



# Changing circumstances: Implications for trophic dynamics and species conservation on the Fennoscandian Tundra



**John-André Henden**

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**UNIVERSITY OF TROMSØ**  
**Faculty of Sciences**  
Department of Biology

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**Changing circumstances: Implications for trophic  
dynamics and species conservation in the  
Fennoscandian Tundra**

*John-André Henden*

## **Advisors**

Prof. Nigel G. Yoccoz

Prof. Rolf A. Ims

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## **This thesis is based on the following papers:**

These papers will be referred to by their roman numerical

### **I.**

Ims, R. A., Henden, J.-A., and Killengreen, S. T. 2008. Collapsing population cycles. *Trends In Ecology & Evolution* **23**:79-86.

### **II.**

Henden, J.-A., Ims, R. A., and Yoccoz, N. G. 2009 Non-stationary spatio-temporal small rodent dynamics: Evidence from long-term Norwegian fox bounty data. *Journal of Animal Ecology, Online Early*

### **III.**

Henden, J.-A., Bårdsen, B.-J., Yoccoz, N. G., and Ims, R. A. 2008. Impacts of differential prey dynamics on the potential recovery of endangered arctic fox populations. *Journal of Applied Ecology* **45**:1086-1093.

### **IV.**

Henden, J.-A., Ims, R. A., Yoccoz, N. G., Hellström, P., and Angerbjörn, A. Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: The case of foxes in tundra.  
(Submitted: *Oikos*)

### **V.**

Henden, J.-A., Yoccoz, N. G., Ims, R. A., Bårdsen, B.-J., and Angerbjörn, A. Phase-dependent effect of conservation efforts in cyclically fluctuating populations of Arctic fox (*Vulpes lagopus*).  
(Submitted: *Biological Conservation*)

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## **Abstract**

A special case of population fluctuations is multi-annual population cycles. While such population cycles exist in several ecosystems, they are more prominent in northern (e.g. tundra) ecosystems, especially among key stone herbivore species. These herbivores provide an important ecosystem function in the sense of pulsed flows of resources (i.e. for predators) and disturbances (i.e. for vegetation) throughout the ecosystem. However, the circumstances on the tundra are changing. For instance, large scale collapse of population cycles of many herbivores has been reported, as well as northward expansion of novel predators (e.g. red fox). These changes, heavily connected to climate change, are capable of disrupting the function and structure of such systems. Overall this thesis aims to outline and evaluate the recent dramatic changes in multi-annual population cycles of many herbivores and the possible implications of such changes on the trophic dynamics and species conservation in the Fennoscandian tundra ecosystem. First I show that the recent collapse of multi-annual population cycles is now a widespread phenomenon, extending several species and ecosystem barriers. Next I show, based on long time series of fox bounty data, that these recent changes have some historical analogies. Specifically, I show that the highly publicized patterns (e.g. geographic gradients, large scale synchrony) in Fennoscandian small rodent cycles have been subject to large spatio-temporal transitions in their patterns, being highly non-stationary. I also demonstrate that collapse of cycles similar to the recent events, though on a smaller spatial extent, have occurred earlier and that these incidents seem to concur with shifts between cold and warm climatic periods. Then I demonstrate which aspects of the recent changes in the dynamics of key prey species is likely to heavily affect the viability and existence of tundra predators strongly adapted to the pulsed flow of resources provided by cyclically fluctuating prey populations. Furthermore, the effect of recent and future projections of climate change may facilitate the establishment of novel predator species,



which may act as dominant competitors for native species for habitat and prey. I here show that increased competition with red fox may be detrimental to arctic fox viability, especially if subsidies (e.g. reindeer carcasses) are available to the dominant competitor. Finally, I show that attempts to conserve native predators, such as the arctic fox, should take into account the factors that govern their demography and thus population dynamics. I show that the effect of management action is highly dependent on the phase of the demographic cycle of arctic fox. This means that management intervention should be continuous, but most focused to moments in time where the effect is expected to be most pronounced.

**Keywords:** climate change, conservation, cyclic prey dynamics, intraguild competition, non-stationary small rodent dynamics, population synchrony, predator-prey dynamics, matrix model, stochasticity, stochastic growth rate, viability, *Vulpes lagopus*.

# **Introduction and background**

## **Characteristics of Tundra**

The tundra constitutes areas above the tree line (i.e. latitude and altitude) and is considered the coldest of all the biomes. It is often recognized for its frost-moulded landscapes, permafrost, extremely low temperatures, little precipitation, nutrient limitations, and short growing seasons. However, the tundra can roughly be separated into two types: The arctic tundra and the alpine (mountain) tundra.

The tundra is located in the northern hemisphere and roughly represents about 10% of the earth's land areas (Fuglei & Ims 2008). It is located as a relatively narrow circumpolar belt situated between the boreal forest in the south and the Arctic Ocean in the north (Walker et al. 2005). The arctic is known for its cold, desert-like conditions and large seasonality with mainly two seasons, summer and winter. The average winter temperature can in some regions be very low, as low as  $-34^{\circ}\text{C}$ , but this varies within the circumpolar range (Eugster et al. 2000). For instance, in the north-eastern part of the Fennoscandian peninsula, which constitutes the south-western fringe of the arctic tundra biome in Eurasia (i.e. low arctic tundra, Figure 1), the climate is characterized by relatively mild winters due to the North Atlantic current, which also means that permafrost only occurs quite scattered in the low lands (Virtanen et al. 1999), but as recognized more recently, more common at altitudes above 350-400m above sea level (Farbrot et al. 2008; Isaksen et al. 2008). The average summer temperature in the arctic tundra varies in the range of  $3-12^{\circ}\text{C}$ , but may occasionally creep below zero. Thus, the relatively mild summer is probably the main reason why this biome is able to sustain life. The growing season on the tundra is quite short, often no longer than 50 to 60 days. While rainfall may vary in different regions of the arctic, the yearly precipitation, including melting snow, is often in the range of 150 to 300 mm (Bliss et al. 1973; Eugster et al. 2000). However, eastern and western reaches in North America and Eurasia, respectively, can have nearly double this amount due to the influence of the ocean (Callaghan et al. 2004c). During the summer rising temperatures melts the top layer of the permafrost, often leaving the soil completely soaked. When water saturates the upper surface, bogs and ponds may form, providing moisture for plants.

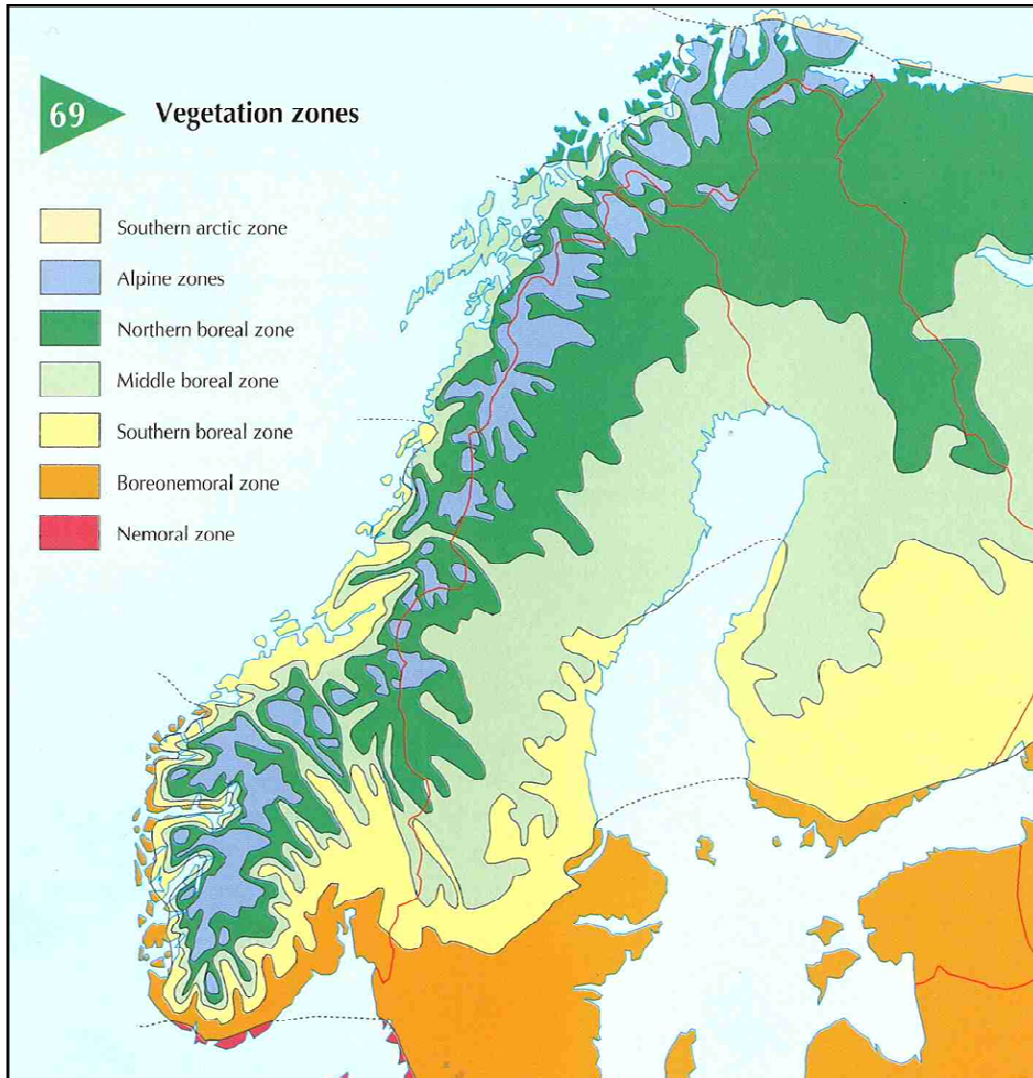
While permafrost often prevents the vegetation of the arctic tundra to hold deep root systems (Bliss et al. 1973), there are still a wide variety of plants that are able to resist the severity of the climate. In the low-arctic tundra the vegetation is often dominated by shrubs (i.e. erect-shrub tundra) (Walker et al. 2005). However, beside shrubs (e.g. willows, bilberry,

