

Vole cycles and predation in temperate and boreal zones of Europe

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Summary

1. Graham & Lambin (2002) have reported on a weasel-reduction experiment, concluding that the impact of weasel predation on field vole survival was neither sufficient nor necessary to initiate and drive the cyclic decline of field vole populations in Kielder Forest, northern England. They also stated that their findings contradict conclusively the specialist predator hypothesis put forward to explain population cycles of voles in North Europe.

2. Straightforward inferences from Kielder Forest to the northern boreal zone are misleading, because the population cycles of voles in Kielder Forest differ essentially from North European vole cycles. The low amplitude of the vole cycles in Kielder Forest, their restricted spatial synchrony in comparison to northern Europe and the virtual lack of interspecific synchrony in Kielder Forest suggest that there are essential differences between the mechanisms responsible for the two types of cyclic fluctuations of voles.

3. The weasel-reduction experiment may provide a misleading picture on the role of predators, even in the Kielder Forest cycle. The experimental reduction of weasels alone may not stop the population decline of voles, because competing larger predators are expected to increase their hunting in the weasel-reduction areas. The small spatial scale of the experiment, which produced only slight, short-term differences in weasel densities between reduction and control areas, also suggests that other predators could have compensated easily for the weasels that were removed.

4. We propose a new version of the predation hypothesis to explain low-amplitude population cycles of voles in temperate Europe, including the Kielder Forest. The interaction between generalist predators and vole populations might account for these cycles because generalists can have a functional response that is destabilizing in the neighbourhood of the equilibrium point. As most generalists are orders of magnitude larger than weasels, and thus need much more food for survival, generalist-driven cycles should be characterized by high prey minima, as observed in Kielder Forest.

Key-words: functional response, generalist predators, herbivores, population cycles, specialist predators

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Vole cycles in Kielder Forest and North Europe

Graham & Lambin (2002) have reported a weasel-reduction experiment, concluding that the impact of common weasel (*Mustela nivalis vulgaris* L.) predation on field vole (*Microtus agrestis* L.) survival was neither

sufficient nor necessary to initiate and drive the cyclic decline of field vole populations in Kielder Forest, northern England. They also stated that their findings contradict conclusively the specialist predator hypothesis put forward by North European ecologists to explain population cycles of voles. Here we present an alternative interpretation of the results, which may serve as a starting-point for new research on temperate vole populations.

Inferences from the vole cycle in Kielder Forest to the 3–5-year population cycles of voles in northern Europe

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(referred to hereafter as northern vole cycles) should be made with caution for the following five reasons. First, the northern vole cycles cover hundreds of thousands of km² in pristine boreal and arctic ecosystems, and in man-made forest plantations and agricultural fields (Kalela 1962), whereas the 3-year population cycle of field voles in Kielder Forest is a small-scale phenomenon covering approximately 600 km² in man-made forest plantations (Lambin, Petty & MacKinnon 2000). Secondly, the low phases of northern vole cycles reach densities 1–2 orders of magnitude lower than in Kielder Forest (< 1 per ha vs. 25–50 per ha) (Henttonen *et al.* 1987; Oksanen *et al.* 1999; Lambin *et al.* 2000). Thirdly, northern vole cycles are high-amplitude fluctuations, characterized by 50–500-fold (sometimes up to 1000-fold) differences between peak and minimum densities (Hanski, Hansson & Henttonen 1991; Oksanen & Oksanen 1992), whereas in Kielder Forest differences between peaks and lows are only about 10-fold (Lambin *et al.* 2000). Fourthly, the cycles of Kielder Forest are spatially synchronous at small scales only (8–20 km; Lambin *et al.* 1998), whereas the northern vole cycles are synchronous at an essentially larger spatial scale (70–500 km; Henttonen *et al.* 1987; Hanski *et al.* 1991; Huitu, Norrdahl & Korpimäki 2003b; Sundell *et al.* 2004). Fifthly, in northern Europe field voles fluctuate in close temporal synchrony with other herbivorous voles (*Microtus* and *Clethrionomys* spp.) and even with insectivorous shrews (*Sorex* spp.), all showing their lowest densities simultaneously (Henttonen *et al.* 1987; Henttonen *et al.* 1989; Hanski & Henttonen 1996; Korpimäki *et al.* 2005), whereas interspecific synchrony with the forementioned species or other small mammals has not been documented in Kielder Forest or elsewhere in temperate Europe. These five differences in the population dynamical syndromes between the Kielder Forest and northern Europe indicate clear differences in underlying mechanisms, i.e. large-scale community dynamics vs. more local single-species dynamics (see Hansson & Henttonen 1988).

The differences outlined above help to discriminate among the putative mechanisms responsible for cyclic dynamics. Specialist-driven predator–prey cycles inevitably have high amplitude. To keep the amplitude from becoming unrealistically large, population dynamic models must include explicit or implicit refuges for prey (Oksanen 1990), or a model structure assuming strong interference between predators (Hanski *et al.* 1991). Before the prey can recover, the vast majority of predators must have starved to death and/or failed to reproduce while having a relatively high mortality rate (Klemola, Pettersen & Stenseth 2003). Obviously, the specialist predator population will not vanish for these reasons until vole densities are much lower than the 25–50 voles per ha, which is the minimum observed in Kielder Forest. In fact, these ‘lows’ correspond to the peak densities observed in North European taiga and tundra habitats of moderate quality (Henttonen *et al.* 1987; Oksanen *et al.* 1999). Moreover, dynamics in

specialist-driven cycles must show wide geographical synchrony, because specialists become mobile when facing an acute shortage of prey (Korpimäki, Lagerström & Saurola 1987; Oksanen, Oksanen & Norberg 1992; Klemola *et al.* 1999).

Methodological issues

Methodological constraints appear to undermine the conclusion of Graham & Lambin (2002) that ‘the impact of weasel predation on field-vole survival was neither sufficient nor necessary to initiate and drive the cyclic decline of field-vole populations in Kielder Forest’. Indeed, methodological issues may account for the lack of response by voles to the weasel-reduction experiment in Kielder Forest (Graham & Lambin 2002). While previous papers by Lambin *et al.* (1998, 2000) render us sympathetic to their claim that weasels hardly play a major role in the field-vole dynamics of Kielder Forest, we do not see that the experiment of Graham & Lambin (2002) would have done much to strengthen this case for the reasons discussed in the following three paragraphs.

