. The drawback of complex models, however, is that they include many parameters that cannot be estimated from the empirical data that are currently available.

Top-down controlled cycles: Predator–herbivore interactions. It is obvious that predators may play an important role in the dynamics of the plant-based arctic food web. In particular, the high number of avian predators in barren tundra habitat, which does not provide much protection for the prey in terms of vegetation cover, may prevent peak-year lemming populations from increasing over the summer after the protective snow cover has disappeared (Batzli et al. 1980). However, that predators can retard the growth of lemming populations does not necessarily imply that cyclic dynamics are generated by predator–prey interactions (Korpimäki and Krebs 1996).

Mathematical models of predator–prey interactions have taught us what are the most plausible cycle-generating features of such interactions (Hanski et al. 2001, Turchin 2003). Critical features include the species of predators that are present at any given locality and their types of functional and numerical response to changes in prey abundance. In particular, the predominance in tundra food webs of specialized rodent predators that exhibit delayed numerical responses to increased prey availability is thought to be important for the commonness of population cycles in the Arctic. But predator–prey models are also sensitive to many other features, such as the intrinsic demographic rates in both predators and prey, and the ways that these rates change with population density (Korpimäki et al. 2004). A serious problem with the many sensitive parameters of predator–prey models is that there are many degrees of freedom for subjective model adjustments when precise empirical data are lacking.

The most serious attempt to parameterize a mathematical model with relevant data obtained from a lemming–predator system is that of Gilg and collegues (2003). Their simple study system in eastern Greenland consisted of lemmings (the collared lemming, *Dicrostonyx groenlandicus*) and four predator species. Among the predators, there are two year-round resident mammals (the ermine and the arctic fox) and two migrant birds (the snowy owl and the long-tailed jaeger). Population dynamics of the lemming and their predators were monitored over three full 4-year cycles, and consumption rates (i.e., predator functional response curves) were estimated to parameterize a fairly detailed mathematical model. The resemblance between the observed population trajectories and those predicted from the model was good, especially in respect to the period of the cycle and the time lag between peaks of the lemming and ermine populations (figure 7). A sensitivity analysis of the model showed that the occurrence of cycles appears to be jointly dependent on avian predators limiting lemming summer growth at peak densities and on the delayed numerical response by ermine. Although most parameters in this model were empirically based, critical details about the ermine's functional and numerical response were nevertheless based on untested assumptions. Moreover, it is questionable whether this case study from Greenland is representative of trophic interactions in more complex and productive continental tundra systems, where *Lemmus* species usually dominate.

The best evidence for predator-controlled cycles would be provided by experimental studies in which the density of predators is manipulated. Wilson and colleagues (1999) excluded all predators from an 11-ha plot in the Northwest Territories in arctic Canada during the decline phase of the population cycle of the collared lemming. Nonmanipulated plots served as controls. The decline of the lemming population in the predator exclosure plot was significantly reduced compared to that in the control plots, and it was concluded that predators depressed lemming populations at both peak and minimum densities during the cycle. Thus, this experiment, together with the combined observational and modeling study from eastern Greenland, suggests that at least the interaction cycles involving *Dicrostonyx* may be predator controlled.

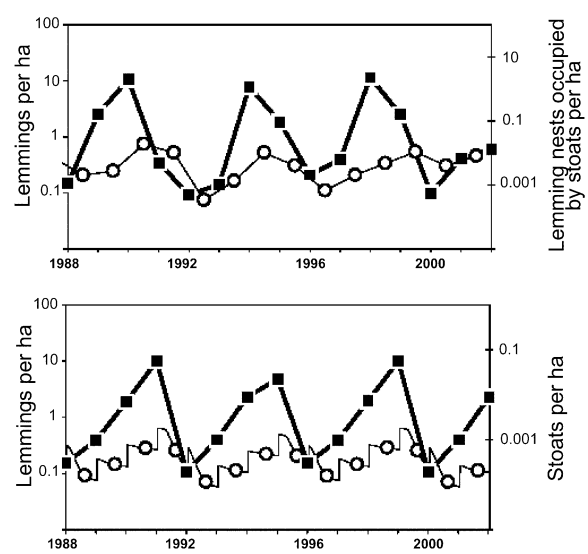

Figure 7. Observed (upper panel) and model-generated (lower panel) population fluctuations in the collared lemming (thick lines, squares) and the stoat (thin lines, circles) at eastern Greenland. Modified from Gilg and colleagues (2003).

