Collapsing population cycles

Rolf A. Ims, John-André Henden and Siw T. Killengreen

Department of Biology, University of Tromsø, NO-9037 Tromsø, Norway

During the past two decades population cycles in voles, grouse and insects have been fading out in Europe. Here, we discuss the cause and implication of these changes. Several lines of evidence now point to climate forcing as the general underlying cause. However, how climate interacts with demography to induce regime shifts in population dynamics is likely to differ among species and ecosystems. Herbivores with high-amplitude population cycles, such as voles, lemmings, snowshoe hares and forest Lepidoptera, form the heart of terrestrial food web dynamics. Thus, collapses of these cycles are also expected to imply collapses of important ecosystem functions, such as the pulsed flows of resources and disturbances.

Introduction

Multi-annual population cycles (i.e. the regular, high-amplitude density oscillations displayed by some animal populations) are among the most studied and discussed ecological phenomena. Prime examples of cyclic population dynamics include the three–four-year cycles in voles and lemmings, the four–ten-year cycles in ptarmigan and forest grouse, and the nine–eleven-year snowshoe hare and forest insect cycles. Ecologically, population cycles, where they occur, have profound influences on the functioning of ecosystems. Population cycles are also important because they provide unique insights into the mechanisms of population and community dynamics. Modern textbooks exploit the examples of cyclic populations to introduce students to state-of-the-art theory of population regulation and trophic interactions, to analytical tools for analyzing ecological dynamics and to discussion of the effects of pulsed disturbance and flows on ecosystem structure and function.

However, there is now reason to believe that some of the most well-known examples of cyclic dynamics have become lessons of history rather than analyses of contemporary ecology. During the past two decades, cycles in voles, forest grouse and forest insects have been fading out in Europe. The first indications of such changes were published during the mid-1990s [1–3], although their significance then was questioned [4]. Here, we provide an updated evaluation of the phenomenon of collapsing cycles, in the light of both the most recent empirical evidence and relevant insights derived from earlier research on population cycles. Although drifting in and out of cyclic dynamics might be expected to be within the range of normal nonlinear population dynamics, we argue that the recent events of collapsing cycles are more widespread and simultaneous than would be expected from an accumulation of independent events.

Modeling collapsing cycles

Mathematical and statistical modeling is a central issue in research on population cycles. The modeling literature is vast, but many useful syntheses have been made [4–7]. Models differ along a continuum from complex mechanistic models to rather simple phenomenological models. Whereas the mechanistic models are primarily used to deduce population dynamics from assumed or known biological mechanisms [5], the phenomenological models are mainly tools for inferring processes from patterns contained in population time series data [4,8].

Theoretically, there are at least as many ways that population cycles can be lost as there are ways that they can be generated. Mechanistic modeling has shown that population cycles can originate from many different types of nonlinear biological interaction, either intrinsic (e.g. maternal effects) or extrinsic (i.e. resources or enemies) to the populations [5]. However, the identity of the decisive interactions, even in much studied cases, such as the vole cycle, is still in dispute [9]. The precise empirical information needed for feeding mechanistic models, and thus for pinpointing the cycle-generating mechanism, can usually be obtained only from laboratory populations [10]. By contrast, data from natural populations are typically represented by short and noisy time series of crude indices of yearly abundance based on hunting bags, catch per effort or damage levels. Such data provide information that is amenable only to phenomenological analysis.

Inferences from log–linear modeling

The most influential phenomenological approach is stochastic log–linear models fitted to time series data by autoregression analysis. In this approach, population dynamics are interpreted in terms of different orders of density dependence. Recent studies have shown that second-order log–linear models (Box 1) parsimoniously describe the population dynamics for a wide range of species and ecological settings. In this model, the first-order term quantifies direct density dependence, which phenomenologically represents population self-regulation or predator functional response. The second-order term quantifies delayed density dependence and reflects trophic interactions (e.g. predator numerical response or pathogen dynamics). The magnitude of the direct and delayed density-dependent parameters determines whether the population displays cyclic oscillations and, eventually, the period and amplitude of the cycle. Incrementally changing the parameter values can lead to the collapse of cycles through period shortening or lengthening and/or amplitude dampening (Box 1). The second-order log–linear model has been instrumental in elucidating how cyclic

Corresponding author: Ims, R.A. (rolf.ims@ib.uit.no).

Box 1. Collapsing cycles in second-order log–linear models

The second-order, stochastic log–linear model has played a promi-
nent role in the analysis of cyclic dynamics [4,8,16,45], including
changes in cycle period and collapse of cyclicity in time and space.
The model is written as Equation I:

$$x_t = \beta_0 + \beta_1 x_{t-1} + \beta_2 x_{t-2} + \varepsilon_t, \qquad \text{(Equation I)}$$

where x_t is the logarithm of population density in year t, β_1 and β_2 are
the parameters of the direct and the delayed density dependence,
respectively, and ε_t is a noise term quantifying the stochastic variation
(e.g. in the environment). This model gives rise to sustained cycles for
certain combinations of β_1 and β_2, given that $\varepsilon_t > 0$. Figure I shows the
dynamics of the model as defined by two density-dependent
parameters.

   Proper multi-annual cycles (i.e. cycle period two years) occur in the
region under the thick semi-circle as defined by $(1 + \beta_1)^2 + 4\beta_2 < 0$.
The lines within the region of the semi-circle define isoclines of
different cycle periods (cycle periods >8 years are not shown). Arrows
and associated letters depict three ways by which cycles can collapse
into noncyclic dynamics. A: period lengthening by weakening of the
delayed density dependence (β_2); B: period shortening by strengthen-
ing the direct density dependence $(1 + \beta_1)$ and C: amplitude dampen-
ing with no change of a cycle period. Amplitude dampening will in
most cases be associated with weakened delayed density depen-
dence (e.g. alternative A).

   The magnitude of the noise term of the log–linear model (ε_t) affects
the variance of both cycle amplitude and period. Thus realizations of
the stochastic process might sometimes produce dynamics that
appear to deviate from a cyclic pattern (Figure II) especially if the
noise term is large.