crowberry and dwarf birch) there are also other plant groups present, such as sedges, grasses, mosses and lichens (Walker et al. 2005). Most plant growth forms are quite short, often grouped together to resist the cold temperatures, wind and erosion and, thus almost entirely protected by the snow during the winter. Moreover, they can carry out photosynthesis at low temperatures and low light intensities.

While biodiversity is generally low (Chernov 2002; Chernov & Matveeva 1997) the vertebrate fauna on the arctic tundra can be quite diverse (Callaghan et al. 2004e; Ims & Fuglei 2005). Herbivorous mammals (such as lemmings, voles, caribou, arctic hares and ptarmigans), carnivorous mammals (such as the arctic fox, recently the red fox, least-weasel and stoat), migratory birds (like shore and water birds, falcons, buzzards, skuas, owls and ravens), insects and many more are represented, sometimes in large quantities. Many species on the tundra display pronounced population cycles in their population dynamics, resulting in years of very high abundance of both small herbivores and carnivores (mammals and birds). Animals permanently situated in the arctic tundra are adapted to handle long, cold winters and to breed and raise young quickly in the summer. Animals such as mammals and birds also have additional insulation from large fat reserves (Callaghan et al. 2004e), but several migrate (i.e. birds) south during the winter because food is not abundant. Thus, the characteristics of arctic tundra can roughly be summarised as: extremely cold climate, low biotic diversity, simple vegetation structure, limited drainage, short season of growth and reproduction and large population oscillations of animals.

The alpine tundra constitutes treeless areas that extend from the tree line to the highest mountain peaks (e.g. Fennoscandian mountain tundra which extends far south on the Fennoscandian Peninsula, Figure 1 (Moen 1999)). This biome is not restricted to certain latitudes and not determined by either temperature or rainfall gradations. Instead, this biome can be found at any latitude on earth, only dependent on altitude. The alpine tundra is similar to the arctic tundra in many ways, but some differences are apparent. Unlike the arctic tundra, the soil in the alpine tundra is well drained and the lower part does not have permafrost. The growing season is also quite long in comparison, with a length of more than 120 days. A main difference is also precipitation and snow depth – as most alpine tundra areas are characterized by large precipitations and deep snow (Oksanen & Virtanen 1995). While plants are often very similar to those found in the arctic tundra (e.g. tussock grasses, dwarf trees, small-leaved shrubs, and heaths) (Oksanen & Virtanen 1995), there is greater variation in the composition of the animal communities between different alpine tundra areas in the arctic tundra circumpolar range, as alpine tundra is found quite widespread in high altitudes

throughout the world. Moreover, there are some differences between northern and southern alpine areas in that respect, as northern alpine areas such as in Fennoscandia is considered more similar to arctic tundra in the composition of the animal communities. For instance, the Fennoscandian mountain tundra (Figure 1) is possibly the only alpine area which holds lemmings (Stenseth & Ims 1993a). This is likely the reason why these areas also are the only alpine tundra areas (except maybe Iceland) which hold populations of arctic fox and snowy owls (at least earlier).



**Figure 1.** Vegetation zones in Scandinavia, Finland, the Baltic States and adjacent areas. The map shows the distribution of the nemoral, boreonemoral, southern boreal, middle boreal, northern boreal and southern arctic zones. The occurrence of continuous zones in the lowlands is emphasised. Large areas of alpine zones with northern boreal vegetation are depicted as islands (Moen 1999).

## **Tundra – ruled by multi-annual population cycles**

Fluctuation in population size is clearly the norm in natural animal populations (Elton 1924; Elton 1942). Such fluctuations in population abundance may be brought about by both abiotic (e.g. environmental stochasticity) and biotic factors (e.g. consumer-resource interactions). However, regular population density cycles form a special case of such fluctuations in population size (Krebs et al. 2001a; Krebs & Myers 1974; Myers 1988). Multi-annual population cycles are characterized by rapid population growth following a few years of low densities. This rapid increase is then succeeded by a major crash one or two years later, where these highs and lows are repeated in a quite constant periodic (the time between successive peaks) manner (Krebs & Myers 1974). The ultimate cause(s) of what generates such regular population cycles have fascinated and captivated population ecologists ever since Elton's (Elton 1924) paper on periodic fluctuations in animal populations. From then on, his paper has spawned more than 80 years of research on multi-annual population cycles in a number of species. These studies have not only contributed to the understanding of population cycles, but has also been instrumental to the current understanding of animal population dynamics in general (Lindström et al. 2001). During the past 80 years a myriad of hypotheses have been put forward to explain the causes underlying such periodic fluctuations in population size (review in Lindström et al. 2001; Stenseth & Ims 1993b; Turchin 2003), however most have been abandoned due to little or no empirical support (Stenseth & Ims 1993b). The current view among many ecologists is that population cycles most likely originate from trophic interactions within the food web (i.e. consumer – resource interactions, such as between plants and herbivores or between herbivores and their parasites/predators) (Ims & Fuglei 2005; Stenseth & Ims 1993b; Turchin 2003).

While the population cycles in lemmings, snow shoe hare and the arctic fox may be among the most well-known, multi-annual population cycles are also common in several other species throughout the tundra (cf. Ims & Fuglei 2005) and elsewhere (Paper I, and references therein). While the phenomenon of population cycles is not reserved to arctic species, they are certainly most common in northern areas (Ims & Fuglei 2005; Kendall et al. 1998). Accordingly, the high prevalence of population cycles in the north probably highlights their ultimate link to northern climate, in the sense of long, cold and stable winters with thick snow cover. Moreover, it is evident that population cycles on the tundra constitute an integral part of the functioning of the entire ecosystem. For instance, voles and lemmings are directly (and indirectly) connected to several species on every trophic level in the plant-based food