Indirect effects of lemming cycles on food webs. As we noted earlier, several arctic bird species that do not prey on lemmings nonetheless exhibit population cycles synchronized with those of the lemmings. Geese and waders are among the best examples (figure 3). For some time it has been hypothesized that predators could link the dynamics of these birds and those of lemmings (Summers and Underhill 1987). An alternative hypothesis could be that cycles in both lemmings and, for instance, geese populations are regulated by cycles in shared food plants (see above).

Recent field studies have revealed the intimate relationship between lemmings, predators, and geese and given support to the so-called "alternative prey hypothesis" (e.g., Bêty et al. 2001, Gauthier et al. 2003). According to this hypothesis, predators switch from lemmings to alternative prey in lemming crash years. Indeed, the large population of arctic fox opportunistically turns to the eggs and young of breeding birds following lemming peak years, and this ultimately gives rise to the demographic cycles in geese that can be observed in wintering flocks (figure 3). The snowy owl may be a third actor in this ecological play between predators and geese, acting in a manner that reinforces the cycles (Bêty et al. 2001). Snowy owls are large and powerful birds that fiercely defend their breeding territories against foxes. Other ground-breeding birds, such as geese and sandpipers, nest close to snowy owl nests as protection against nest predators. This protection effect is clearly reflected in the decreasing breeding success of geese with increasing distance from owl nests (figure 8). As snowy owls normally are not present on the tundra when there are few lemmings, they provide protection only in peak years of the lemming cycle. Thus, the temporally variable protection caused by snowy owls acts to strengthen the fluctuation in goose and sandpiper breeding success during the lemming cycle.

Indirect effects in food webs are probably more common and influential than is usually assumed. The "apparent mutualisms or competition" (Abrams et al. 1998) resulting from shared predators among prey species at the same trophic level (e.g., geese and lemmings) are only one of several possible ways by which lemming cycles may lead to other cyclic phenomena. Another example is diseases that are shared among species. Human settlements in the Arctic often have direct or indirect contact with wildlife through hunting, gathering, and keeping dogs, and certain wildlife diseases (zoonoses) may spill over to populations of humans and domestic animals. Tularemia (transmitted from rodents) varies cyclically in the human population as a result of the cycles in lemmings and voles in Fennoscandia (Hörnfeldt 1978). Rabies exhibits cyclic epidemics in arctic fox populations, and these spill over to sledge dogs (Elton 1931).

Ecosystem productivity and interaction cycles. Plant primary productivity is low on arctic tundra because of low temperatures, a short snow-free season, and low concentrations of nutrients in the soil (Callaghan et al. 2004). Low primary productivity may restrict food chain length (Post 2002), and it has been suggested that the northernmost high-arctic tundra may not be productive enough to provide subsistence for any herbivores (Oksanen and Oksanen 2000). Other, slightly more productive systems may harbor some herbivores, but at densities too low to sustain populations of resident predators. In this latter situation, one may expect that such simple, bitrophic-level food webs (i.e., consisting only of plants and herbivores) would be ruled by consumer–resource interactions involving overgrazing, with violent cycles as a result. As noted above, the erratic dynamics of Norwegian lemmings in high-alpine habitats (equivalent to high-arctic environments) have been proposed as an example of such kinds of cycle (Turchin et al. 2000). On the other hand, in low-arctic and low-alpine regions, where productivity is high enough to sustain predators on a year-round basis, these predators may limit the herbivore populations so that plants are not overgrazed (Ekerholm et al. 2005). In this case, cycles may originate from an interaction between herbivores and predators (e.g., Gilg et al. 2003).