   Usually log–linear models are fit by autoregression analysis (e.g.
autoregressive moving average (ARMA) models [16]) to time series
on the basis of annual population indices. However, if more than one
population index per year is available (e.g. spring and autumn
indices), the analysis can be elaborated so that the density-dependent
parameters can be made conditional on season (summer and winter)

[28,46,47]. This elaboration has been helpful for highlighting the
expected outcome of climate change. For instance, if delayed density
dependence acts primarily over the winter *season*, shorter winters
are expected to dampen cycle amplitude. Moreover, continuously
time varying parameters can be fitted to explore the extent to which
the density-dependent structure and the period of the cycle change
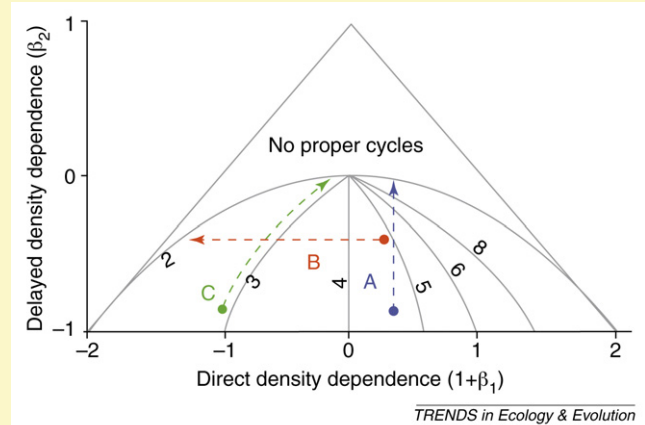through time (Figure 4, main text).

Figure I. The parameter plane of the second-order log–linear model showing the
region with proper multi-annual cycles (under the semi-circle). Curved isoclines
under the semi-circle show parameter combinations with different cycle periods
in years (periods >8 years are not shown). Colored broken arrows labeled with
capital letters indicate three alternative routes towards collapse of cyclic
dynamics. Blue arrow **(A)** shows decreased delayed density dependence and
period lengthening. Red arrow **(B)** shows increased direct dependence and
period shortening. Green arrow **(C)** shows a decrease in both direct and delayed
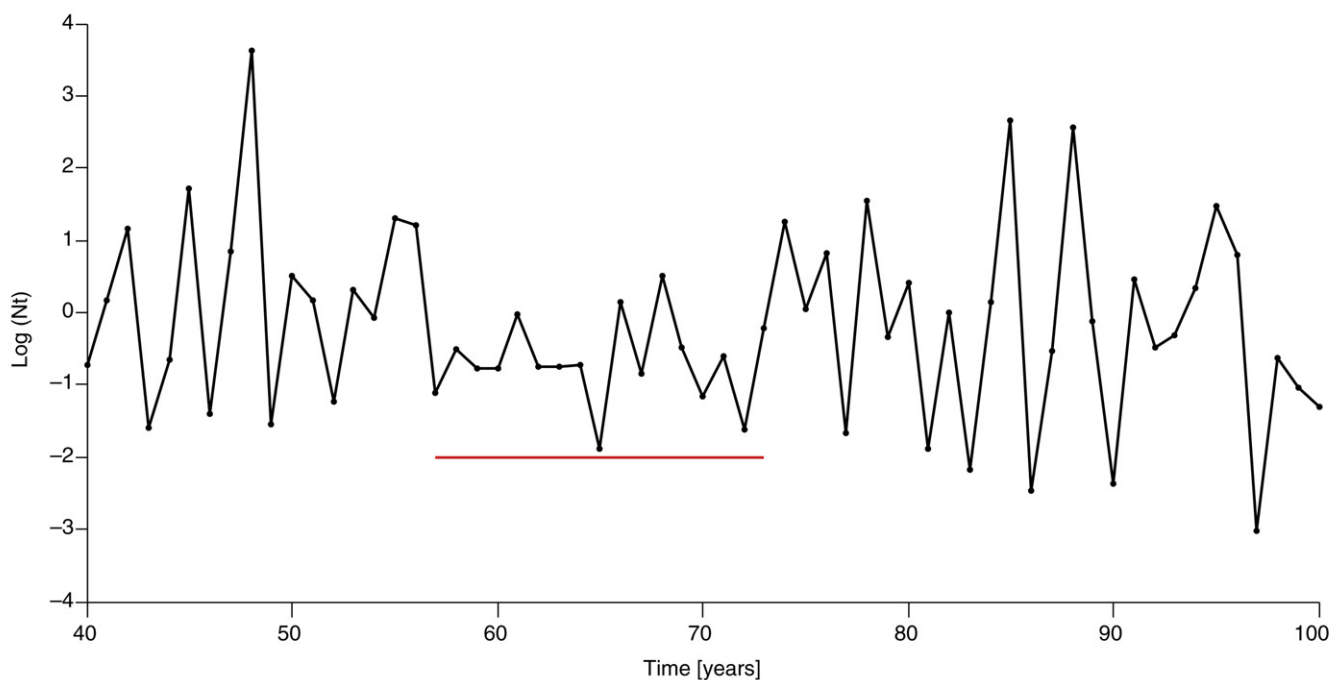density dependence without any change in the three-year period before the cycle
disappears.

Figure II. Simulated time series of population density (N_t) from a model with parameter $(1 + \beta_1) = 0$, $\beta_2 = -0.625$ and $e_t = 0.5$. According to the density-dependent
parameters, a four-year cycle is expected (Figure I). A high degree of stochasticity yields a period of transient, apparently noncyclic dynamics (denoted by the red line).

populations collapse in space and time based on time series data.