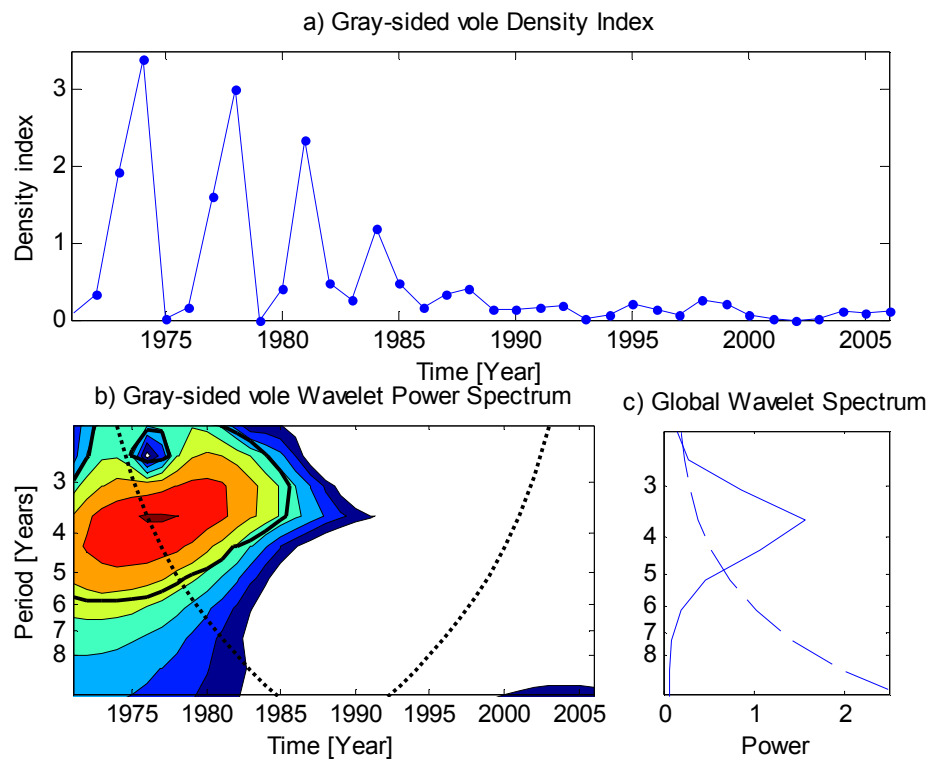
webs of the tundra (Ims & Fuglei 2005), providing an important ecosystem function in the sense of pulsed flows of resources (i.e. for predators) and disturbances (i.e. for vegetation) throughout the ecosystem. However, recently indications of large-scale collapse of population cycles in small rodent and other cyclic species have surfaced, capable of disrupting the function and structure of such systems. In Paper I, we review the increasing number of studies that show temporal and spatial changes in cyclic population dynamics, transcending species and ecosystems, and discuss the cause and implications of these changes.

### **Spatio-temporal small rodent dynamics**

The 3-5 year population cycles and high degree of spatial synchrony of these cycles (review in Bjørnstad et al. 1999) in Fennoscandian small rodents have, in particular, received much attention. Already in the late 19<sup>th</sup> century (Collett 1911-12) and early parts of the 20<sup>th</sup> century Norwegian naturalists (Johnsen 1929; Wildhagen 1949, 1952) started to gather and organize qualitative (e.g. 0 = low and 1 = high abundance) records of lemming and vole peak years, with some time series going back as early as the 1870s and extending almost 80 years (i.e. to 1949; Wildhagen 1952). However, more recently (mostly since 1970) time series from several areas in Fennoscandia, based on more elaborate trapping studies providing quantitative measures of small rodent dynamics (e.g. Ekerholm et al. 2001; Henttonen & Wallgren 2001; Hörnfeldt et al. 2006; Kausrud et al. 2008), have emerged. These trapping data, which have been thoroughly analysed by means of time series analysis, have provided one of the richest sources of information on the spatial dimension of cyclic population dynamics. First of all, these studies have revealed a consistent geographic gradient in their density-dependent structure (Bjørnstad et al. 1995; Stenseth 1999), reflecting the prevalence of non-cyclic dynamics in the south, through cyclic dynamics with a relatively short 3-4 year period in the central parts, to a longer 5-year cycle in the very north of Fennoscandia (Bjørnstad et al. 1995; Hanski et al. 1991; Hanski & Henttonen 1996; Hansson & Henttonen 1985; Strann et al. 2002; Sundell et al. 2004). This gradient in cyclicity and cycle period length has most often been explained by differences in the composition of the predator assembly in northern versus southern parts of Fennoscandia, in the sense of a higher proportion of generalist predators in the south and a higher proportion of specialist in the north (Begon et al. 2006; Hansson & Henttonen 1985; Turchin 2003). These differences have ultimately been connected to the thickness and temporal deviations of snow cover in winter (Hansson & Henttonen 1985). In addition to gradients in the pattern of population dynamics, analyses have also provided evidence for large-scale spatial synchrony of the cycles

(Angerbjörn et al. 2001; Christiansen 1983; Myrberget 1973), especially within the regions with equivalent cycle period. Several hypotheses have been invoked to explain this large-scale synchrony, including climate (Huitu et al. 2005; Huitu et al. 2003) and the action of nomadic predators (Ims & Steen 1990). While these spatial patterns of cyclicality, periodicity and spatial synchrony now seems to have been established among many as a consistent pattern of Fennoscandian small rodent population dynamics (Begon et al. 2006), there are reasons to question this on several grounds. First, these spatial patterns are founded on relative short time series (2-3 decades, but see Henttonen & Wallgren 2001) and mainly from a restricted time period (i.e. most time series starts after 1970). Just due to the shortness of the time series, there are reasons to question whether these patterns are representative for Fennoscandian small rodent dynamics in a longer timeframe. Second, several studies have documented the sensitivity of small rodent dynamics in northern areas to climate (Bierman et al. 2006; Kausrud et al. 2008; Yoccoz & Ims 1999; Aars & Ims 2002). Thus, it could be expected that temporal shifts and trends in climate, such as the alternations between relatively warm and cold periods during the 20<sup>th</sup> century in Europe (Nesje et al. 2005), is capable of causing shifts in population dynamics patterns. Accordingly, while based on relatively poor data (i.e. qualitative time series), some studies (Bjørnstad 2000; Steen et al. 1990) have reported periods of interrupted cyclicality and spatial synchrony in the beginning of the 20<sup>th</sup> century (i.e. 1910-1930), concurrent with a relative warm period (Nesje et al. 2005). Additionally, it has recently been reported that the multi-annual population cycles displayed by several vole species in Fennoscandia have become severely dampened and even completely lost over large areas (e.g. Figure 2), especially in the northern boreal forest (Hanski & Henttonen 1996; Henttonen & Wallgren 2001; Hörnfeldt 2004; Hörnfeldt et al. 2005; Steen et al. 1996). Also this recent shift took place concurrently with a warming period from the late 1970s onwards (Jones et al. 1999). Even breakdown of spatial population synchrony have been reported (Henttonen & Wallgren 2001). Third, several modelling studies have shown that temporal shifts from cyclic to non-cyclic dynamics (i.e. non-stationary dynamics) might be expected from the processes (i.e. non-linear trophic interactions) underlying cyclic population dynamics (Hanski & Henttonen 1996; Hastings & Higgins 1994; Kendall et al. 1999), i.e. without any external abiotic forcing. In Paper II, we use an alternative source of data that provides a better basis for evaluating the long-term stationarity of the spatio-temporal patterns of Fennoscandian small rodent population dynamics. The data consist of an almost century long (1880–1976) panel of fox bounty time series including 18 counties of Norway, thus spanning the whole range of latitudes of

Fennoscandia (i.e. 15 latitudinal degrees). These fox time series mirror the dynamics of their dominant small rodent prey, in particular, with respect to cycle period length and spatial synchrony. The purpose of the analyses is: 1) To document instances of nonstationary population dynamics both in terms of local (i.e. county-wise) characteristics (density dependence and periodicity) and in large spatial dynamics (regional population synchrony between counties) and, 2) To investigate the degree of coherence between historical and more recent small rodent dynamics in Fennoscandia so as to evaluate the temporal consistency of the geographical patterns of density-dependent structure and periodicity on a centennial time-scale.



**Figure 2.** Cycle amplitude dampening toward a temporal collapse of the four-year cycle in boreal gray-sided vole *Clethrionomys rufocanus* in northern Sweden (Hörnfeldt 2004). (a) Time series of combined fall catches from a region covering 10 000 km<sup>2</sup>. (b) The normalized wavelet power spectrum (Torrence & Compo 1998) for the time series showing the statistical significance of the change in dynamics. The cyclic nature of the dynamics gradually disappears, perhaps with a decreasing periodicity, until no periodic signal remains after 1990. (c) The global wavelet power spectrum, showing the significant periodic signal at approximately four years. The dashed line shows the 5% significance level. The time series data were obtained from (Hörnfeldt et al. 2005).