It is well known that even least weasels (*M. nivalis nivalis* L.), a very small and ecologically distinct subspecies of North Europe adapted to hunt voles in their tunnels below snow, can move several kilometres (Oksanen *et al.* 1992; Klemola *et al.* 1999; Aunapuu & Oksanen 2003) and they, together with stoats (*M. erminea* L.; body size closer to common weasel than least weasel) can easily find local vole patches and rapidly bring out-of-phase patches to the level of surrounding areas (Korpimäki *et al.* 2002). However, the experiment by Graham & Lambin (2002) was conducted at a small spatial scale: three paired reduction and control areas, each only 5–12 ha and 2–4 km apart. As the home-range size of common weasels (body size double that of the least weasel) is 10–40 ha at high densities and 120–220 ha at low densities of main prey (voles) (Jedrzejewski, Jedrzejewska & Szymura 1995), each reduction area was smaller than the home range of a single weasel. In addition, invading individuals from surrounding areas rapidly replaced most weasels removed from the treatment areas, in particular when vole densities in the reduction areas started to increase to higher levels than in surrounding areas. This is a possible reason why only a short-term difference in weasel densities during the two study years (in midsummer 1999) was documented in one of the three reduction areas, whereas during most of the time and, particularly, in winter to spring, weasel densities were similarly low in reduction and control areas (Fig. 1 in Graham & Lambin 2002). The lack of efficacy of the predator-density manipulation in Kielder Forest resembles the situation in a large-scale experiment in Finland, in which captive-born least weasels released in three ‘predator addition islands’ soon starved to death or were killed by larger predators, so that there was an obvious treatment effect on population dynamics of voles on only one of the three treatment-control island pairs (Sundell 2003).

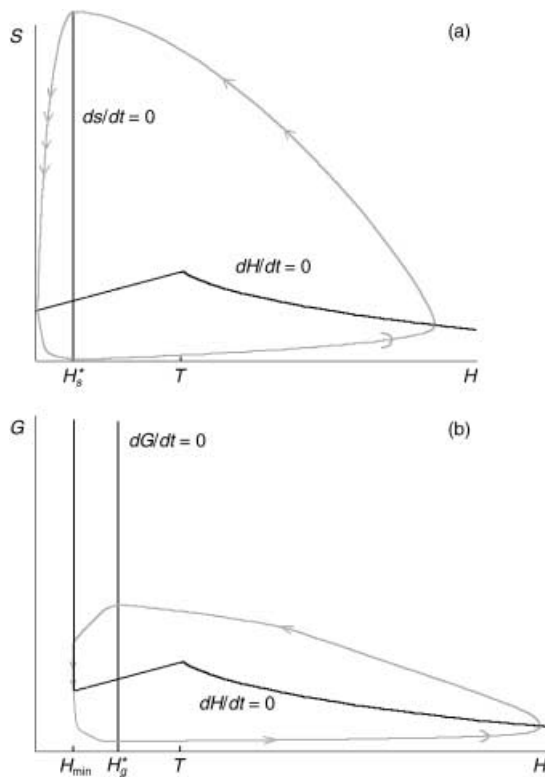


Fig. 1. A phase plane presentation of predator (S , G) and prey (H) isoclines in specialist-dominated (a) and generalist-dominated (b) *laissez-faire* predation systems where the prey guild is heavily dominated by *Microtus* spp. H_s^* and H_g^* stand for the prey density at which the predator in question has zero growth rate, H_{\min} represents the prey density at which the generalist leaves the system, and T is the prey density at which all female territories are occupied. The course of the limit cycle is indicated by the grey line, where the pace of the cycle is indicated by the shape of the arrows (round = slow, pointed = fast) and their number.

Only the densities of the smallest member of vole-eating predator assemblage, the common weasel, were reduced (Graham & Lambin 2002). Because the densities of other mammalian and avian predators subsisting on voles (particularly red foxes *Vulpes vulpes* L. and tawny owls *Strix aluco* L.) were high in Kielder Forest (Lambin *et al.* 2000; Petty *et al.* 2000), it seems likely that, even in the absence of invading weasels, these other predators could have compensated easily for the weasels that were removed. In principle, the reduction of one predator species decreases interspecific competition for food among predators (Korpimäki & Norrdahl 1998) and/or intraguild predation, which should trigger a compensatory response of other predators. Earlier, using large-scale replicated experiments (Korpimäki & Norrdahl 1998), we showed that the reduction of the densities of the smallest member of the vole-eating predator assemblage (in our case the least weasel) is insufficient to prevent a summer decline of northern voles, at least in a system where considerable numbers of avian and generalist predators occur.

Small live-trapping grids were used to estimate vole densities and survival (one permanent 0.3-ha

live-trapping grid per removal and control area) (Graham & Lambin 2002). As daily movements of field voles average 20–30 m and are even higher for males and in the decline phase of the vole cycle (Norrdahl & Korpimäki 1998; Banks, Norrdahl & Korpimäki 2000), many voles may have emigrated from the live-trapping grids. In addition, on trapping grids, live-traps were set at 5-m intervals and prebaited with wheat and carrots 2–3 days before each monthly 3-day trapping session (Graham & Lambin 2002). This apparently means that live-trapping grids were food-supplemented during about 1 week per each month (see also Henttonen 2000). It is possible that food-supplemented grids attracted voles, in particular adult individuals, from surrounding areas, which may have masked effects of weasel reduction.

Predator-reduction experiments in the north

The extrapolation from Kielder Forest to boreal vole cycles is especially surprising when seen against the background of experimental work conducted in northern Europe. Our earlier large-scale experiments, where either least weasel densities or avian predator densities have been reduced, showed that it is not sufficient to manipulate only densities of one predator group to alter the population dynamics of cyclic northern voles (Norrdahl & Korpimäki 1995; Korpimäki & Norrdahl 1998). Compared to the experiment by Graham & Lambin (2002), our experiments have been conducted on > 10 times larger spatial scale and with as many or more replicated study areas (3–5) in equally natural settings (Norrdahl & Korpimäki 1995; Korpimäki & Norrdahl 1998; Korpimäki *et al.* 2002, 2005; see also May 1999). We have reduced experimentally the densities of all main mammalian and avian predators in three (in 3 years) or four (in 3 years) large unfenced areas (2.5–3 km² each) in each phase of the 3-year vole cycle. These large-scale replicated manipulations increased the autumn density of *Microtus* voles (main prey of predators) by fourfold in the low phase, by twofold during the increase phase and by twofold in the peak phase. Moreover, the manipulations retarded the initiation of decline of the vole cycle and prevented the summer decline of vole populations (Korpimäki & Norrdahl 1998; Korpimäki *et al.* 2002). In addition, predator reduction also increased the densities of bank voles (*Clethrionomys glareolus* Schreb; the most important alternative prey of predators) in the low and increase phases of the cycle (Korpimäki *et al.* 2005). Nevertheless, Graham & Lambin (2002) regarded these experiments as non-instructive, because we used snap-trapping methods to monitor the small mammal populations and could therefore, in their opinion, say little about the demographic changes which supposedly accounted for changes in vole numbers.