Collapsing cycles in space

More than eighty year ago Charles Elton was the first to realize that population cycles of snowshoe hares and voles were regionalized in the sense that they were mainly northern phenomena. His conjecture has been verified analytically and extended taxonomically to many species of mammals, birds and insects [11]. Although ecologists initially emphasized a north–south dichotomy between cyclic and noncyclic dynamics, the focus later changed to explore clinal geographical patterns, whenever panels of time-series data with adequate spatial coverage were available [12]. Such geographical clines in cycle amplitude or periodicity ending in 'spatial collapses of cyclicity' have now been demonstrated by log–linear autoregression analyses for different taxa and geographical areas (Table 1). In all these cases, there is a gradual amplitude dampening towards the regions where the cycles disappear. However, the cases differ with respect to whether the route towards loss of cyclicity is associated with a change in period duration and, eventually, whether period lengthening or shortening is involved (Table 1). For instance, in Fennoscandian voles, there is a period shortening from a five-year cycle in the northernmost region to a mainly three-year cycle in the south–central Fennoscandia, before the population cycle collapses into stable dynamics in the far south [13,14]. The period shortening is due to the increased strength of direct density dependence [15], which is attributed to an increased abundance of generalist predators towards the south [13]. In American forest grouse, the cycles appear to collapse towards the south by means of period lengthening and a decrease in the strength of delayed density dependence [16]. Moreover, in Hokkaido (Japan) the clinal period shortening in the gray-sided vole

Myodes rufocanus is due to a decrease in both direct and delayed density dependence [17].

Not all population cycles are boreal or arctic [18], neither do all spatial clines in cycle amplitude or period end in a southern collapse [19]. Thus, collapses of cycles in other directions occur along certain coast–inland gradients [19,20] or altitudinal gradients [21,22]. There seems, however, to be a common denominator for all the cases of spatial clines: the cycles appear to fade with shorter winters. In closing this short review of collapsing cycles in the spatial domain, we note that in the case of red grouse *Lagopus lagopus scoticus* in the UK, where both cyclicity and period duration appear to be regionalized, evidence for consistent clines in dynamics is at the best weak [23]. Moreover, the more erratic dynamics of the famous Norwegian lemming *Lemmus lemmus* (Figure 1) might not quite adhere to the general pattern of Fennoscandian voles [24], although period shortening towards the southern part of the mountain chain is suggested in this case too [25].

Collapsing cycles in time

The cases

Among all cases of cyclic population dynamics, the vole cycle in Fennoscandia is probably the most celebrated owing to the many long time series and the richly geographically patterned dynamics. The first recent incidence of a deviation from the 'normal Fennoscandian vole cycle' was reported from northern Finnish taiga two decades ago [26]. Soon similar events of missed cyclic peak years were reported to have taken place at approximately the same time (i.e. mid-1980s) over vast tracts of the boreal forest zone [1–3]. This initiated an era of regime shift in population dynamics, leading to a collapse of the boreal vole cycle. The aberrant dynamics has lasted until present and, thus, for a period of four–six cycles. The shifted dynamics

Table 1. Species and geographical areas with spatial clines in population dynamics from clear multi-annual population cycles to more stable dynamics within their distribution range

Species	Geographical area	Cline type[a]	Density dependence (DD)[b]	Proposed mechanism[c]	Refs
Myodes and *Microtus* voles	Fennoscandia	North–south amplitude dampening and period shortening	Increased direct DD	North–south gradient in winter season duration and number of generalist predators	[15]
Common vole *Microtus arvalis*	Central Europe	Inland–coast amplitude dampening	Decreased direct and delayed DD	Inland–coast gradient in winter season duration	[19]
Grey-sided vole *M. rufocanus*	Hokkaido, Japan	South–west north–east amplitude dampening	Decreased direct and delayed DD	South–west, north–east gradients in winter season duration	[17]
Ermine *Mustela erminea*	Canada	North–south amplitude dampening	Decreased delayed DD	Geographical cline in prey dynamics	[48]
Bonasa and *Tympanichus* forest grouse	North America	North–south period lengthening	Decreased delayed DD	Increased number of generalist predators towards the south	[16]
Tetrao, *Lagopus* and *Bonasa* grouse spp.	Europe	North–south amplitude dampening	Decreased DD	N/A	[49]
Snowshoe hare *Lepus americanus*	North America	North–south amplitude dampening	Decreased DD	Increased amount of generalist and environmental heterogeneity towards south	[50,51]
Autumnal moth *Epirrita autumnata*	Fennoscandia	North–south amplitude dampening and less regular outbreaks	N/A	Increased number of generalist parasitoids and predators towards the south	[52]

Abbreviation: N/A, not available.
[a]Described with respect to direction and change in density dependence (DD) towards regions with collapsed cycles.
[b]Estimated by log–linear time series analysis in all studies.
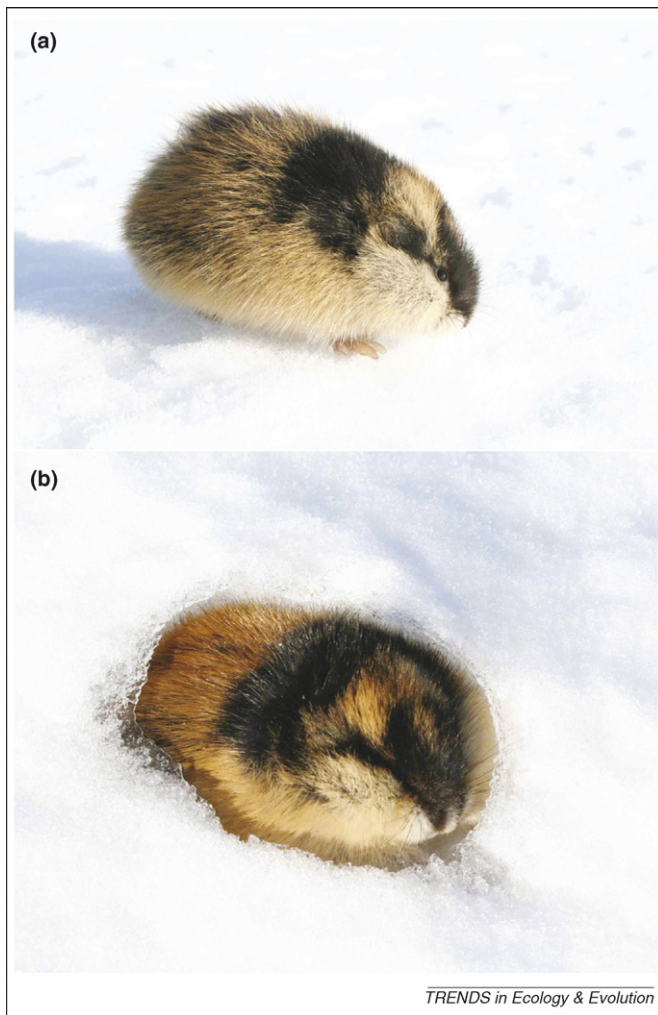[c]Noted when such a proposition was available.