### **Tundra predators – specialists on small rodents**

Voles and lemmings form the heart of the terrestrial food web dynamics of the Fennoscandian tundra, constituting key prey for many predators (Ims & Fuglei 2005; Korpimäki & Krebs 1996), such as the arctic fox (*Vulpes lagopus*) (Fuglei & Ims 2008). The arctic fox is one of the vertebrates that are best adapted to life on the tundra (Fuglei & Ims 2008), in the sense of a life-cycle specifically adjusted to the seasonal and multi-annual fluctuations in resources. The arctic fox is regarded as a specialist of small rodents in inland tundra areas of Fennoscandia (Elmhagen et al. 2002; Tannerfeldt & Angerbjörn 1998) and in many other regions of tundra biome (Angerbjörn et al. 1999). In small rodent peak years arctic fox experience an overabundance of food which is reflected in their reproductive investment by a distinct increase in the number of breeding foxes and their litter size (up to 24 cubs have been reported) (Angerbjörn et al. 1999; Roth 2003), whereas they often completely refrain from breeding in low density small rodent years. Consequently, these strong pulses in resource availability and the subsequent response in terms of increased reproduction give rise to the pronounced population cycles displayed by arctic fox (e.g. Angerbjörn et al. 1991; Angerbjörn et al. 1995; Kaikusalo & Angerbjörn 1995). The arctic fox is a flagship species for the arctic and alpine tundra (Fuglei & Ims 2008) being one of the few truly arctic vertebrate species (NB: only in alpine areas in Fennoscandia). Being at the top of the food chain, the arctic fox is likely to be a suitable indicator species of ecosystem state and change (Schmitz et al. 2003; Voigt et al. 2003). Although found in large numbers throughout its circumpolar range, arctic fox populations at the edge of its distribution in southern arctic tundra and the northern mountain tundra are declining (Hersteinsson & Macdonald 1992). This is especially the case for the Fennoscandian arctic fox. The arctic fox in Fennoscandia was severely decimated, probably owing to overhunting in the early 20<sup>th</sup> century (Johnsen 1929; Lønnberg 1927). However, despite full protection in 1928, 1930 and 1940 in Sweden, Norway and Finland, respectively, the arctic fox has failed to recover to former numbers (Hersteinsson et al. 1989 and reference therein). Quite to the contrary, since the 1970s the arctic fox has been subject to a further decline in Fennoscandia (Angerbjörn et al. 1995) and is now considered to be on the verge of regional extinction (Dalén et al. 2006; Ims & Fuglei 2005; SEFALO 2004). The decline and range contraction of the Fennoscandian arctic fox has, at least partly, been attributed to dampened peak abundances of cyclically fluctuating vole and lemming populations (Angerbjörn et al. 2007; Angerbjörn et al. 1995; Fuglei & Ims 2008; Ims & Fuglei 2005) and increased interspecific competition with the northward expanding red fox (Elmhagen 2003; Hersteinsson & Macdonald 1992; Ims &

Fuglei 2005; Killengreen et al. 2007; Tannerfeldt et al. 2002). However, also several other putative causes of the “Fennoscandian arctic fox problem” have been proposed (Hersteinsson et al. 1989; Hersteinsson & Macdonald 1992).



**Figure 3.** Arctic fox and Norwegian lemming in southern Arctic tundra at the Varanger Peninsula, NE Norway, in April.

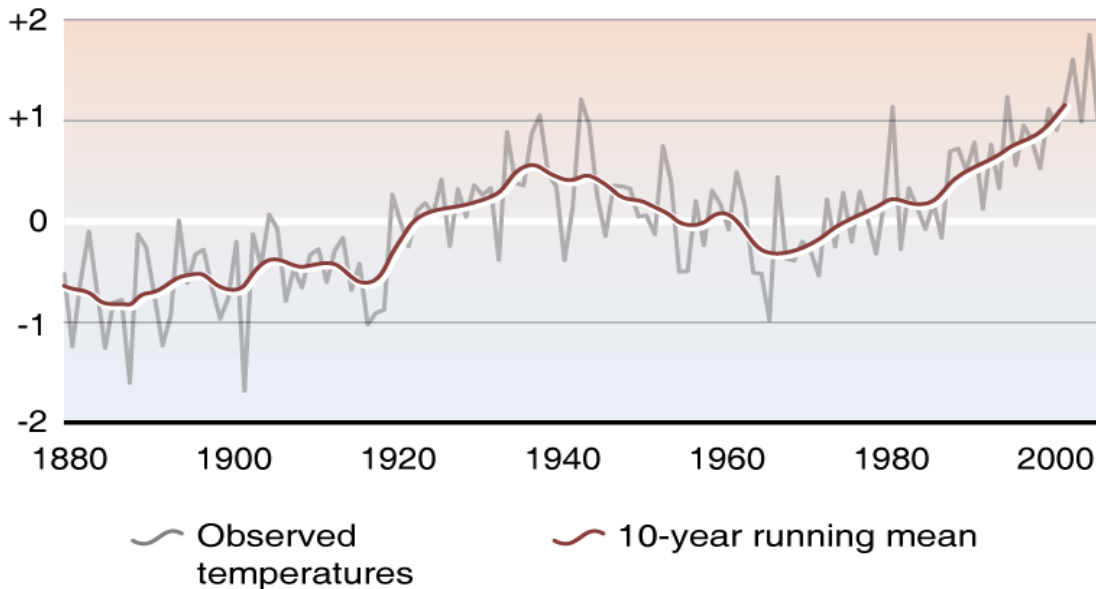
### **Climate change – impact on Fennoscandian tundra**

The arctic is currently subject to large changes capable of disrupting the structure and functioning of tundra ecosystems (ACIA 2005). Climate change, with the largest changes expected in polar areas (Gillett et al. 2008; Hanssen-Bauer et al. 2005), has been highlighted as the major component of change in this region (Callaghan et al. 2004a; Callaghan et al. 2004d). During the 20<sup>th</sup> century there has been a significant warming which cannot be explained by natural climate variations alone (Rosenzweig et al. 2008), where warming rates have been most pronounced in northern areas and especially in winter (Jones et al. 1999). The last hundred years have consisted of an alternation between relatively warm and cold periods in the northern hemisphere (Beck et al. 2007; Jones et al. 1999), where especially two periods of warming have been identified; the period between 1925-1944 and 1978-onwards (Jones et al. 1999), intersected by periods of cooling (Figure 4). In recent decades the average warming in arctic areas have been around 3°C (Callaghan et al. 2004e). However, climate projections suggest a continuation of the warming trend, possibly as much as 4-5°C by 2080 in mean annual temperature (Callaghan et al. 2004e).

Downscaled climatic scenarios for Fennoscandia (review in Hanssen-Bauer et al. 2005) have revealed several interesting trends in components of climate change, especially temperature and precipitation. For temperature, warming rates are expected to be larger in inland compared to more coastal areas. For instance, predicted January warming rates during

the 21<sup>st</sup> century is projected to be less than 0.3°C per decade along the west coast of Norway, while more than 0.5°C in inland areas. Furthermore, warming rates are predicted to be larger in winter than summer, especially in northern inland areas, and there are indications of larger warming rates at higher altitudes. Projections for precipitation, however, hold more uncertainty. Nevertheless, there are projections of increased precipitation in northern inland parts of Fennoscandia. Furthermore, there are projections of increased precipitation intensity almost year round and especially during winter, increased frequency of wet days during winter and more precipitation in the form of rain in the north. Consequently, the shifts between warm and cold periods during winter, especially as the precipitation intensity of rainy days seems to increase all year round (Hanssen-Bauer et al. 2005), could lead to increased frequencies of wet weather, deep snow and/or ice crust formation. Finally, there are also projections regarding an increase of the growing season of as much as 3 weeks over the next 60 or so years.

### Temperature anomaly (°C)



**Figure 4. Trends in Arctic temperature, 1880-2006 (60°-90°N).** Arctic land temperature anomalies from 1880 through 2006 is shown in this figure. The zero line represents the average temperature for 1961–1990. In the late 1800s the Arctic was relatively cold. There was a warm period in the 1920s to 1940s and cold periods in the early 1900s and in the 1960s. Over the last decades the temperatures were about 1.0°C above the 20th century average. **Sources:** CRU (2007). CRUTEM3v dataset. Climate Research Unit, University of East Anglia. <http://www.cru.uea.ac.uk/cru/data/temperature> [Accessed 6 April 2007]

It is now documented that global warming will strongly affect the distribution and abundance of both plants and animals (Callaghan et al. 2004e). The arctic tundra is predicted to shrink under global warming as the boreal forest zone will be moving to the north (ACIA 2005). However, such northward expansion of the boreal forest is likely to be a rather slow process. Thus, there are reasons to believe that ecological processes and characteristic species within the tundra ecosystem are likely to be affected long before the open tundra becomes forested. For instance, a warmer climate will result in longer growth season for plants and thus more plant biomass for tundra herbivores to consume. One of the most evident examples is the rapid expansion of shrubs such as willows and dwarf birch reported in several areas of the tundra (Chapin et al. 2005; Sturm et al. 2001). Since shrubs are already present in the tundra an increase in the amount of shrubs is likely much faster than the northward expansion of the boreal forest. Increased biomass of shrubs and other plant species will facilitate the existence and increase of herbivores other than small rodents, such as hare and grouse (but possibly also voles). Consequently, this is likely to increase the overall biomass, diversity and stability of herbivore prey for carnivores, possibly leading to establishment of novel, invasive species, such as the red fox. Invasion of novel predators have been shown to have dramatic effects on the structure and functioning of food webs (Roemer et al. 2002). However, the establishment and success of invasive species seem to be connected to the complexity of the “target” food web, in the sense that more diverse food webs limits the establishment of invaders (Kennedy et al. 2002). Accordingly, tundra ecosystems may be particularly sensitive to such invasions due to their simplicity. Additionally, climate warming is likely to result in dramatic changes in the population dynamics of key prey species (e.g. small rodents) on the tundra, especially through events that affect snow and ice conditions (Callaghan et al. 2004e). Being at the top of the food chain and with their specific adaptation to the seasonal and multi-annual fluctuations of tundra ecosystems native predators, such as the arctic fox, may therefore be particularly sensitive to such changes (Callaghan et al. 2004e; Fuglei & Ims 2008; Ims & Fuglei 2005; Voigt et al. 2003).