Indeed, the use of snap-trapping (10 trap lines with 11 snap-traps 10 m apart in each; see Korpimäki & Norrdahl 1998; Korpimäki *et al.* 2002) instead of live-trapping was the only feasible choice in experiments

conducted on such a large spatial scale. Moreover, snap-trapping is practically the only method that can yield reliable estimates of vole densities, even in the low phase of the northern vole cycle when densities are normally of the order of 0.1–0.5 voles per ha (see above), making it very difficult to obtain reliable density estimates with live-trapping (Viitala 1977; Henttonen *et al.* 1987; Oksanen *et al.* 1999). As the areas were large and trap lines were at least 100 m apart, snap-trappings hardly affected the dynamics of vole populations (see also Christensen & Hörnfeldt 2003). There also is no logical mechanism by which snap-trapping could have inflated the estimate of treatment effect. Besides being the only feasible method in large-scale experiments in the north, snap-trapping provides knowledge of several demographic parameters (age structure, sex ratio, proportion of breeding females and litter size) and body condition of voles (Klemola *et al.* 1997; Klemola, Norrdahl & Korpimäki 2000; Norrdahl & Korpimäki 2002a,b).

Moreover, we have conducted experiments in an arctic–alpine habitat complex in North Norway. In one of the experiments, a large (2 ha) mammalian predator-proof enclosure was maintained for five summers. Vole densities on this treatment area and on five comparable control areas with free access to predators were quantified by live-trapping (Oksanen *et al.* 1999; Ekerholm *et al.* 2004). The 2-ha enclosure encompassed the entire range of habitat variation available in the landscape and allowed free dispersal from optimal to suboptimal habitats within the enclosure. In the increase phase of the cycle, vole density did not differ between the reduction area and control areas, in the peak phase of the cycle density on the reduction area was 30% higher than on control areas and in the decline phase of the cycle vole density on the reduction area was two- to fourfold greater than on control areas (Ekerholm *et al.* 2004). As the treatment lacked replication for logistic reasons, interval estimates for the magnitudes of treatment effects cannot be computed, but the existence of a significant treatment effect can nevertheless be inferred, as the enclosure became a statistical outlier every autumn. In the other experiment, voles were introduced to four treeless islands in a large lake. The densities of island populations were compared to the reference areas with vegetation comparable to the two most productive islands and to the reference areas in heath-dominated tundra, comparable to the less productive islands. Even the most conservative comparisons (all islands against the most productive mainland references) revealed two- to fourfold higher vole densities on the islands, where recurrent severe devastation of woody vegetation indicated that voles had increased to carrying capacity (Hambäck *et al.* 2004). Due to the virtual lack of vole immigration, the island populations were not only protected against predators but possibly also against pathogens potentially present on the mainland. Note that the islands cannot be regarded as fenced, because the lake is frozen for most of the year, enabling emigration, and the voles in question can also swim.

The collective message of these experiments is that the reduction of predators changes the dynamics of cyclic vole populations profoundly throughout the boreal and arctic zones of northern Europe (Korpimäki & Norrdahl 1998; Korpimäki *et al.* 2002, 2005; Norrdahl *et al.* 2002; vs. Oksanen *et al.* 1999; Ekerholm *et al.* 2004; Hambäck *et al.* 2004). In addition, collared lemming (*Dicrostonyx groenlandicus* Traill) abundance in Canadian tundra was two- to ninefold higher in a predator enclosure than in control areas in the peak and decline years of the cycle, and protection from predators prevented the decline of lemming populations (Wilson, Krebs & Sinclair 1999). In another site of Canadian tundra, control populations of collared lemmings declined in summer, whereas a population protected from predators remained more stable (Reid, Krebs & Kenney 1995). Observational evidence for the importance of predators in governing cyclic dynamics of collared lemmings has also been obtained in Greenland: the 4-year lemming cycle appears to be driven by a 1-year delay in the numerical response of stoats, whereas the cycle is apparently dampened by direct density-dependent predation by arctic foxes (*Alopex lagopus* L.), owls and skuas (Gilg, Hanski & Sittler 2003). This consistency of results is remarkable, given the marked differences in habitats, in small rodent and predator assemblages and in the methods used to manipulate predator densities and to quantify rodent abundances.

Statistical time-series analyses and mathematical models have suggested that population cycles of northern voles are generated by the combined effects of delayed and direct density-dependent mechanisms (Stenseth 1999; Hanski *et al.* 2001; Klemola *et al.* 2003). On the basis of our observational and experimental results, regulation by predators is the most likely candidate for delayed density dependence, and food limitation in winter for direct density dependence (Korpimäki & Norrdahl 1998; Oksanen *et al.* 1999; Korpimäki *et al.* 2002; Huitu *et al.* 2003a; Ekerholm *et al.* 2004). Moreover, cycles give way to relative stability in areas where transit distances between favourable patches are long (Oksanen *et al.* 1999), as predicted by the predation theory (Murdoch 1977). We have previously refined the specialist predation hypothesis (Henttonen *et al.* 1987; Hanski *et al.* 1991), so that the delayed density-dependent regulation by all the main predators, not only weasels, is the main cause of population cycles of northern voles (the synergic predation hypothesis) (Norrdahl & Korpimäki 2002c). At present, there are large-scale replicated experimental results in North Europe that provide support for this hypothesis, and also for a more general hypothesis that northern vole cycles are indeed generated by predators.

Can generalist predators induce cyclic dynamics?