Figure 1. (a) Live and (b) dead Norwegian lemmings *Lemmus lemmus* on the snow surface in the Norwegian Arctic in March 2007. Although the Norwegian lemming has become famous for its three–five-year population cycles [4], these cycles have typically been less stable than those of other sympatric small rodent species (i.e. voles) in alpine and arctic tundra [24,25,27]. When lemming population outbreaks occur, they are generally synchronous with those of sympatric vole species [24]. However, Norwegian lemmings are quite frequently missing in the research catches in the summer of small rodent peak years [24,27]. In such years, there have sometimes been signs of a build-up of the lemming population in the preceding winter, but observations of live and dead lemmings on the snow have coincided with population crash. It has been suggested that Norwegian lemmings are especially sensitive to variation in winter climate conditions [25]. One reason for this might be that they rely on mosses as their main winter food, whereas arctic–alpine voles rely mainly on vascular plants. As the lowest vegetation stratum, mosses are probably more readily locked in ice after mild spells [37,38] than are the more erect vascular plants. Photographs: Rolf A. Ims.

in the boreal forest later appeared to expand northwards to other ecosystems. In subarctic birch forest in north-western Finland, where the time series extends back nearly 60 years, the cyclic peaks have been missing since the early 1990s [27]. In hemi-arctic Norwegian tundra even further north, a five-year cycle in voles still prevails, but now has distinctly shifted to lower spring densities and dampened cycle amplitude [24]. Population cycles have also prevailed, at least until recently, in some other localities in Fennoscandia (e.g. see Ref. [20]). However, the overall picture from Fennoscandia is that the vole cycle has collapsed over vast areas, in particular in forested ecosystems.

Outside Fennoscandia, there is statistical evidence for recent collapses of vole cycles in northern England [28] and

central Europe [18]. Recent regime shifts between cyclic and noncyclic dynamics in the Japanese gray-sided vole occurred between the late 1970s and the early 1990s on Hokkaido [29]. Unfortunately, there are no reports on how gray-sided vole dynamics have developed in Hokkaido since then. There is no statistical evidence for collapsing vole cycles in North America. This might be due to the scarcity of continuous long-term population time series from the northern taiga and arctic tundra, which were the regions where the North American vole and lemming cycles were known to prevail [4]. There are also fewer reports on collapsing cycles in taxa with longer cycle periods than the three–five-year vole cycle. Obviously, demonstrating altered dynamics in populations with long cycle periods will require longer time series. Nevertheless, the six–seven-year cycle in Finnish black grouse *Tetrao tetrix* became noncyclic during the mid-1980s [30]. At the same time, the cyclic mass outbreaks of the larch budmoth *Zeiraphera diniana* in the European Alps were lost or severely dampened [31]. The latter case is exceptional as it could be demonstrated that the recent gap in the astonishingly regular nine-year moth outbreak clockwork is the first and only for a period of 1200 years (Figure 2).

Patterns of transition in time

Whereas the shift from cyclic to noncyclic dynamics appeared to happen abruptly in some cases, it was preceded by a period of gradual amplitude dampening in others (Table 2). The most astonishing example of gradual amplitude dampening before loss of cyclicity is from Birger Hörnfeldt's spatially extensive monitoring program of boreal voles in northern Sweden (Figure 3). Statistical evidence for change in period duration (i.e. period lengthening) preceding the collapse of the cycle has so far been reported only for the field vole *Microtus agrestis* in northern England [28] (Figure 4). Demonstrating shifts in cycle period in the temporal domain requires sophisticated statistical analyses [28,29] and adequate data. The clearest demonstrations of gradual temporal change (e.g. see Refs [28,30,32]) are based on data obtained from population monitoring with extensive spatial sampling frames. Thus, the apparent discrepancy between the abrupt and gradual transitions can to some extent originate from spatial averaging of locally asynchronous collapses. Cyclicity and spatial synchrony appear to be intertwined [33]. Consequently, in northern England [28] and northern Fennoscandia [27], temporal loss of cyclicity was associated with loss of spatial synchrony.

Collapsing cycles: a case for intrinsic systemic variability?

Except in the extreme case of the larch budmoth (Figure 2), all other cases of collapsing cycles have been demonstrated in time series shorter than 60 years, usually shorter than 30 years. Obviously, the duration of the time series constrains empirically based inferences about the causal mechanism. A challenge is thus to distinguish between 'normal' intrinsic variability and systemic changes due to some external force. The inherent variability in stochastic log–linear systems sometimes leads to accidental deviations from the dominant cyclic pattern (Box 1). However,
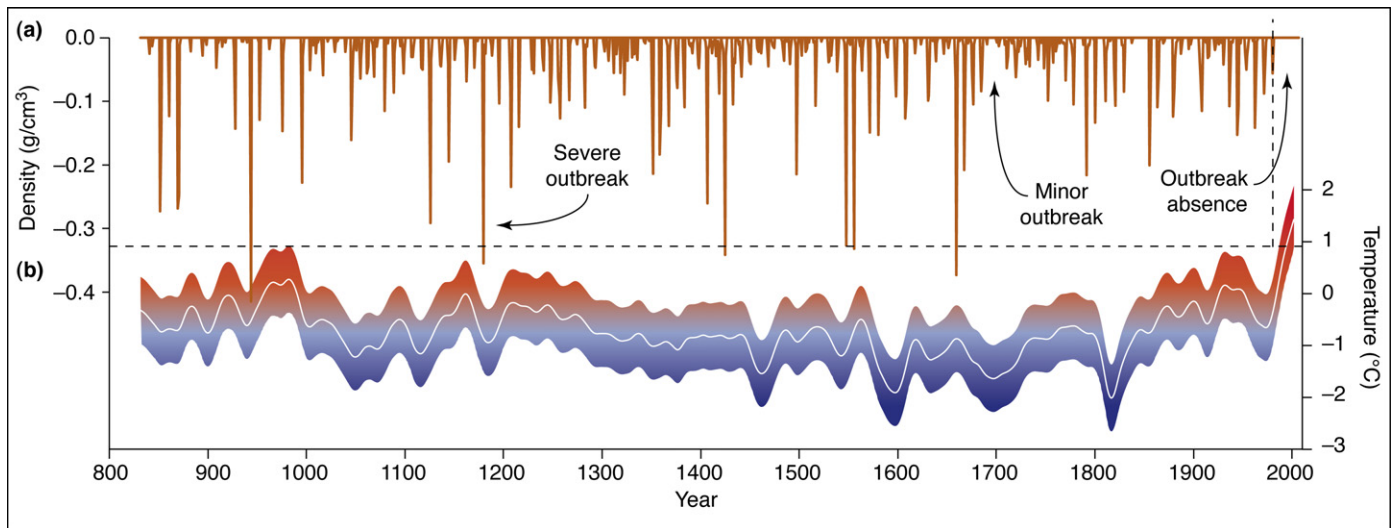
Figure 2. Long-term outbreak dynamics of larch budmoth *Zeiraphera diniana* and temperature variation for the European Alps in the past 1200 years demonstrating how the cyclic moth outbreaks disappear at the end of the time series coincident with rapidly increasing temperatures. **(a)** Larch budmoth outbreak reconstruction since AD 832 based on tree-ring density variation. The bars denote tree-ring 'density declines' resulting from moth outbreaks. The vertical dashed line indicates the last mass outbreak in 1981, and the horizontal dashed line indicates the upper standard error limit recorded during the late 9th century. **(b)** Long-term variation in temperature reconstructed on the basis of tree-ring width. The white curve is the annual mean derived from a temperature model and the colored band is the standard error. Reproduced, with permission, from [31].