### **Small rodents and arctic fox**

The predominance of population cycles in the north appears to be strongly linked to long, cold and stable winters (Hansson & Henttonen 1988), and should therefore be vulnerable to climate change. Thus, as climate becomes warmer there are reasons to believe that the population cycles of small rodents will become less regular and even disappear. Accordingly, it has recently been reported of changes in small rodent population dynamics through large

parts of Fennoscandia, mainly involving declining spring densities of key vole species (Ekerholm et al. 2001; Hörnfeldt 2004; Hörnfeldt et al. 2005; Yoccoz et al. 2001), extended periods without distinct peak years in lemmings (Oksanen et al. 2008; Tannerfeldt et al. 2002), and recently loss of cyclicity in lemmings furthest south in the Fennoscandian mountain tundra (Kausrud et al. 2008). The recent tendency of more shifts between warm and cold periods during winter, resulting in repeated freeze-thaw events (i.e. ice crust formations), is likely to be detrimental to small rodents that depend on food located in the snow pack close to the ground (Korslund & Steen 2006; Yoccoz & Ims 1999; Aars & Ims 2002). Of the different small rodent species, lemmings may be particularly sensitive to such incidents of ice-crust formations since they almost entirely depend on moss during winter, which is likely the first vegetation to become encapsulated by ice. Voles, on the other hand, may be less vulnerable since they forage on other types of plants (e.g. shrubs) that often will extend above the lower ice crust. Although these changes in rodent dynamics have coincided with the recent decline in the Fennoscandian arctic fox (Ims & Fuglei 2005; SEFALO 2004) and other predators connected to the tundra (e.g. Rough-legged buzzard: Kjellen & Roos 2000; Snowy owl: Marthinsen et al. 2008), the direct connection has yet to be demonstrated. Predators located on the tundra possess particular adaptations to the “boom and bust” nature of the tundra, such as the high reproductive output connected to small rodent peak years. This high reproductive output seems like a necessity in sustaining a decent population number until the next small rodent peak. Consequently, missed or low amplitude small rodent peak years may thus pose a major demographic challenge (e.g. low litter size) for small rodent specialists like the arctic fox, eventually resulting in a pronounced decline. However, in an attempt to preserve such species it is important to identify which aspects of the underlying prey dynamics (e.g. periodicity, amplitude or mean density) are likely to be most crucial to the arctic fox, as this may provide guidelines for how to adequately characterize and monitor prey dynamics and, more importantly, provide information on where to concentrate management efforts. Thus, in paper III, we address how the mean, temporal variance and the periodicity of small rodent population density cycles impact long-term stochastic growth rate of arctic fox populations. We do this in a modeling framework where the vital rates of the fox are linked to realistic, quantitative realizations of small rodent density dynamics.

### **Arctic fox – In contest with larger predators**

The arctic fox is a small-sized predator that is an inferior competitor, and may even serve as a prey to many other carnivores, such as snowy owls, wolverines, eagles, red fox and wolves.

Increased ecosystem productivity, due to increased cover of shrubs on the tundra, will lead to invasion of more southerly-distributed species acting as competitors and predators of the arctic fox. Most important in this context is the larger sized red fox (*Vulpes vulpes*). Arctic and red foxes are sympatric in a narrow overlap zone in the low Arctic (Hersteinsson & Macdonald 1992). As with other closely related canids (Clark et al. 2005; Fedriani et al. 2000; Nelson et al. 2007; Switalski 2003), competition between arctic fox and red fox can be expected to be fierce. Indeed, many studies have indicated that the red fox can expel the arctic fox in cases where their distribution range comes to overlap (Chirkova 1968; Killengreen et al. 2007; Linnell et al. 1999; Tannerfeldt et al. 2002). The importance of competition between the two fox species has been particularly emphasized in Fennoscandia where the decline of the arctic fox to near extinction have, at least partly, been attributed to the expansion of the red fox into the mountain and southern arctic tundra (Kaikusalo & Angerbjörn 1995; Killengreen et al. 2007; Tannerfeldt et al. 2002). In regions where vole and lemming cycles prevail, both fox species prey to a large degree on small rodents (Elmhagen et al. 2002). Thus, both species respond numerically to rodent dynamics and can themselves exhibit population cycles that mirror the cycle of their rodent prey (Angerbjörn et al. 1995; Butler 1951; Elton 1942). However, while the arctic fox appears to be a resident rodent specialist in inland tundra ecosystems (Angerbjörn et al. 1999), the red fox is capable of utilizing a greater span of suitable habitats, for instance, the boreal forest (Hersteinsson & Macdonald 1992). As a result, the red fox is capable of displaying a functional response in both habitat and prey when such alternatives are available. Such differences in terms of the degree of specialization on habitat and prey, in turn affects predators numerical and functional responses (Andersson & Erlinge 1977; Gilg et al. 2003; Krebs et al. 2001b; Wiklund et al. 1999). Consequently, to assess the outcome of asymmetric competition in such a system one must consider the underlying prey dynamics as well as the competing predators' numerical and functional responses to the prey cycle. For instance, if the dominant predator species (i.e. red fox) operates as a typical resident specialist (cf. Andersson & Erlinge 1977), and responds numerically to the prey cycle (i.e. with a time-delay), the largest effect on the subdominant competitor (i.e. arctic fox) could be expected in the crash phase of the prey cycle. On the other hand, if the dominant species responds like a generalist that functionally shifts habitat and/or diet to track peak prey density populations (Korpimäki 1994), the greatest effect on the subdominant species could be expected in the increase and peak phases of the cycle. However, while the phases of the prey cycle with the most intense competition for different numerical and functional responses of the dominant predator may be rather

straightforward to deduce, the outcome in terms of long-term viability of the subdominant species, and thus the likelihood for species co-existence within guilds, is in need of more elaborate analyses. In Paper IV, we develop a model to predict how population dynamics of a dominant and versatile predator (red fox) may impact the long-term growth rate of a subdominant and less versatile predator (arctic fox).



**Figure 5.** Arctic and red fox with their common prey, the Norwegian lemming, in southern Arctic tundra at Varanger Peninsula, NE Norway.

### **Implications for conservation**

The present and future predicted changes in tundra ecosystems have implications for the conservation of tundra predators. Both changes in the dynamics of key prey as well as increased competition with invading species pose a great challenge for native species, such as the arctic fox. While the predicted changes could, in the long term, result in larger biomass and diversity of prey species for the arctic fox (see above), the short-term changes (i.e. collapse of small rodent cycles) are nevertheless capable of driving the arctic fox to extinction long before that happens. Moreover, due to the simplicity of tundra ecosystems in the sense of few enemies, competitors and available food resources, arctic animals have evolved relatively few traits related to predator avoidance and competition for resources (Callaghan et al. 2004b; Callaghan et al. 2004e). Hence, the increasing threat posed by the gradual invasion of the red fox, in the form of displacement of arctic fox from high-productive habitats (Tannerfeldt et al. 2002), will further limit prey availability and consequently viability of the arctic fox.

In an attempt to conserve the arctic fox the first aim would be to locate areas with remnants of small rodent cycles with moderate to high spring peak densities. Due to the close connection between small rodent density and the demography of arctic fox, such areas would constitute a prerequisite for successful recovery of the arctic fox. Moreover, management action aiming to reverse declines of endangered populations ought to explicitly take into

account factors that govern demography and temporal dynamics of the population in question (Bradbury et al. 2001). For instance, much can be gained by targeting management action to moments in time in which the population is most responsive to any given action. Specifically, for species with pronounced multi-annual population cycles, like the arctic fox, it might be expected that the effect of a management intervention will depend on the particular phase of the demographic cycle. Knowledge of such phase-dependency would enable managers to focus management action to specific “high-receptive” phases, making management action more effective both ecologically as well as financially. The latter is important due to the fact that most conservation endeavours are associated with limited funding. In Paper V we analyse, by means of modelling, to what extent demographic perturbations exhibit phase-dependent effects on arctic fox population growth. Based on this analysis we provide recommendations on how management actions could be temporally allocated as to be most effective.