The tacit point of departure in the work of the Kielder team and in its interpretation (Graham & Lambin 2002; Lambin & Graham 2003; Oli 2003a,b) appears

to be that the existence of sustained population cycles is something peculiar that needs to be explained preferentially with a single factor, accounting for all cyclic population fluctuations. For us, the existence of cycles is trivial. Instability and multi-annual cycles emerge easily from all kinds of simple consumer-resource models, and complexity *per se* simply confuses matters (May 1972; Pimm 1982). As residents or frequent visitors of boreal and arctic life zones, we see cycles wherever we decide to look: in arvicoline rodents (see above), in forest grouse (Lindström *et al.* 1995), in hares (Krebs *et al.* 2001), in folivorous insects (Klemola *et al.* 2002) and even in reindeer (Oksanen 1998). Different cycles are associated with different population dynamical syndromes. The cycles are displayed both in the presence of predators (voles, hares) and in their virtual absence (reindeer, lemmings). The impacts of cyclic herbivores on main winter food plants are variable (only reindeer and lemmings having strong and long-lasting impacts: Moen *et al.* 1993; Johansen & Karlsen 1998). The heterogeneity of the causal mechanisms accounting for these cycles thus seems obvious. For us, the interesting issue in the context of cyclic populations is therefore not 'why cycles' but 'what drives a given set of cyclic populations?'. Indeed, a considerable mystery is the relative rarity of violent population cycles at middle and low latitudes. In this context, intermediate cases such as Kielder Forest, displaying regular cycles with low amplitude, may prove pivotal, especially if the empirical studies are connected to theoretical analyses of the impact of specific, potentially stabilizing types of food-web complexity on population dynamics (Oksanen *et al.* 2001).

True numerical responses of consumers (deriving from changes in natality and mortality) have inevitably a built-in time delay, which is potentially destabilizing. Hence, the occurrence of sustained population cycles is not especially remarkable, nor is it necessary to assume that the same consumer–resource interaction would account for all sustained population cycles. Indeed, the difference between the northern vole cycles, characterized by extended peak phases and gradual declines, and the boom–crash dynamics of high arctic lemming populations, characterized by sharp, short-lived peaks, abrupt crashes with profound impacts on the vegetation, and extremely deep lows (Batzli *et al.* 1980; Moen *et al.* 1993; Turchin *et al.* 2000; Ekerholm, Oksanen & Oksanen 2001; Turchin & Batzli 2001) suggest that even the arvicoline rodent cycles at high latitudes may be a heterogeneous phenomenon, where different trophic interactions account for different cycles. Moreover, the case of the Kielder Forest (Graham & Lambin 2002) and data from other areas of temperate Europe (Mackin-Rogalska & Nabaglo 1990; Jedrzejewski & Jedrzejewska 1996; Tkadlec & Stenseth 2001) suggest that the influence of predators on population fluctuations of voles is more multifaceted than previously thought. Besides, in temperate zone with high minimum vole densities diseases may have

a larger role than in cold northern areas (Cavanagh *et al.* 2004).

The time trajectories documented from Kielder Forest (Graham & Lambin 2002) have a roughly similar shape to the northern vole cycles, but the characteristics of Kielder trajectories are nevertheless inconsistent with the conjecture of weasel–vole limit cycles. The diagnostic features in this context are the high minima and the low amplitude (see above), which imply that only such predator species which have much larger daily energy needs than weasels can possibly be in a pivotal role for the dynamics of the voles in Kielder Forest. On the basis of profound differences between the low-amplitude cycles at Kielder Forest and the high-amplitude northern vole cycles, we suggest that the Kielder cycle might be driven by the interaction between field voles and their generalist, resident predators. The argument for generalist-driven cycles has been presented formally by Oksanen *et al.* (2001) and was inspired by the extensive Polish data from vole–predator interactions (review in Jedrzejewska & Jedrzejewski 1998). Below, we will summarize briefly the main points.

Specialists, generalist and predator–prey cycles

The classical argument that systems dominated by generalist predators have a locally stable predator–prey equilibrium point (Andersson & Erlinge 1977; Hanski *et al.* 1991) derive from Holling's (1959) inference that some predators appeared to concentrate on the most abundant prey types, thus generating a potentially stabilizing type III functional response curve. However, Oksanen *et al.* (2001) found that this interpretation has little support in the cited data. Normally, the experimental predators included the most profitable resource in their diets regardless of its density. The much-discussed 'switching' amounted to abandonment of less profitable resources when the density of the profitable one exceeded a threshold. Rather than indicating a type III functional response, the results thus supported the optimal foraging theory (Stephens & Krebs 1986), generating an 'odd' type of functional response (a combination of two or more type II functional response curves; Abrams 1987), which is destabilizing for almost all densities of preferred prey.

Evidence for a type III functional response was obtained only in those cases where different resource types were found in different habitats, so that simultaneous searching for both was not possible. Even so, it took several additional assumptions to generate a functional response curve that actually leads to local stability of the predator–prey equilibrium point, even in the absence of density-dependence in prey (see Oksanen *et al.* 2001). One central premise was that the predator had to perceive both habitats as roughly equally profitable when prey density was barely sufficient for zero population growth of predators. Below, we will explore what happens when the secondary habitat provides enough resources for survival but not for

reproduction. The point of departure of the analysis is *laissez-faire* predation models (Rosenzweig 1977), which suit for qualitative analyses of stability conditions in predator–vole systems (Oksanen 1990; Oksanen *et al.* 2000).

Let H and C stand for the densities of voles and their predators, respectively. Let r be the intrinsic growth rate of the vole population, $g(H)$ be a function representing direct density dependence in voles, a be the intrinsic searching efficiency of predators, $f(H)$ be the part of the functional response of predators, which is influenced by prey density, m be the maintenance cost of predators and their per capita death rate when starving, and k be the efficiency by which predators convert captured prey to energy for maintenance and reproduction. Then:

$$dH/dt = rHg(H) - af(H)HC \text{ and} \quad \text{eqn 1}$$

$$dC/dt = -mC + kaf(H)HC \quad \text{eqn 2}$$

The equations for zero isoclines can be solved setting the partial derivatives equal to zero.

$$dH/dt = 0 \Rightarrow C = \frac{r g(H)}{a f(H)} \text{ and} \quad \text{eqn 3}$$

$$dC/dt = 0 \Rightarrow H^* = \frac{m}{kaf(H^*)} \quad \text{eqn 4}$$

Because arguments uniquely define function values, equation 4 implies that the equilibrium prey density is constant (i.e. the predator isocline in a predator–prey phase space is vertical) regardless of the details of the predator's functional response. Basic theory of differential equations tells that, with this isocline structure, the local stability of the predator–prey equilibrium depends only on the slope of the prey isocline at $H = H^*$, where H^* is the prey density at which predators are barely acquiring enough energy to replace themselves during their lifetimes (Rosenzweig 1971). Because r/a is a constant, the slope is determined by the behaviour of the ratio $g(H)/f(H)$ when $H \approx H^*$. If the ratio is a decreasing function of H in the neighbourhood of H^* , the equilibrium is locally stable. In the converse case, the equilibrium is locally unstable and generates cyclic dynamics.