we doubt that this can explain the large extent of the recent cases of collapsed cycles (Table 2). This conclusion is also bolstered by log–linear analyses demonstrating that the temporal changes are statistically significant [28,29,32].

However, the problem of nonstationary (or transient) cyclic dynamics due to intrinsic systemic variability is accentuated in the presence of strongly nonlinear density dependence [6,34]. Transient noncyclic dynamics in voles,
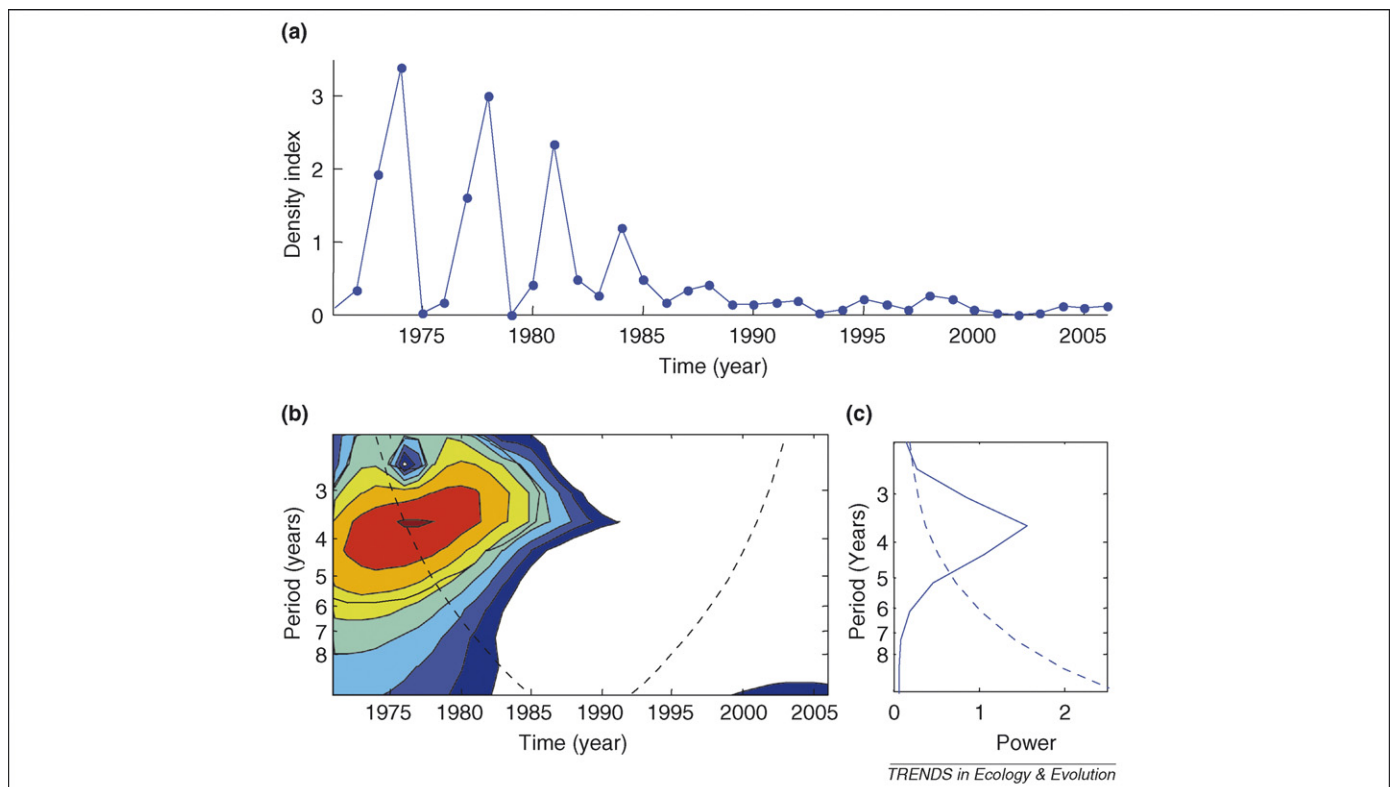

Figure 3. Cycle amplitude dampening towards a temporal collapse of the four-year cycle in boreal gray-sided vole *Myodes rufocanus* in northern Sweden [32]. **(a)** Time series of combined fall catches from a region covering 10 000 km². **(b)** The normalized wavelet power spectrum [43] for the time series showing the statistical significance of the change in dynamics. The likelihood of the power spectrum increases from blue to red. The black contour line encloses the region with greater than 95% confidence, thus showing a significant approximately four-year periodicity until 1985. Thereafter, the cyclic nature of the dynamics gradually disappears, perhaps with a decreasing periodicity, until no periodic signal remains after 1990. The dotted envelope indicates the 'cone of influence'. Outside this 'cone' the interpretations are dubious, because the inferences are weaker at the end and start of the time series. **(c)** The global wavelet power spectrum, showing the significant periodic signal at approximately four years. The broken line shows the 5% significance level. The time series data were obtained from [44].