Whether these conjectures regarding ecosystem productivity and food web structure and function match reality is uncertain. Indeed, some of the northernmost islands of the high Arctic lack lemmings and other mammalian herbivores. However, this may be because the open sea and sea ice have acted as a barrier against colonization since the last ice age. Other extreme high-arctic environments, such as the northern tip of Greenland and some of the northernmost large islands in the Canadian Arctic, have both lemmings and resident predators despite very low terrestrial primary productivity (Gauthier et al. 2003). Moreover, even in these unproductive environments, the predators seem to be able to consume most of the secondary production (i.e., herbivores), which suggests that the system is top-down controlled even there (Krebs et al. 2003). It is possible that predators are resident in these high-arctic environments only because they are subsidized by the nearby marine food webs (Roth 2003). Truly inland high-arctic areas with no ecological connectivity to the marine food web are often polar deserts at high altitudes with hardly any bioproduction. Some low-elevation, inland high-arctic areas do exist, however, and could provide valuable test beds for the role of terrestrial primary productivity on food chain length and trophic dynamics in the Arctic. To the best of our knowledge, lemmings exist nowhere in the absence of year-round resident predators. If exceptions could be identified and studied, they would provide a crucial test of some influential ideas on the function of arctic ecosystems.

Interaction cycles in the Arctic and climatic change

The extreme climate in the Arctic underlies most characteristics of the tundra ecosystem (Callaghan et al. 2004). Although trophic interaction cycles are also found south of the tundra biome (e.g., Kendall et al. 1998), such cycles appear to be most pronounced in the Arctic because of the very short plant growth season, low primary productivity, and simple food web structure (Oksanen and Oksanen 2000). Recent evidence from more southern terrestrial biomes has shown that the

effect of climate change on ecosystem functioning may be amplified through altered trophic interactions involving plants, herbivores, and predators (Schmitz et al. 2003). We suspect that such amplifier effects resulting from climate-induced "trophic dysfunctioning" may be even more profound in tundra ecosystems, where the trophic interactions are already delicately balanced in a realm of strong seasonal and multiannual cycles.

Most ecological field studies in the Arctic have been conducted in the summer season, when plants are productive and when reproduction and population growth take place in most Arctic animals. Yet the Arctic winter (defined here as the months when the ground is covered with snow) makes up more than half of the year. Hence, the climatic conditions during the winter may be more important for the ecological dynamics than the summer conditions. How Arctic winters affect plant and animal population dynamics has received relatively little attention until recently, since the impacts of climatic change have come into focus.