## Methods

**Detailed description of the methods, results and a more elaborate discussion are presented in the attached manuscripts referred to by their Latin number (I–V)**

### Second-order log-linear autoregressive (AR[2]) model

Paper I, II, III, IV and V:

The second-order log-linear autoregressive (AR[2]) model has played a prominent role in the analysis of cyclic dynamics (Bjørnstad et al. 1995; Royama 1992; Stenseth 1999) including changes in cycle period and collapse of cyclicity in time and space. The model is written as:

$$(X_t - \beta_0) = \beta_1(X_{t-1} - \beta_0) + \beta_2(X_{t-2} - \beta_0) + \varepsilon_t \quad \text{Eq. 1}$$

where  $X_t$  is the logarithm of population density in year  $t$ ,  $\beta_0$  is the intrinsic process mean (i.e. mean population density on log scale),  $1 + \beta_1$  is the coefficient of direct density dependence,  $\beta_2$  is the coefficient of delayed density dependence and  $\varepsilon_t$  denotes externally induced noise (i.e. environmental stochasticity). This model gives rise to sustained cycles for certain combinations of  $1 + \beta_1$  and  $\beta_2$ , given that  $\varepsilon_t > 0$  and  $\beta_2 < 0$  (Royama 1992; Shumway & Stoffer 2006).



**Paper I:**

In this paper the second-order log-linear model (AR[2]) is used to show the potential challenge of distinguishing between “normal” intrinsic variability and systemic changes due to some external force, in analyses of short ecological time series. In the framework of the second-order log-linear model the amount of extrinsic variance (i.e. the environmental stochasticity) quantified by the noise-term of the log-linear model ( $\varepsilon_t$  in Eq. 1), is an important determinant of the variance of both the cycle amplitude and period (Royama 1992). Accordingly, the inherent variability in stochastic log-linear systems sometimes leads to accidental deviations from the dominant cyclic pattern (i.e. periods of *transient dynamics*).

**Paper II:**

In this paper the second-order log-linear model (AR[2]) was used to assess spatio-temporal stationarity in density depend structure of time series of fox bounty statistics from all counties of Norway, covering a period of almost 100 years (1880-1976). From the second-order log-linear autoregressive (AR[2]) model (estimated using the Yule-Walker function (Kendall & Ord 1990) *ar.yw* in R (R Development Core Team, 2006)) we extracted, for each county (i.e. time series) and time period (three time periods), coefficients of direct DD ( $1+\beta_1$ ) and delayed DD ( $\beta_2$ ). To provide a flexible visualization of the geographic pattern in the extracted period-specific DD coefficients they were regressed against latitude using additive models (i.e. GAM) (Wood 2006). The reason for the choice of the framework of second order log-linear models was to provide a direct comparison to the seminal study of Bjørnstad et al. (1995) on which much of the current knowledge of gradients in population cycles is based. In their paper they provided similar plots of autoregressive parameters and cycle period lengths as used in paper II, but for a more recent time period.

**Paper III, IV and V:**

In paper III the second-order log-linear model (AR[2]) is used as a tool to generate the small rodent dynamics (function *arima.sim* in the software R (R Development Core Team 2006)) in the context of modelling the resultant resource driven demography of arctic fox. To highlight different aspects of the temporal and spatial trends in small rodent dynamics in Fennoscandia, we parameterized Eq. 1 to investigate three aspects of the dynamics: (i) cycle period, (ii) the process mean of the rodent density ( $\beta_0$ ), and (iii) externally induced variance in rodent density ( $\sigma^2_\varepsilon$ ). Specifically, we chose parameters to yield a 3\*3\*3 design with cycle period of 3, 4 and 5 years,  $\beta_0 = 2.1, 2.3$  and  $2.5$  (on log scale) and  $\sigma^2_\varepsilon = 0.1, 0.2$  and  $0.3$ .

In paper IV and V we parameterized Eq. 1 to yield small rodent dynamics with a typical 4 year periodicity.

## **Wavelet and Spectral analysis**

### **Paper I:**

In nature, non-linear and non-stationary processes are the rule rather than the exception, and many classical tools for time series analysis, such as Fourier analysis, require stationarity. Wavelet analysis (Torrence & Compo 1998) employs a time-scale and/or time–frequency decomposition of the signal (e.g. an ecological time series) that overcomes these problems and provides a powerful tool for analyzing non-stationary, aperiodic and noisy signals often found in ecological time series (Torrence & Compo 1998). Wavelet analysis was used in this paper to show the significance of the periodic signal (i.e. 4 year periodicity) and the temporal change in the signal (via 3 year periodicity), by period shortening, towards a dampened non-cyclic dynamics in the time series of boreal gray-sided vole from Northern Sweden (Hörnfeldt et al. 2005).

### **Paper II:**

In this paper an initial investigation of each of the time series' wavelet spectra (Torrence & Compo 1998) was made as to assess whether significant temporal changes in the time series not captured by periodic divisions and analysis was missed (see below). This seemed not to be the case. However, while wavelet analysis might provide a very good scope for exploring the details of changes in separate time series (e.g. Grenfell et al. 2001; Paper I), they provide however no simple means for quantitative comparisons of the panel of multiple time series (Rouyer et al. 2008) analysed in paper II. Thus, we used spectral analysis to assess cyclicity and estimate periodicity in three distinct time periods within the entire time frame of the fox bounty series.

Spectral analysis (Kendall et al. 1998) was implemented by using the function *spec.pgram* in R. This function calculates the periodogram using a fast Fourier transform (fft) (i.e. decomposing a sequence of values into components of different frequencies) of the time series. We estimated the spectra of the different time series using the smoothed (i.e. average) periodogram (Shumway & Stoffer 2006) and focused on the dominant spectral peak in the smoothed spectrum with frequencies corresponding to the range in cycle period length in Fennoscandia (i.e. 3-5 years). For instance, if the dominant spectral peak was located at a

frequency of 0.25 (frequency per cycle) this means that the dominant period length is 4 years ( $0.25 = 1/4$  years etc.).

## **Spatial covariance – Synchrony in population dynamics**

### **Paper II:**

Due to the expected connection between “common pattern” (i.e. signals oscillating with the same periodicity) and large scale synchrony (Bjørnstad 2000; Kendall et al. 2000), we performed analysis of spatial synchrony on cyclic and non-cyclic time series separately. We used the classification of cyclic and non-cyclic time series derived from the spectral analysis as the basis for this analysis. To analyse spatial synchrony, we used the nonparametric spatial covariance function (Sncf) from the package *ncf* (Bjørnstad & Falck 2001) written for R, where splines are applied to estimate the (average) spatial covariance based on the pairwise cross-correlation coefficients calculated from the time series.

## **Mathematical model**

### **Paper III, IV and V:**

#### **General modelling framework**

The general framework of the model consists of two (Paper III and V) or three (Paper IV) interlinked compartments (Figure 6). The first model compartment provides realizations of small rodent prey dynamics, by means of AR[2] models, that phenomenologically simulate the characteristics (i.e. cycle period and amplitude) of typical vole and lemming cycles (Stenseth 1999). The second compartment links the small rodent dynamics to a model predicting the population growth rate of the arctic fox. In paper IV, a third compartment is added where small rodent dynamics is linked to a model predicting the abundance dynamics of the red fox, which further form the basis for intraguild competition with arctic fox. The growth of the arctic fox population, and the abundance of red fox, is predicted by the use of projection matrix models (Caswell 2001) where the vital rates (species specific) are made functions of the prevailing abundance of small rodents. In our modelling framework the arctic fox-small rodent relationships is driven as a bottom-up resource-consumer dynamics with no feedback from the consumer (i.e. the arctic fox) on the resource (i.e. the small rodent populations).

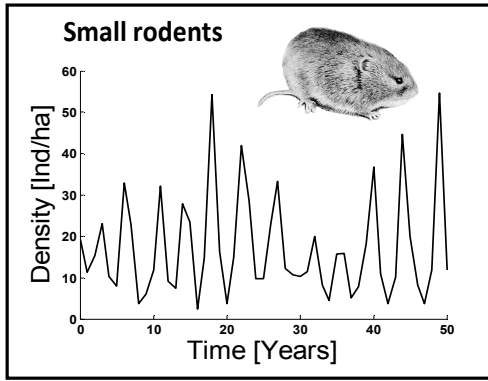
**Paper I:**

In this paper a two compartment model (i.e. compartment 1 and 2) is used to address how changes in the mean, temporal variance and the periodicity of small rodent population density cycles impact long-term stochastic growth rate of arctic fox populations. This is done to address which aspects of the recent changes in small rodent dynamics, seen over large parts of Fennoscandia (Paper I), might be most devastating for arctic fox long-term population growth (i.e. viability).