Table 2. Examples of cyclic population dynamics subjected to temporal changes

Cases	Geographical area	Type of change	Onset of change	Proposed cause	Refs
Myodes and *Microtus* voles	Middle boreal forest, central Scandinavia	Loss of three–four-year cycles; possibly decreased winter survival	Mid-1980s	Poor winter survival	[1,3]
Myodes and *Microtus* voles	Northern boreal forest, northern Sweden	Loss of four-year cycles; amplitude dampening; decreased delayed DD; decreased winter survival	Early 1980s	Adverse winter quality, landscape changes	[32]
Myodes and *Microtus*, lemmings and voles	Northern boreal forest, northern Finland	Loss of four–five-year cycles; loss of delayed DD; decreased winter survival	Mid-1980s	N/A	[36]
Lemmus, Myodes and *Microtus,* lemmings and voles	Subarctic birch forest, north-western Finland	Loss of five-year cycles; decreased winter survival	Late 1980s	N/A	[27]
Myodes and *Microtus* voles	Mountain tundra, northern Norway	Amplitude dampening of four–five-year cycle	Late 1980s	N/A	[24]
Field vole *Microtus agrestis*	Clear-cuts in spruce plantations, northern England	Loss of four-year cycles; amplitude dampening and period lengthening; loss of delayed DD	Early 1990s	Shorter winters, altered trophic interactions	[28]
Common vole *Microtus arvalis*	Agricultural fields, France	Amplitude dampening	Early 1990s	N/A	[18]
Grey-sided vole *M. rufocanus*	Mixed forest, North East Hokkaido, Japan	Shifting in and out of cyclic dynamics; changes in DD	Late 1970s until 1980s	Temporary climate regime shift	[29]
Black grouse *Tetrao tetrix*	Boreal forest, Finland	Amplitude dampening	Mid-1980s	Reduced chick survival due to climate change	[30]
Larch budmoth *Zeiraphera diniana*	Subalpine larch forest, central Europe	Loss of mass outbreaks; amplitude dampening	1980s	Climatic warming	[31]

Abbreviation: N/A, not available.

generated by nonlinear community dynamics models, can persist for long periods [2]. In this case, conclusions about externally enforced systemic shifts, based on log–linear analyses of local and short-term time series, will be deceptive. Moreover, a similar conclusion based on the (large) spatial extent of the change phenomena might be unwar-ranted, because spatial coupling, for instance owing to dispersal, can act to regionalize temporally transient dynamics [35]. However, because the recent large-scale collapse of cycles in Europe transcends ecosystem borders and geographical barriers, we argue that the phenomenon is not due to intrinsic system variability.
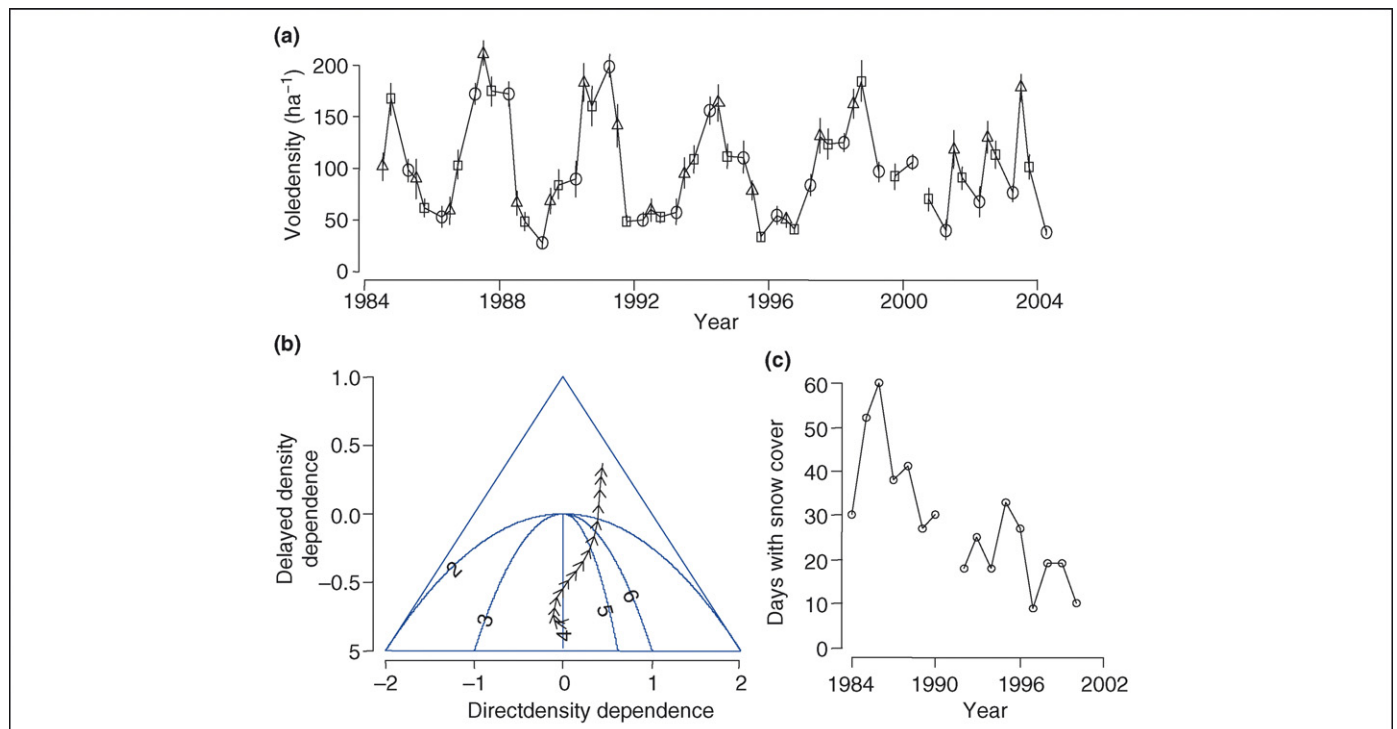