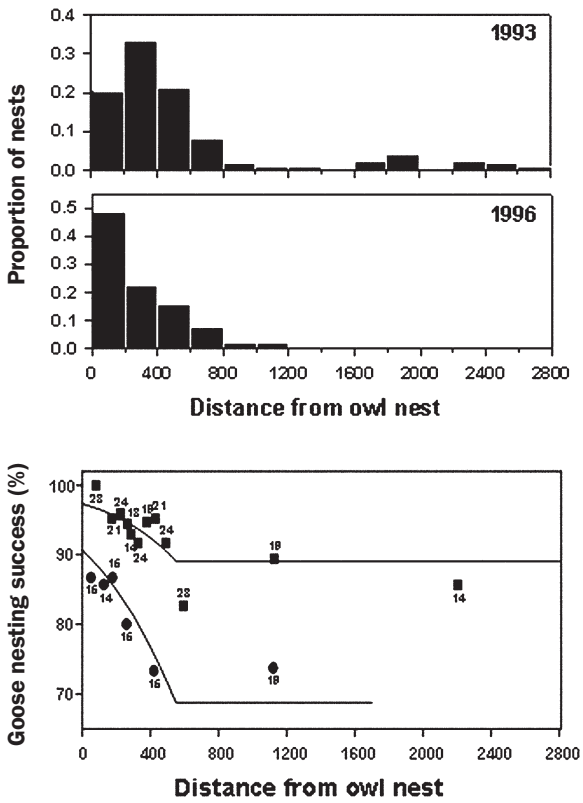

Figure 8. Protection of snow goose breeding success provided by snowy owls on Banks Island in arctic Canada. Upper panel: Distribution of snow goose nests in relation to distance (in meters) from the nearest snowy owl nest in 1993 (a large lemming peak year) and in 1996 (a smaller peak year). Lower panel: Relationship between goose nesting success and distance from nearest owl nests during the same two lemming peak years (1993, squares; 1996, circles). The regression curves (solid lines) were obtained with the best-fit logistic model with an inflection point of 550 m. Reprinted from Bêty and colleagues (2001).

Although a thick snow carpet poses a problem for large herbivores such as reindeer, by increasing the costs of movements and foraging (Schmitz et al. 2003), it is rather beneficial for small herbivores such as lemmings and voles. For small mammals, deep snow offers protections both from low ambient temperatures and from many predators. Indeed, for voles in Fennoscandia, there is a correlation between the length and strength of the winter (the number of months with snow and the snow cover thickness), on the one hand, and the amplitude of population fluctuations, on the other (Hansson and Henttonen 1988). In areas with short winters and a shallow snow cover, it seems that voles always decline to very low population densities in the spring. In particular, short episodes with mild weather (and especially rain-on-snow events leading to ice crust formation that "locks" the vegetation) can lead to population crashes (figure 9). A moderate climatic change scenario predicts that the region of the Arctic in which such events will occur frequently will increase by 40% by the year 2090 (Putkonen and Roe 2003).

Even though both arctic lemmings and boreal voles exhibit multiannual cycles, the seasonal characteristics of their population curves seem to differ, especially in the population peak years (figure 10). Intense winter breeding, leading to rapid population growth under the snow, precedes peak years in arctic lemmings (Batzli et al. 1980). Seasonal peak densities are then reached in the spring. In contrast, boreal vole populations typically decline through the winter, because winter breeding is less common, and population growth first resumes in the summer, giving rise to peak densities in the fall. Also, alpine populations of the Norwegian lemming currently seem to exhibit seasonal dynamics, with yearly peaks in the fall (which contrast with the spring peaks in truly arctic lemming populations; compare the population curves for alpine Norwegian and arctic brown lemmings in figure 1).

The ecosystem consequences of these two different types of seasonal population dynamics may be considerable. One

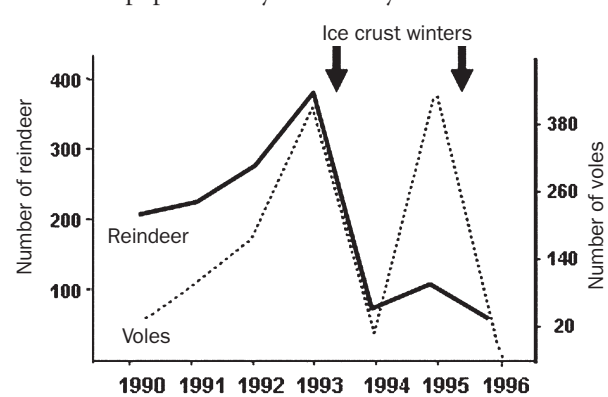

Figure 9. Population dynamics of Svalbard reindeer at Brøggerhalvøya (solid line) and of sibling voles at Fuglefjella (broken line) in Svalbard, Norway Modified from Callaghan et al. (2004).