Let us assume that the only source of density dependence in the prey is female territoriality (reflecting, e.g. quality and quantity of food). With this assumption, the $g(H)$ function will be specified as follows:

$$g(H) = \min\left(1, \frac{T}{H}\right) \quad \text{eqn 5}$$

where T is the population density at which all territories available for maturing females become occupied. As for functional response, we must assume that there is some H_{\min} such that $f(H) = 0$ for all $H < H_{\min}$. This

parameter represents the vole density at which hunting in the vole habitat is no longer profitable, and the predators either move out of it (generalists) or become passive and try to survive on caches and on body reserves. When hunting in the vole habitat, both generalists and specialists can be expected to have type II functional response (see above). Consequently, we can assume that for $H_{\min} < H$, the $f(H)$ function corresponds to equation 6:

$$f(H) = \frac{1}{1 + ahH} \quad \text{eqn 6}$$

where h is the time used by the predator when handling one prey. Substituting equation 6 to equation 4 we obtain the equation for the predator isocline as:

$$H^* = \frac{m}{a(k - mh)} \quad \text{eqn 7}$$

where H^* refers to prey density at the predator isocline. The vertical form of the predator isocline now becomes visible without excursions to higher mathematics. For $H_{\min} < H \leq T$, the prey isocline obtains the following shape:

$$C = \frac{r}{af(H)} = \frac{r}{a} + hrH \quad \text{eqn 8}$$

which is a linearly increasing function of H . For $T < H$, we obtain:

$$C = \frac{rg(H)}{af(H)} = \frac{rT + ahrTH}{aH} = \frac{rT}{aH} + hrT \quad \text{eqn 9}$$

i.e. the prey isocline declines asymptotically towards $C = hrT$ when H goes to infinity (although, in reality, other factors such as depletion of winter forage, not included in the equation system, would enter the scene at very high values of H). For $H < H_{\min}$, prey isocline is not defined, which means that this range represents a 'technical prey refugium' where predators have no impact on prey dynamics (as they are in another habitat or do not hunt at all).

The contrast between specialists and generalists lies in parameter values. For specialists we can expect a to be large, because a specialist should, almost by definition, be very efficient in finding its prey, and m to be very small, because a specialist need not be larger than it takes to safely tackle its prey, and small size means low costs of maintenance and locomotion. Moreover, the parameter H_{\min} is likely to be very close to zero, as no significant alternative prey exists. For generalists, the converse applies: a is likely to be smaller, m larger and H_{\min} larger by orders of magnitude.

These differences have major dynamical consequences. The isocline for the specialists, running at $H = H_s^*$ (Fig. 1a), is almost guaranteed to meet the vole isocline where it has a positive slope (i.e. $H_s^* < T$), unless either resources of the prey are so scanty that the

females defend very large territories (e.g. in the case of taiga populations of bank voles, see Oksanen *et al.* 2000) or the occurrence of prey is so patchy that the long transit times (increasing the value of the parameter m) boost the value of H_s^* (see Oksanen *et al.* 1999). For productive *Microtus*-dominated systems we can safely assume that $H_s^* \ll T$. Hence, large amplitude limit cycles are generated (Fig. 1a).

Next let us assume that the small specialists have been replaced by medium-sized generalists (which could, in practice happen, e.g. so that the generalists act as intraguild predators on specialists; see Latham 1952; Korpimäki & Norrdahl 1989; Oksanen *et al.* 2001). Because of their considerably higher m/a ratio, the predator isocline of the generalists (H_g^*) is likely to lie at a much higher H -value than the isocline of the specialists (i.e. $H_s^* \ll H_g^*$). It is thus likely that $T < H_g^*$, which means that the prey isocline has a negative slope at the equilibrium, making it locally stable. Note that stability is obtained here in spite of a destabilizing functional response and the existence of alternative prey plays no stabilizing role whatsoever. (If alternative prey were available in the same habitat, their impact would be destabilizing because they would add a positive term to the predator equation 2, thus reducing the magnitude of H_g^* .) The high likelihood for stability is simply a consequence of the relative inefficiency of generalists as predators on voles and their large daily energy requirements, which increase the value of H_g^* .

While the low searching efficiency and large food needs of a medium-size generalist increase the likelihood of a stable equilibrium point, this is by no means guaranteed. For systems where voles have many resources and are thus characterized by weak female territoriality (e.g. field voles in a productive grassland, see Myllymäki 1977) T can be very large, rendering a situation where $H_g^* < T$ likely. Such systems will display limited cycle dynamics (Fig. 1b). However, the relatively high value of H_{\min} guarantees that the minima of the vole cycles are orders of magnitude higher than in the case of specialist-dominated cycles. Even prey maxima will be higher, as limit cycles inevitably cross the prey isocline well past the point where its slope becomes negative. Where they occur, generalist-driven cycles should thus have low amplitudes, high maxima and extraordinarily high minima (Fig. 1b), compared to specialist-driven cycles in a similar habitat (Fig. 1a). The characteristics of the Kielder Forest cycle (Lambin *et al.* 2000; Petty *et al.* 2000) conform to these theory-based predictions of generalist-driven population cycles.