Figure 4. Gradual change in population dynamics from cyclic to noncyclic in the field vole *Microtus agrestis* population in Kielder Forest, northern England. The collapsing population cycles are analyzed in terms of density-dependent parameters of a second-order log–linear model (Box 1) and are related to a change in winter *season* duration. **(a)** The time series of the mean (standard errors given by vertical lines) of the estimated seasonal densities (voles per hectare) of the vole populations averaged over all locations from 1984 to 2004. Triangles summer; squares autumn; circles spring. **(b)** The change in direct and delayed density dependence over the time period based on a log–linear model of annual autumn densities. The black curve with arrowheads superimposed on grey parameter isolines (explained in Box 1) shows that the dynamics change gradually from a four-year cycle in the beginning of the time series, through a five–six-year cycle, until the delayed density dependence eventually becomes zero and there are no more cyclic dynamics at the end of the time period. **(c)** Evidence for a shorter winter *season* over the twenty-year time period. The number of days with ground snow cover in Kielder Forest from the 1 November to the 31 March during the winter from 1984–1985 to 2000–2001. Reproduced, with permission, from [28].

Collapsing cycles resulting from climatic forcing

The strongest causal inferences have been derived from analyses in which the collapse process has been related to concurrent climate change. A particularly illuminating case is the detailed analysis of the process of collapse of the field vole cycles in northern England [28], where the increasingly shorter winters since the early 1990s have been decisive (Figure 4). This study complements the earlier studies of geographic clines in vole dynamics along gradients of seasonality. Indeed, vole cycles appear to vanish when winter becomes shorter both in the spatial and the temporal domain. In northern England [28] and Fennoscandia [36], the collapses of vole cycles appeared to be driven by a loss of delayed density dependence in the rate of change over the winters. However, whereas a drastically shortened season with snow cover (<1 month) appeared to be decisive in northern England, such a connection has not been made for northern Fennoscandia, where snow cover still lasts for about half a year. Indeed, the fact that winter climate differs vastly between the geographical regions with collapsing cycles indicates that the change mechanisms are also likely to differ. In boreal and alpine Fennoscandia, detailed demographic analyses of tundra vole *Microtus oeconomus* populations have pointed to melting–freezing events during the winter, leading to ground ice-crust formation, as being detrimental for winter survival [37,38]. An increasing frequency of such events in northern areas due to increased climatic variation [39] might have shifted the winter dynamics into a regime in which weather-induced mortality overrides density-dependent processes. For instance, spring densities of voles might never exceed the threshold for which specialized predators are able to respond numerically.

The principle of disrupted density dependence and cyclicity through climatic forcing can apply widely to different species and ecosystems. However, the specific season and mechanisms involved are likely to vary. For instance, the Finnish black grouse cycle appears to have collapsed owing to severely reduced chick survival after a mismatch between the grouse breeding phenology and the progress of the spring season developed [30]. In addition, in the case of the dampening of larch budmoth outbreaks in the European Alps, which commenced simultaneously with the onset of the warmest period of the past 1200 years (Figure 3), mismatched phenologies in spring might have been involved. The added complexity of the many climate-sensitive life stages and trophic interactions in insects provides more scope for weather-induced changes in the outbreak dynamics than in homeothermic vertebrates.

Conclusions and perspectives

Paradigms on how population cycles vary in space have shifted as more and longer population time series have accumulated and more refined analytical tools have been used. Hence, to some extent, the current realization of temporally changing cycles might also be data and method driven. Indeed, drifting in and out of cyclic dynamics over long time scales can be expected to be within the range of the normal behavior of some populations and ecosystems. However, the many cases of collapsing cycles 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. 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 noncyclic populations currently are on the move after changing climatic isoclines and that the regions with cycles are shrinking. Exactly how climate change interacts with population dynamics in each case is likely to differ between taxa and ecosystems. Identifying the mechanism(s) will require hypothesis-targeted study approaches beyond the uninformed surveillances [40] normally giving rise to time-series data.

Identifying the mechanisms behind the collapses of cyclic dynamics will not be easy, shown by the fact that the cause of the vole cycle is still in debate after >80 years of research. Ironically, however, the way in which cycles eventually disappear can provide the best (and last) clues as to how they were generated. The collapse of population cycles will also demonstrate their role in the ecosystems to which they belonged. The latter aspect represents a sincere concern. Herbivores with high-amplitude population cycles, such as voles, lemmings, snowshoe hares and forest Lepidoptera, form the heart of terrestrial food-web dynamics [41]. Thus, collapses of these cycles will also imply collapses of important ecosystem functions, such as the pulsed flows of resources and disturbances throughout the ecosystem. The consequences of dampening of spring abundance of northern lemmings and voles are already reflected in severe population declines in northern predators [41] owing to reduced abundance of rodent prey, and increasing cover of mosses owing to reduced rodent-induced disturbance of vegetation [42]. Indeed, if we are to predict the effect of climate change on northern ecosystems, we need to be able to understand processes of the collapsing population cycles and their consequences.

References

1 Lindström, E.R. and Hörnfeldt, B. (1994) Vole cycles, snow depth and fox predation. *Oikos* 70, 156–160
2 Hanski, I. and Henttonen, H. (1996) Predation on competing rodent species: A simple explanation of complex patterns. *J. Anim. Ecol.* 65, 220–232
3 Steen, H. *et al.* (1996) Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology* 77, 2365–2372
4 Stenseth, N.C. (1999) Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87, 427–461
5 Kendall, B.E. *et al.* (1999) Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology* 80, 1789–1805
6 Bjørnstad, O.N. and Grenfell, B.T. (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science* 293, 638–643

7 Turchin, P. (2003) *Complex Population Dynamics: A Theoretical / Empirical Synthesis,* Princeton University Press

8 Royama, T. (1992) *Analytical Population Dynamics,* Chapman and Hall

9 Oli, M.K. (2003) Response to Korpimaki *et al*: vole cycles and predation. *Trends Ecol. Evol.* 18, 495–496

10 Costantino, R.F. *et al.* (1995) Experimentally-induced transitions in the dynamic behavior of insect populations. *Nature* 375, 227–230