aspect is the effect of different seasonal grazing pressures on vegetation. A high herbivore population (and grazing impact) at the start of the growing season in the spring is likely to have impacts different from those of the same population in the fall. Another aspect is the consequences of differential seasonal availability of small rodent prey on the community of predators. Notably, specialist predators depend on a high density of prey in the spring to breed successfully. Nomadic predators such as the snowy owl will not settle and breed at all if the lemming density is below a certain threshold in the spring (e.g., approximately 2 lemmings per ha in Greenland; Gilg et al. 2003). Also, for resident specialists, breeding success is strongly dependent on rodent density in spring. For instance, where arctic foxes do not have access to other major food sources, such as seabirds, they do not usually breed unless the spring density of lemmings is high (Angerbjörn et al. 1999). If lemming dynamics on Arctic tundra were to shift from a seasonal pattern with peak densities in the spring to population peaks in the fall (figure 10), it would clearly affect specialist lemming predators negatively. The effect of such a change on tundra vegetation is harder to predict, but may still be considerable.

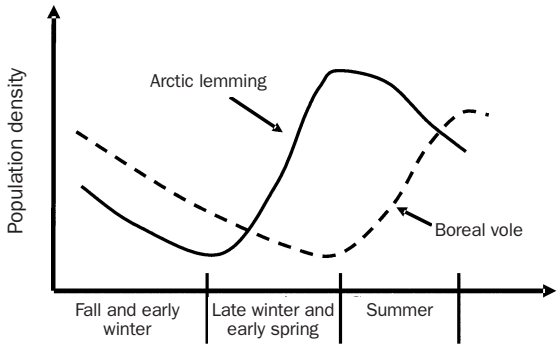

Figure 10. A depiction of some principal differences in the seasonal dynamics during cyclic peak years for arctic lemmings and boreal voles.

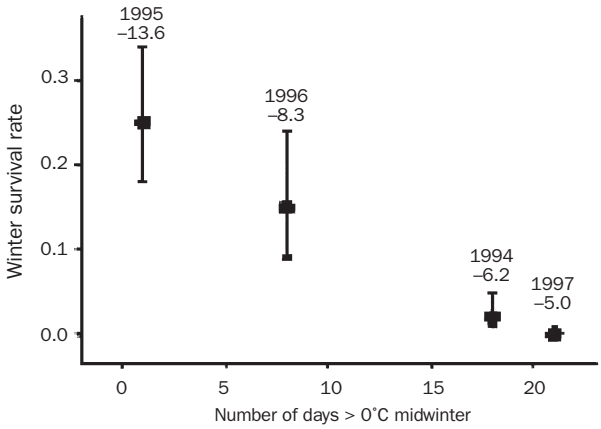

Figure 11. Yearly winter survival rate (with 95% confidence intervals) of several local tundra vole (*Microtus oeconomus*) populations plotted against the number of days with temperatures above 0 degrees Celsius (°C) during the middle of winter (December–February). Mean winter temperature and year are denoted above the survival rate estimates. Reprinted from Aars and Ims (2002).

Models of climate change predict that winters in the Arctic will become considerably warmer and more variable (Callaghan et al. 2004). In fact, some arctic and subarctic regions seem to have warmed already. Given that the seasonal characteristics of arctic lemming population dynamics, and thus their trophic interaction cycles, are dependent on a long and cold winter, we may expect that the dynamics and structure of the tundra ecosystem will change quite dramatically. In fact, climate may not need to change much to have a large effect. It has been shown that just a few more days with above-zero temperatures during the winter may dramatically lower the survival rate of voles and disrupt the dynamics of local populations (figure 11; Aars and Ims 2002). Moreover, climatic anomalies taking place at a large scale may act to synchronize distant lemming populations (Korpimäki et al. 2004) that otherwise would fluctuate asynchronously. Such large-scale synchrony could have negative impacts on nomadic predators of lemming, as a nomadic strategy would not work in such a situation (Ims and Steen 1990).