Conclusions and suggestions for future research

We agree that the documentation of the low-amplitude cycles of Kielder Forest (Lambin *et al.* 2000) and cyclic vole populations in Central and Eastern Europe (Jedrzejewski & Jedrzejewska 1996; Tkadlec & Stenseth 2001) has vastly increased our understanding of vole dynamics in the temperate zone, as has the documentation of

destabilizing functional responses in many medium-sized predators of the temperate zone (Zalewski, Jedrzejewski & Jedrzejewska 1995; Jedrzejewski *et al.* 1996; Jedrzejewska & Jedrzejewski 1998; Oksanen *et al.* 2000). The bottom line of these studies is that the generalist vs. specialist issue is but one aspect of the question, whether predator–vole interactions lead to stable or oscillatory dynamics. While the task of constructing a testable hypothesis for the low-amplitude, asynchronous cycles of the Kielder Forest is primarily the task of ecologists working with the system, we can point out that a plausible hypothesis for the low-amplitude temperate zone cycles is that they are driven mainly by generalist predators. Such a conjecture places these systems under the same umbrella of consumer–resource cycles, which has proved a fertile point of departure in studies of many cyclic populations (reviews in Hansson & Henttonen 1988; Oksanen 1990; Norrdahl 1995, Batzli 1996, Korpimäki & Krebs 1996, Stenseth 1999, Oksanen *et al.* 2000, 2001; Hanski *et al.* 2001, Krebs *et al.* 2001, Turchin & Batzli 2001, Berryman 2002; Hanski & Henttonen 2002, Klemola *et al.* 2002, 2003, Turchin 2003, Korpimäki *et al.* 2004).

While we appreciate the contribution of the studies in Kielder Forest and East Europe to the understanding of vole dynamics in the temperate zone, we regard the experiment of Graham & Lambin (2002) and its interpretations (Graham 2001; Lambin & Graham 2003; Oli 2003a, 2003b) as representing a somewhat backward step (see also Korpimäki *et al.* 2003). Several examples of compensatory predation and intraguild predation among vole predators did exist prior to their study (e.g. Norrdahl & Korpimäki 1995; Oksanen *et al.* 1999; see also Sundell 2003), where we learnt the hard way that nature is not a laboratory where ecological field experiments could be conducted as controlled manipulation of the putative causal factor without the need for other precautions. Besides the factors with which we wish to work, nature harbours many mobile predators whose fitness is determined largely by their ability to assess prey density and to redistribute their hunting effort accordingly. Thus, these predators are likely to outperform our capture–recapture methods in the reliable assessment of vole density, and the changing habitat use of these predators can abolish detectable treatment responses. In temperate and south boreal zones of Europe, where the predator guild is reasonably species-rich and both mammalian and avian predators are at least moderately abundant, the critical experiment is to remove *all* predators of voles or to essentially reduce their *collective* density. This can be achieved by non-lethal means, e.g. by enclosing the sites with a chicken-net fence with a nylon-net roof. This method excludes large predators, but allows the movement of voles and small predators. Small predators can be manipulated by removal trapping, covering sufficiently large areas around the trapping grids (see Korpimäki & Norrdahl 1998). More specific predator manipulations may turn out to be competition experiments between

predators, where the predicted response is that other predators increase their use of the treatment areas and prevent any detectable impacts on vole dynamics. Moreover, we do not see any logical connection between the conjecture that a given population cycle is driven by predators and the 'prediction' that removal of predators should stop the cycle. Predator removal amounts to simplification of the food web. If stability is generated by some specific forms of food-web complexity (Hanski *et al.* 1991, 2001; Oksanen *et al.* 2001; Klemola *et al.* 2002), further simplification of a cyclic system may, rather, increase the amplitude of cycles or make dynamics totally chaotic, depending on the characteristics of herbivore–plant interactions (Oksanen 1990; Turchin *et al.* 2000, Turchin & Batzli 2001).

If we are to make progress in our studies on cyclic and non-cyclic herbivore populations, it is vital (1) to define the problem before trying to solve it, (2) to have clear, theory-based predictions concerning the outcomes of planned experiments and (3) to understand the community-level mechanisms that can interfere with our experiment and to eliminate these confounding factors by appropriate countermeasures.

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References

- Abrams, P.A. (1987) The functional responses of adaptive consumers of two resources. *Theoretical Population Biology*, **32**, 262–288.
- Andersson, M. & Erlinge, S. (1977) Influence of predation on rodent populations. *Oikos*, **29**, 591–597.
- Aunapuu, M. & Oksanen, T. (2003) Habitat selection of co-existing competitors: a study of small mustelids in northern Norway. *Evolutionary Ecology*, **17**, 371–392.
- Banks, P.B., Norrdahl, K. & Korpimäki, E. (2000) Non-linearity in the predation risk of prey mobility. *Proceedings of the Royal Society London B*, **267**, 1621–1625.
- Batzli, G.O. (1996) Population cycles revisited. *Trends in Ecology and Evolution*, **11**, 488–489.
- Batzli, G.O., White, R.G., McLean, S.F.J., Pitelka, F.A. & Collier, B. (1980) The herbivore-based trophic system. *An Arctic Ecosystem: the Coastal Plain of Northern Alaska* (eds J. Brown, P.C. Miller, L. Tieszen & F.L. Bunnell), pp. 335–410. Dowden, Hutchinson & Ross, Stroudberg, PA.
- Berryman, A.A. (2002) Do trophic interactions cause population cycles. *Population Cycles: the Case of Trophic Interactions* (ed. A.A. Berryman), pp. 177–187. Oxford University Press, Oxford.
- Cavanagh, R.D., Lambin, X., Ergon, T., Bennett, M., Graham, I.M., van Sooling, D. & Begon, M. (2004)