**Paper IV:**

In this paper we use the three compartment model (Figure 6) to predict how population dynamics of a dominant and versatile predator (red fox) may impact the long-term growth rate of a subdominant and less versatile predator (arctic fox). We compare three realistic scenarios of red fox performance: (1) *A numerical response scenario* where red fox act as a resident rodent specialist exhibiting population cycles lagging one year after the rodent cycle (i.e. similar to that of arctic fox), (2) *a functional response scenario* where red fox shift between tundra and a nearby ecosystem (i.e. boreal forest) so as to track rodent peaks in tundra without delay, and (3) *a constant subsidy scenario* in which the red fox population is stabilized at the same mean density as in the other two scenarios, by some external subsidy such as reindeer. For all three scenarios it is assumed that the arctic fox respond numerically as a rodent specialist and that the mechanisms of competition is of a interference type, in which the arctic fox is excluded from the most resource rich patches in tundra. We assume that red fox affects arctic fox demography by reducing (i.e. % reduction, Figure 4) the amount of resources available for arctic fox.

**Compartment 1**



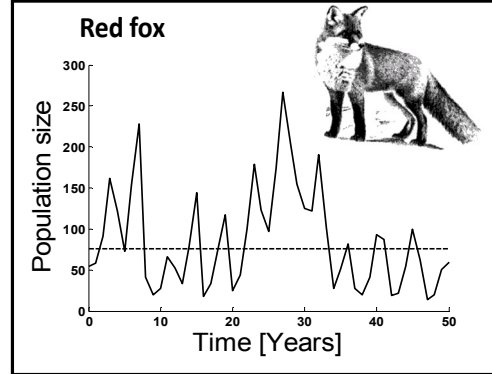
Stochastic auto-regressive rodent model

$$(X_t - \beta_0) = \beta_1(X_{t-1} - \beta_0) + \beta_2(X_{t-2} - \beta_0) + \varepsilon_t$$

1. Numerical response
2. Functional response

3. Constant subsidy

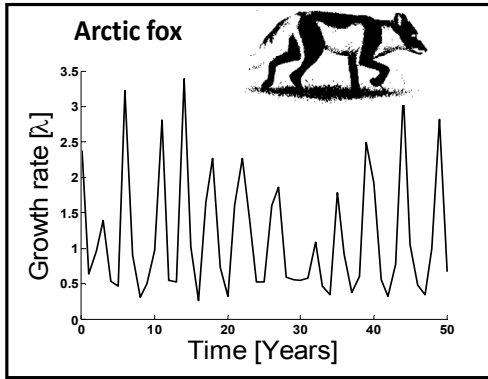
**Compartment 3**



Demographic red fox model

$$\begin{bmatrix} 0.5 * S_{juv} * LF_{juv} * PB_{juv} & 0.5 * S_{juv} * LF_{ad} * PB_{ad} \\ S_{yl} & S_{ad} \end{bmatrix}$$

**Compartment 2**



Demographic arctic fox model

$$\begin{bmatrix} 0.5 * S_{juv} * LF_{juv} * PB_{juv} & 0.5 * S_{juv} * LF_{ad} * PB_{ad} \\ S_{yl} & S_{ad} \end{bmatrix}$$

**Figure 6. Schematic representation of the model framework.** Compartment 1 hold the small rodent time series generated from the stochastic second-order autoregressive model. Compartment 2 hold the resulting population growth rate of arctic fox, where vital rates are made functions of the prevailing small rodent density (compartment 1). Compartment 3 gives the fluctuations in population size of red fox, based on the prevailing density of small rodents (i.e. for the numerical and functional response scenarios). However, in compartment 3 there is also a scenario where external subsidies result in a stable density of red fox (i.e. constant subsidy scenario). In paper IV, we assume that red fox affect arctic fox demography by reducing (i.e. % reduction) the amount of resources available for arctic fox.

**Paper V:**

In this paper we use the two compartment model to evaluate the phase-dependent effect of demographic perturbations (i.e. management action) on the growth rate of arctic fox. We assume that management action affect the population growth rate of arctic fox by increasing

the amount of resources available to the arctic fox. In the model this improvement is mediated through a change (i.e. percentage increase) relative to the baseline demographic rates as determined by the prevailing small rodent density (Figure 1 in Paper V). Due to the lack of knowledge about how management actions actually work to improve arctic fox vital rates, two contrasting scenarios of increased resource availability resulting from management action were tried. Management actions were then directed to each phase of the demographic cycle of arctic fox separately. We also distinguish between the effects of management action (of some sort) capable of affecting reproductive parameters (i.e. vital rates) and those capable of affecting survival parameters only, as well assessing the possibility that the magnitude (i.e. proportional increase) of the management induced increase in resource availability may have a disproportional effect on arctic fox growth rate. This is done by simulating and comparing three levels of the magnitude of change in the response scenarios (i.e. *diminishing return scenario* (maximum levels): 20%, 50% and 100%, *constant scenario*: 10%, 25% and 50%).

## **Results and Discussion**

### **The collapse of cycles (Paper I)**

The many cases of collapsing cycles, in small rodents and in some other herbivores such as forest grouse and insects, occurring at the end of the last century are exceptional in the sense that they are more widespread and simultaneous than would be expected from a coincidental accumulation of independent events (i.e. transient periods due to intrinsic systemic variability). Collapsing cycles in some of the longest time series available, and thorough analyses of the processes of change in spatially extensive datasets, have shown compelling connections to climatic warming. Moreover, the consistency between the recent demonstrations of shifted dynamics and the largely analogous, well-known spatial transitions adds significantly to the weight of evidence for a common climatic cause. Our interpretation of the space–time connection is that the geographical borders between cyclic and non-cyclic populations currently are on the move following changing climatic isoclines and that the areas with cycles in boreal and arctic regions are shrinking. Exactly how climate change interacts with population dynamics in each case is likely to differ between taxa and ecosystems. However, in small rodents it seems to be linked to changes in the quality of winter conditions (i.e. Fennoscandia) (Korslund & Steen 2006; Aars & Ims 2002) or the length of winter (i.e. northern England) (Bierman et al. 2006). In the former, an increasing frequency of melting-freezing events in northern areas due to increased climatic variation

might have shifted the winter dynamics into a regime in which weather-induced mortality overrides density-dependent processes. In the latter, however, shorter winters may lead to the collapses of vole cycles through a reduction of delayed density dependence in the rate of change over the winters (Bierman et al. 2006).

### **Non-stationary small rodent dynamics (Paper II)**

Based on the analysis of exceptionally long-term and large-scale fox bounty data from Norway, we demonstrate that the dynamics of northern voles and lemming, which is a major component of the community dynamics of boreal and arctic regions (Ims & Fuglei 2005), have been liable to substantial transitions of their spatial–temporal dynamics over the last century. In the first period of these time series (period 1 in our analysis (1880-1910)), there was a clear geographical separation between cyclic and non-cyclic populations in Norway, where non-cyclic dynamics was located on the southernmost tip of Norway and spatially synchronous, uniform 4-year cycles dominated most of Norway (north of 60°N). This clear latitudinal separation of cyclic and noncyclic populations was also reflected in a south-north gradient of increasingly negative delayed DD, implying larger amplitudes of the dynamics towards the north (also north of 60°). In the second time period (1911-1932), a less clear geographical separation between cyclic and noncyclic populations became apparent. While cycles still prevailed in the northern and central parts of Norway, cycle period diversified according to a geographical pattern with prevalence of short population cycles (3 year) in the south and long cycles (5 year) in the very north. As expected (Bjørnstad 2000; Kendall et al. 2000), the diversification of cycle period was associated with a decrease in the extent of spatial synchrony among the cyclic populations. In the last time period (period 3 (1948-1976)), the number of populations displaying cyclic dynamics dropped as populations with the shortest and longest periodicities in the preceding period (period 2) turned non-cyclic. Correspondingly, the geographical separation between northern cyclic and southern non-cyclic completely broke down in this period. The generally less cyclic dynamics in this last period was also reflected in a substantial increase in direct DD in the time series.