11 Kendall, B.E. *et al.* (1998) The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. *Ecol. Lett.* 1, 160–164

12 Hansson, L. and Henttonen, H. (1988) Rodent dynamics as community processes. *Trends Ecol. Evol.* 3, 195–200

13 Hanski, I. *et al.* (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* 60, 353–367

14 Sundell, J. *et al.* (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *J. Anim. Ecol.* 73, 167–178

15 Bjornstad, O.N. *et al.* (1995) Geographic gradient in small rodent density-fluctuations – a statistical modeling approach. *Proc. Biol. Sci.* 262, 127–133

16 Williams, C.K. *et al.* (2004) The collapse of cycles in the dynamics of North American grouse populations. *Ecol. Lett.* 7, 1135–1142

17 Saitoh, T. *et al.* (1998) The population dynamics of the vole *Clethrionomys rufocanus* in Hokkaido, Japan. *Res. Pop. Ecol.* 40, 61–76

18 Lambin, X. *et al.* (2006) Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? *J. Anim. Ecol.* 75, 340–349

19 Tkadlec, E. and Stenseth, N.C. (2001) A new geographical gradient in vole population dynamics. *Proc. Biol. Sci.* 268, 1547–1552

20 Strann, K.B. *et al.* (2002) Is the heart of Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. *Ecography* 25, 81–87

21 Baltensweiler, W. (1993) Why the larch bud-moth cycle collapsed in the sub-alpine larch-cembran pine forests in the year 1990 for the first time since 1850. *Oecologia* 94, 62–66

22 Tenow, O. *et al.* (2007) Waves and synchrony in *Epirrita autumnata / Operophtera brumata* outbreaks. I. Lagged synchrony: regionally, locally and among species. *J. Anim. Ecol.* 76, 258–268

23 Haydon, D.T. *et al.* (2002) Analysing noisy time-series: describing regional variation in the cyclic dynamics of red grouse. *Proc. Biol. Sci.* 269, 1609–1617

24 Ekerholm, P. *et al.* (2001) Long-term dynamics of voles and lemmings at the timberline and above the willow limit as a test of hypotheses on trophic interactions. *Ecography* 24, 555–568

25 Angerbjörn, A. *et al.* (2001) Geographical and temporal patterns of lemming population dynamics in Fennoscandia. *Ecography* 24, 298–308

26 Henttonen, H. *et al.* (1987) How much do weasels shape microtine cycles in the Northern Fennoscandian taiga. *Oikos* 50, 353–365

27 Henttonen, H. and Wallgren, H. (2001) Rodent dynamics and communities in the birch forest zone of northern Fennoscandia. In *Nordic Mountain Birch System* (Wielgolaski, F.E., ed.), pp. 261–278, UNESCO

28 Bierman, S.M. *et al.* (2006) Changes over time in the spatiotemporal dynamics of cyclic populations of field voles (*Microtus agrestis* L.). *Am. Nat.* 167, 583–590

29 Saitoh, T. *et al.* (2006) Effects of regime shifts on the population dynamics of the grey-sided vole in Hokkaido, Japan. *Climate Res.* 32, 109–118

30 Ludwig, G.X. *et al.* (2006) Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proc. Biol. Sci.* 273, 2009–2016

31 Esper, J. *et al.* (2007) 1200 years of regular outbreaks in alpine insects. *Proc. Biol. Sci.* 274, 671–679

32 Hörnfeldt, B. (2004) Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. *Oikos* 107, 376–392

33 Bjornstad, O.N. *et al.* (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol. Evol.* 14, 427–432

34 Hastings, A. (2004) Transients: the key to long-term ecological understanding? *Trends Ecol. Evol.* 19, 39–45

35 Ranta, E. *et al.* (1997) The spatial dimension in population fluctuations. *Science* 278, 1621–1623

36 Yoccoz, N.G. *et al.* (2001) Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. *J. Anim. Ecol.* 70, 713–720

37 Aars, J. and Ims, R.A. (2002) Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. *Ecology* 83, 3449–3456

38 Korslund, L. and Steen, H. (2006) Small rodent winter survival: snow conditions limit access to food resources. *J. Anim. Ecol.* 75, 156–166

39 Putkonen, J. and Roe, G. (2003) Rain-on-snow events impact soil temperatures and affect ungulate survival. *Geophys. Res. Lett.*, 30 DOI: 10.1029/2002GL016326

40 Nichols, J.D. and Williams, B.K. (2006) Monitoring for conservation. *Trends Ecol. Evol.* 21, 668–673

41 Ims, R.A. and Fuglei, E. (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* 55, 311–322

42 Rydgren, K. *et al.* (2007) Moss species benefits from breakdown of cyclic rodent dynamics in boreal forest. *Ecology* 88, 2320–2329

43 Torrence, C. and Compo, G.P. (1998) A practical guide to wavelet analysis. *Bull. Am. Meteorl. Soc.* 79, 61–78

44 Hörnfeldt, B. *et al.* (2005) Fading out of vole and predator cycles? *Proc. Biol. Sci.* 272, 2045–2049

45 Ives, A.R. (1995) Measuring resilience in stochastic-systems. *Ecol. Monogr.* 65, 217–233

46 Hansen, T.F. *et al.* (1999) Multiannual vole cycles and population regulation during long winters: An analysis of seasonal density dependence. *Am. Nat.* 154, 129–139

47 Stenseth, N.C. *et al.* (2003) Seasonality, density dependence, and population cycles in Hokkaido voles. *Proc. Natl. Acad. Sci. U. S. A.* 100, 11478–11483

48 Johnson, D.R. *et al.* (2000) Cyclic dynamics of eastern Canadian ermine populations. *Can. J. Zool.* 78, 835–839

49 Cattadori, I.M. and Hudson, P.J. (1999) Temporal dynamics of grouse populations at the southern edge of their distribution. *Ecography* 22, 374–383

50 Wolff, J.O. (1980) The role of habitat patchiness in the population-dynamics of snowshoe hares. *Ecol. Monogr.* 50, 111–130

51 Murray, D.L. (2000) A geographic analysis of snowshoe hare population demography. *Can. J. Zool.* 78, 1207–1217

52 Klemola, T. *et al.* (2002) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* 99, 83–94