- Disease dynamics in cyclic populations of field voles (*Microtus agrestis*): cowpox virus and vole tuberculosis (*Mycobacterium microti*). *Proceedings of the Royal Society London B*, **271**, 859–867.
- Christensen, P. & Hörnfeldt, B. (2003) Long-term decline of vole populations in northern Sweden: a test of the destructive sampling hypothesis. *Journal of Mammalogy*, **84**, 1292–1299.
- Ekerholm, P., Oksanen, L. & Oksanen, T. (2001) Long-term dynamics of voles and lemmings at the timberline and above the willow limit as a test of theories on trophic interactions. *Ecography*, **24**, 555–568.
- Ekerholm, P., Oksanen, L., Oksanen, T. & Schneider, M. (2004) The impact of short term predator removal on vole dynamics in a subarctic–alpine habitat complex. *Oikos*, **106**, 457–468.
- Gilg, O., Hanski, I. & Sittler, B. (2003) Cyclic dynamics in a simple vertebrate predator–prey community. *Science*, **302**, 866–868.
- Graham, I.M. (2001) *Weasels and vole cycles: an experimental test of the specialist predator hypothesis*. PhD thesis, University of Aberdeen, Aberdeen.
- Graham, I.M. & Lambin, X. (2002) The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. *Journal of Animal Ecology*, **71**, 946–956.
- Hambäck, P.A., Oksanen, L., Ekerholm, P., Lindgren, Å., Oksanen, T. & Schneider, M. (2004) Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos*, **106**, 85–92.
- Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, **60**, 353–367.
- Hanski, I. & Henttonen, H. (1996) Predation on competing rodent species: a simple explanation of complex patterns. *Journal of Animal Ecology*, **65**, 220–232.
- Hanski, I. & Henttonen, H. (2002) Population cycles of small rodents in Fennoscandia. *Population Cycles: the Case of Trophic Interactions* (ed. A.A. Berryman), pp. 44–68. Oxford University Press, Oxford.
- Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001) Small-rodent dynamics and predation. *Ecology*, **82**, 1505–1520.
- Hansson, L. & Henttonen, H. (1988) Rodent dynamics as community processes. *Trends in Ecology and Evolution*, **3**, 195–200.
- Henttonen, H. (2000) Long-term dynamics of the bank vole *Clethrionomys glareolus* at Pallasjärvi, northern Finnish taiga. *Polish Journal of Ecology*, **48** (Suppl.), 87–96.
- Henttonen, H., Haukialmi, V., Kaikusalo, A., Korpimäki, E., Norrdahl, K. & Skarén, U.A.P. (1989) Long-term dynamics of the common shrew *Sorex araneus* in Finland. *Annales Zoologici Fennici*, **26**, 349–355.
- Henttonen, H., Oksanen, T., Jortikka, A. & Haukialmi, V. (1987) How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos*, **50**, 353–365.
- Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, **91**, 385–398.
- Huitu, O., Koivula, M., Korpimäki, E., Klemola, T. & Norrdahl, K. (2003a) Winter food supply limits growth of northern vole populations in the absence of predation. *Ecology*, **84**, 2108–2118.
- Huitu, O., Norrdahl, K. & Korpimäki, E. (2003b) Landscape effects on temporal and spatial properties of vole population fluctuations. *Oecologia*, **135**, 209–220.
- Jedrzejewska, B. & Jedrzejewski, W. (1998) *Predation in Vertebrate Communities. The Bialowieza Primeval Forest as a Case Study*. Springer Verlag, Berlin.
- Jedrzejewski, W. & Jedrzejewska, B. (1996) Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta Theriologica*, **41**, 1–34.

- Jedrzejewski, W., Jedrzejewska, B. & Szymura, L. (1995) Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. *Ecology*, **76**, 179–195.
- Jedrzejewski, W., Jedrzejewska, B., Szymura, A. & Zub, K. (1996) Tawny owl (*Strix aluco*) predation in a pristine deciduous forest (Białowieża National Park, Poland). *Journal of Animal Ecology*, **65**, 105–120.
- Johansen, B. & Karlsen, S.R. (1998) *Changes in Lichen Cover of Finnmarksvidda 1987–86*. NORUT Informasjonsteknologi IT475/1–98. NORUT Informasjonsteknologi, Tromsø, Norway [in Norwegian].
- Kalela, O. (1962) On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. *Annales Academiæ Scientiarum Fennicæ A*, **IV** (66), 1–38.
- Klemola, T., Koivula, M., Korpimäki, E. & Norrdahl, K. (1997) Small mustelid predation slows population growth of *Microtus* voles: a predator reduction experiment. *Journal of Animal Ecology*, **66**, 607–614.
- Klemola, T., Korpimäki, E., Norrdahl, K., Tanhuanpää, M. & Koivula, M. (1999) Mobility and habitat utilization of small mustelids in relation to cyclically fluctuating prey abundances. *Annales Zoologici Fennici*, **36**, 75–82.
- Klemola, T., Norrdahl, K. & Korpimäki, E. (2000) Do delayed effects of overgrazing explain population cycles in voles? *Oikos*, **90**, 509–516.
- Klemola, T., Pettersen, T. & Stenseth, N.C. (2003) Trophic interactions in population cycles of voles and lemmings: a model-based synthesis. *Advances in Ecological Research*, **33**, 75–160.
- Klemola, T., Tanhuanpää, M., Korpimäki, E. & Ruohomäki, K. (2002) Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos*, **99**, 83–94.
- Korpimäki, E., Brown, P.R., Jacob, J. & Pech, R.P. (2004) The puzzles of population cycles and outbreaks of small mammals solved? *Bioscience*, **54**, 1071–1079.
- Korpimäki, E., Klemola, T., Norrdahl, K., Oksanen, L., Oksanen, T., Banks, P.B., Batzli, G.O. & Henttonen, H. (2003) Vole cycles and predation. *Trends in Ecology and Evolution*, **18**, 494–495.
- Korpimäki, E. & Krebs, C.J. (1996) Predation and population cycles of small mammals. A reassessment of the predation hypothesis. *Bioscience*, **46**, 754–764.
- Korpimäki, E., Lagerström, M. & Saurola, P. (1987) Field evidence for nomadism in Tengmalm's owl *Aegolius funereus*. *Ornis Scandinavica*, **18**, 1–4.
- Korpimäki, E. & Norrdahl, K. (1989) Avian predation on mustelids in Europe I: occurrence and effects on body size variation and life traits. *Oikos*, **55**, 205–215.
- Korpimäki, E. & Norrdahl, K. (1998) Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology*, **76**, 2448–2455.
- Korpimäki, E., Norrdahl, K., Huitu, O. & Klemola, T. (2005) Predator-induced synchrony in population oscillations of co-existing small mammal species. *Proceedings of the Royal Society London B*, **272**, 193–202.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. (2002) Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society London B*, **269**, 991–997.
- Krebs, C.J., Boonstra, R., Boutin, S. & Sinclair, A.R.E. (2001) What drives the 10-year cycle of snowshoe hares? *Bioscience*, **51**, 25–35.
- Lambin, X., Elston, D.A., Petty, S.J. & MacKinnon, J.L. (1998) Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proceedings of the Royal Society London B*, **265**, 1491–1496.
- Lambin, X. & Graham, I.M. (2003) Testing the specialist predator hypothesis for vole cycles. *Trends in Ecology and Evolution*, **18**, 493.
- Lambin, X., Petty, S.J. & MacKinnon, J.L. (2000) Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, **69**, 106–118.
- Latham, R.M. (1952) The fox as a factor in the control of weasel populations. *Journal of Wildlife Management*, **16**, 516–517.
- Lindström, J., Ranta, E., Kaitala, V. & Lindén, H. (1995) The clockwork of Finnish tetraonid population dynamics. *Oikos*, **74**, 185–194.
- Mackin-Rogalska, R. & Nabaglo, L. (1990) Geographical variation in cyclic periodicity and synchrony in the common vole, *Microtus arvalis*. *Oikos*, **59**, 343–348.
- May, R.M. (1972) Will large and complex systems be stable? *Nature*, **238**, 413–414.
- May, R.M. (1999) Crash tests for real. *Nature*, **398**, 371–372.
- Moen, J., Lundberg, P.A., Ekerholm, P. & Oksanen, L. (1993) Lemming grazing on snowbed vegetation during a population peak, northern Norway. *Arctic Alpine Research*, **25**, 130–135.
- Murdoch, W.W. (1977) Transit time and predation on a patchily distributed prey. *American Naturalist*, **101**, 1061–1075.
- Myllymäki, A. (1977) Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. *Oikos*, **29**, 553–569.
- Norrdahl, K. (1995) Population cycles in northern small mammals. *Biology Review*, **70**, 621–637.
- Norrdahl, K., Klemola, T., Korpimäki, E. & Koivula, M. (2002) Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos*, **99**, 419–430.
- Norrdahl, K. & Korpimäki, E. (1995) Effects of predator removal on vertebrate prey populations: birds of prey and small mammals. *Oecologia*, **103**, 241–248.
- Norrdahl, K. & Korpimäki, E. (1998) Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology*, **79**, 226–232.
- Norrdahl, K. & Korpimäki, E. (2002a) Changes in individual quality during a 3-year population cycle of voles. *Oecologia*, **130**, 239–249.
- Norrdahl, K. & Korpimäki, E. (2002b) Changes in population structure and reproduction during a 3-year population cycle of voles. *Oikos*, **96**, 331–345.
- Norrdahl, K. & Korpimäki, E. (2002c) Seasonal changes in the numerical responses of predators to cyclic vole populations. *Ecography*, **25**, 428–438.
- Oksanen, L. (1990) Exploitation ecosystems in seasonal environments. *Oikos*, **57**, 14–24.
- Oksanen, L. (1998) Naturförhållanden och dynamik inom den fennoskandiska fjäll-och tundravärlden *Hållbar Utveckling Och Biologisk Mångfald I Fjällregionen* (eds O. Olsson, M. Rolén & E. Torp), pp. 123–159. Forskningsråd-nämnden, Stockholm, Sweden.
- Oksanen, L. & Oksanen, T. (1992) Long-term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. *Ecography*, **15**, 226–236.
- Oksanen, T., Oksanen, L., Jedrzejewski, W., Jedrzejewska, B., Korpimäki, E. & Norrdahl, K. (2000) Predation and the dynamics of the bank vole, *Clethrionomys glareolus*. *Polish Journal of Ecology*, **48** (Suppl.), 197–217.
- Oksanen, T., Oksanen, L. & Norberg, M. (1992) Habitat use of small mustelids in north Fennoscandian tundra: a test of the hypothesis of patchy exploitation ecosystems. *Ecography*, **15**, 237–244.
- Oksanen, T., Oksanen, L., Schneider, M. & Aunapuu, M. (2001) Regulation, cycles and stability in northern carnivore-herbivore systems: back to first principles. *Oikos*, **94**, 101–117.
- Oksanen, T., Schneider, M., Rammul, Ü., Hambäck, P. & Aunapuu, M. (1999) Population fluctuations of voles in North Fennoscandian tundra: contrasting dynamics in adjacent areas with different habitat composition. *Oikos*, **86**, 463–478.