Considering that climate has become warmer at northern latitudes during the last century (Callaghan et al. 2004), a pertinent question is whether the ecological dynamics of the Arctic have changed along the lines we have suggested above. Unfortunately, there are no long-term monitoring programs from arctic tundra proper that can provide definitive answers. However, time series of vole populations at the border of the Arctic in Fennoscandia are sufficiently long to provide indications of recent changes. Such data do suggest that the expected changes have taken place. At Kilpisjärvi in northern Finland, where more than 50 years of vole trapping have been conducted in subarctic birch forest, the population cycle was clearly dampened during the 1990s and exhibited mainly seasonal fluctuations (figure 12; Henttonen and Wallgren 2001). Similar changes took place in northern coniferous taiga in the 1980s (Hörnfeldt 2004). In low-arctic tundra in Finnmarksvidda, northern Norway, winter declines seem to have become more pronounced in voles (Ekerholm et al. 2005). These changes in the population dynamics of small rodents have been accompanied by changes in the community of predators. The arctic fox and the snowy owl have been declining through the last decade (figure 12), and both species are now on the verge of extinction in Fennoscandia (SEFALO 2004). The rough-legged buzzard has also shown a declining trend during the last two decades (Kjellén and Roos 2000). While specialist predators are declining, generalist predators such as the red fox seem to be spreading northward (Hersteinsson and Macdonald 1992). Although there may be many potential causes for the northward expansion of generalist predators, it matches the general trend that many southern species seem to be rapidly moving northward because of climatic warming (Parmesan and Yohe 2003). Invasion of new predators may dramatically alter the dynamics and structure of food webs (Roemer et al. 2002), and this applies

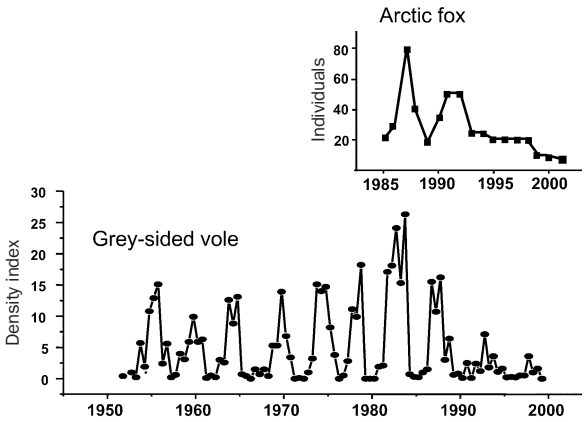

Figure 12. Changed dynamics of the grey-sided vole in Kilpisjärvi, Finland (Henttonen and Wallgren 2001) and population trend for the arctic fox in northern Finland (SEFALO 2004).

perhaps especially to arctic food webs, which, because of their simplicity, may be more easily invaded (i.e., less resistant) and more affected by invasive species (i.e., less resilient) (Kennedy et al. 2002). As population trends in predators often reflect and determine major changes in the ecosystem (Schmitz et al. 2003), it may be prudent for monitoring programs to concentrate on upper-trophic-level predators.

Perspectives for future research and monitoring

Owing to their simplicity, tundra ecosystems are valuable model systems for elucidating fundamental principles of how trophic interactions shape the structure and function of food webs. Moreover, tundra ecosystems are among the most exposed and vulnerable to climate change, and there is an urgent need for predicting and eventually documenting how such changes affect key processes such as the trophic interaction cycles we have described in this article. However, except for some recent instructive field campaigns (e.g., Krebs et al. 2003) and case studies (e.g., Gauthier et al. 2003, Gilg et al. 2003), there are at present few ongoing arctic research projects with a genuine ecosystem perspective (but see Oksanen and Oksanen 2000). There is a particular need for ecosystem-based research protocols with good geographic representation, covering, for example, prevailing climate gradients. Moreover, such projects should have a time horizon long enough to include temporal variability in climate and the time lags in ecosystem responses to such variability (which may be markedly delayed in the Arctic), as well as several normal interaction cycles within the system. There is a striking lack of high-quality, long-term time series for important variables such as plant primary production at tundra sites. Moreover, there is an urgent need for studies conducted during the critical winter season. Much can be achieved by setting up targeted monitoring programs with a standardized protocol at many sites in the Arctic. Such monitoring programs should include quantitative measurements of species that are likely to be the main players in the interaction cycles we have described.

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