The patterns found in this study, especially in time period 1 and 2, conform to earlier studies by Steen et al. (1990) and Bjørnstad (2000), who analysed Wildhagen's (1952) qualitative data on small rodents for the presence of cyclicity and spatial synchrony. They found statistical evidence for cyclicity and large-scale synchrony of the cycles in a period equivalent to period 1 in this study, but on a regional scale. This shifted into non-cyclic dynamics with no evidence for large-scale synchrony in the next period (i.e. equivalent to

period 2). However, analyzing the fox series which had a better resolution it could be shown that the loss of synchrony was due to diversified cycle period length (though cyclic) on the level of counties in central and northern areas. The data analysed by Steen et al., (1990) and Bjørnstad (2000) also spanned into the period not covered by the fox time series analysed here (i.e. 1933-1947). Their analysis of this period showed that the dynamics returned to more pronounced cyclicality and spatial synchrony. In the subsequent period (i.e. period 3, 1948-1976) our analysis shows that the dynamics changed once more towards larger areas of non-cyclic dynamics and weak synchrony. Thus, spatial patterns in cyclicality and cycle period length, as well as equivalent spatial patterns in DD structure, appear not to be stationary on time-scales longer than a few decades.

The recent changes documented in Fennoscandian small rodents (Paper I) seem to fit into this picture of non-stationary dynamics quite well, where the area of non-cyclic dynamics now seems to have become larger than what has been apparent in the last century. The recent changes have been proposed to stem from milder and shorter winters interfering with the density dependent processes underlying cyclic population dynamics (Paper I and references therein). Accordingly, while we have not tested the role of climate specifically in these analyses, the transitions in spatio-temporal dynamics documented in this paper seem to correspond to the alternations between relatively cold and warm periods during the 20<sup>th</sup> century (Beck et al. 2007; Nesje et al. 2005).

### **Aspects of changed prey dynamics on the viability of arctic fox (Paper III)**

Arctic fox population growth rate was found to be highly sensitive to the temporal mean and to some extent to the variance in small rodent density cycles, whereas cycle period in the observed range of 3- to 5-year cycles was surprisingly of minor importance. The relatively insignificant effect of cycle period length may appear counterintuitive in the sense that a 5-year prey cycle would seem to be a much greater demographic challenge to a relatively short-lived species than a 3-year cycle. However, given the same temporal mean rodent density, a long-waved cycle is likely to offer more breeding opportunities for arctic foxes between the cyclic peak years than a more short-waved cycle. This seems to compensate to a large degree for the extended duration between peak years of a long-waved cycle. The positive effect of mean prey density does not need any further explanation in light of the strong positive relationship between arctic fox vital rates and prevailing prey density. The effect of the temporal variance of rodent density fluctuations on fox population growth is, however, more intricate, as it interacted with mean rodent density. The largest effect of externally induced



variance was at low rodent densities, where increased variance acted to increase arctic fox population growth. This result appears to contrast with most modeling studies, which have demonstrated that increased year-to-year variation in vital rates will act to decrease long-term stochastic growth rate (Morris & Doak 2002; Tuljapurkar 1989). However, in contrast to previous studies we entered temporal variance indirectly through rodent population dynamics, not by implementing stochasticity directly on the vital rates. Thus, due to the logistic relationship between rodent density and fox vital rates, increased variance of the rodent dynamics translate non-linearly to either increased or decreased mean and/or variance of fox vital rate depending on mean rodent density (Jensen's inequality; see Fig. 4 in Paper III, for a graphic demonstration). In particular, at low rodent densities, increased temporal variance will act to increase mean fox vital rate, and the positive effect resulting from the increased mean will dominate over the negative effect of the increased variance in the vital rates.

Our analysis shows that small rodent population dynamics characterized by low-amplitude density cycles (irrespective of cycle period length), provide little scope for positive population growth, and thus recovery, of the arctic fox. The recent changes in small rodent dynamics seen over large parts of Fennoscandia thus seems sufficient to explain the recent decline of the arctic fox. Thus, we advise that management actions such as re-introductions and red fox control should be conducted in mountain tundra regions where regular, high-amplitude cycles, of any period, with recurrent high spring densities of rodents still prevail. In order to properly identify geographic areas with the highest potential for arctic fox recovery, the emphasis of current monitoring programmes of small rodent dynamics needs to consider more quantitative metrics than they currently employ.

#### **Interference competition between arctic and red fox (Paper IV)**

Arctic fox is impacted most by the constant subsidy scenario and least by the numerical response scenario. The differential effects of the scenarios stemmed from cyclic phase-dependent sensitivity to competition, mediated by changes in temporal mean and variance of available prey to the subdominant predator (i.e. arctic fox). A general implication from our result is that external resource subsidies (prey or habitats), monopolized by the dominant competitor, can significantly reduce the likelihood for co-existence within the predator guild. In terms of conservation of vulnerable arctic fox populations this means that the likelihood of extinction increases with increasing amount of ungulate carcass in tundra and nearby forest areas, since this will act to both increase and stabilize populations of red fox.

### **Phase-dependent effect of conservation effort (Paper V)**

By using a model in which the management action improved arctic fox vital rate through increased resource availability, we show that arctic fox population growth was most improved when management action was applied in the increase and decrease phase of the cycle. Except in the low phase of the cycle, the growth rate was more affected when the management action worked through improved reproduction than through improved survival. There was a synergistic effect to be gained by performing management action during multiple phases during a demographic cycle. Thus, it is recommended that arctic fox conservation programs ought to be continuous in time, but with the highest intensities of management action in the phases of the cycle in which the target population is most prone to respond.

### **Conclusion**

The arctic is currently subject to large changes capable of disrupting the structure and functioning of tundra ecosystems. Global warming, with the largest impacts expected in polar areas, has been highlighted as the major component of ecosystem change in this region. In this thesis I have explored how such changing circumstances may influence the biotic system of the tundra. I have especially focused on small rodent density cycles, which constitute a major component of the community dynamics of boreal and arctic regions, and the retreat of the arctic fox in Fennoscandia. The many cases of collapsing cycles that have recently occurred are exceptional in the sense that they are more widespread and simultaneous, transcending species and ecosystem borders, than would be expected from a coincidental accumulation of independent events. The evidence of collapsing cycles in some of the longest time series available as well as thorough analyses of the processes of change in spatially extensive datasets has shown compelling connections to climatic warming. Moreover, the consistency between the recent demonstrations of shifted dynamics and the largely analogous, well-known, spatial transitions adds significantly to the weight of evidence for a common climatic cause. Accordingly, it is now clear that the dynamics of northern voles and lemming, at least in Fennoscandia, have been liable to substantial transitions of their spatial-temporal dynamics over the last century, rarely stationary longer than a few decades. Thus, our analysis indicates that the collapse of small rodent cycles that recently has taken place in large parts of Fennoscandia appears to have some historical analogies. In all incidents, the shifts in dynamics patterns seem to concur with shifts between cold and warm climatic periods. Since the way climate change interacts with population dynamics is likely to differ

between species and systems, identifying the mechanism(s) will require hypothesis-targeted study approaches beyond the “process-naïve” monitoring normally giving rise to time-series data.

The recent changes in small rodent population dynamics, characterized by dampened, low-amplitude density cycles, likely have detrimental consequences for tundra predators that depend heavily on small rodents as food. Indeed, although the changes in dynamics in small rodents and other key-stone herbivores also have taken place outside the tundra, the knock-on effects on predators and possible alternative prey species is likely to be strongest in the setting of the arctic, with very simple food webs and strong trophic interactions. Yet, although the recent decrease of several tundra predators have coincided with the reported changes in small rodent density cycles, the direct connection has not been demonstrated. However, we have shown that the recent changes in small rodents is a sufficient explanation for the recent decline of the Fennoscandian arctic fox, as it provide little scope for positive population growth, and thus recovery. However, also other projected climate induced changes pose a threat to the existence of the arctic fox. We have here demonstrated the potentially devastating consequence for arctic fox viability of increased intraguild competition with the northward expanding dominant red fox, especially so if subsidies during winter is available for the dominant competitor. Finally, we have shown that predator populations with demographic cycles driven by multi-annual cycles of their key prey resource are likely to be “cyclic phase sensitive” to management actions. To be successful, management actions such as re-introductions and red fox control should thus be conducted in mountain tundra regions where regular, high-amplitude cycles, of any period, with recurrent high spring densities of rodents still prevail. Moreover, any conservation programs aimed at conserving tundra predators ought to be continuous in time, but with the highest intensities of management action in the phases of the cycle in which the target population is most prone to respond. To identify potential hot-spots of favorable prey dynamics, adequate monitoring of small rodent populations is required. There is also a need to further the understanding on how resource availability translates into demographic rates of the arctic fox, the dynamic nature of the arctic – red fox interaction as well as an improved understanding of how specific management actions works as to improve vital rates.

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