- Oli, M.K. (2003a) Population cycles of small rodents are caused by specialist predators: or are they? *Trends in Ecology and Evolution*, **18**, 105–107.
- Oli, M.K. (2003b) Response to Korpimäki *et al.*: vole cycles and predation. *Trends in Ecology and Evolution*, **18**, 495–496.
- Petty, S.J., Lambin, X., Sherratt, T.N., Thomas, C.J., Mackinnon, J.L., Coles, C.F., Davison, M. & Little, B. (2000) Spatial synchrony in field vole *Microtus agrestis* abundance in a coniferous forest in northern England: the role of vole-eating raptors. *Journal of Applied Ecology*, **37** (Suppl. 1), 136–147.
- Pimm, S.L. (1982) *Food Webs*. Chapman & Hall, London.
- Reid, D.G., Krebs, C.J. & Kenney, A. (1995) Limitation of collared lemming population growth at low densities by predation mortality. *Oikos*, **73**, 387–398.
- Rosenzweig, M.L. (1971) Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. *Science*, **171**, 385–387.
- Rosenzweig, M.L. (1977) Aspects of biological exploitation. *Quarterly Review of Biology*, **52**, 371–380.
- Stenseth, N.C. (1999) Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos*, **87**, 427–461.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Sundell, J. (2003) Population dynamics of microtine rodents: an experimental test of the predation hypothesis. *Oikos*, **101**, 416–427.
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology*, **73**, 167–178.
- Tkadlec, E. & Stenseth, N.C. (2001) A new geographical gradient in vole population dynamics. *Proceedings of the Royal Society London B*, **268**, 1547–1552.
- Turchin, P. (2003) *Complex Population Dynamics: a Theoretical/Empirical Synthesis*. Princeton University Press, Princeton and Oxford.
- Turchin, P. & Batzli, G.O. (2001) Availability of food and the population dynamics of arvicoline rodents. *Ecology*, **82**, 1521–1534.
- Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T. & Henttonen, H. (2000) Are lemmings prey or predators? *Nature*, **405**, 562–565.
- Viitala, J. (1977) Social organization in cyclic subarctic populations of the voles *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). *Annales Zoologici Fennici*, **14**, 53–93.
- Wilson, D.J., Krebs, C.J. & Sinclair, T. (1999) Limitation of collared lemming populations during a population cycle. *Oikos*, **87**, 382–398.
- Zalewski, A., Jedrzejewski, W. & Jedrzejewska, B. (1995) Pine marten home ranges, numbers and predation on vertebrates in a deciduous forest (Bialowieza National Park, Poland). *Annales Zoologici Fennici*, **32**, 131–144.

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