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Regulation, cycles and stability in northern carnivore-herbivore systems: back to first principles

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In studies on dynamics of northern predator-prey systems, two assumptions are often made. First, the bifurcation from stable to cyclic dynamics is seen as a consequence of changing generalist-specialist ratio, ultimately due to reduced prey diversity at high latitudes and the negative impact of snow on the efficiency of generalists as predators of small, folivorous mammals. Supposedly, the primary mechanism is the qualitative difference between the functional response of specialist and generalist predators. Second, the interaction between large predators and ungulates is supposed to be prone to lead to two alternative equilibria, one where predation regulates ungulates at a relatively low equilibrium and another, where ungulate densities are close to carrying capacity. In the first-mentioned issue, our analysis corroborates the general idea of snow favoring specialists and leading to cycles. However, differences in functional response appear to be of secondary importance only, and rather special conditions are required for generalists to have a stabilizing type III functional response. A destabilizing type II functional response or a slight modification of it should be common in generalists, too, as also indicated by the classical experiments. Stability of generalist dominated systems seems primarily to derive from their relative inefficiency, allowing prey's density-dependent mechanisms to play a bigger role in the neighborhood of the equilibrium. Moreover, the main destabilizing impact of deep, long-lasting snow cover appears to lie in the protection it offers to the efficient but vulnerable specialists, which are eliminated or marginalized by intraguild predation in areas with snow-free winters, unless the habitat offers some other form of efficient protection. As for the conjecture of multiple equilibria in northern wolf-ungulate systems, it seems to be derived from an erroneous operational definition of numerical response and has little if any empirical support. Available data suggest that predation limitation of folivorous mammals prevails along the entire gradient from relatively productive low arctic habitats to the humid parts of the temperate zone, provided that the numbers of predators are not controlled by man.

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Scientists' view of nature and how it functions is inevitably influenced by both empiricism and theory. As long as the pieces seem to fit, we tend to retain tacit assumptions, derived from a mixture of past empirical and theoretical work. Whenever a closer look at the explanation reveals logical problems in the underlying framework, it is time for reconsideration. This can open new avenues worthwhile to explore. The problem became actualized for us when we observed that weakened cyclicity in two northern vole populations coincided with the invasion of an alien generalist predator – the American mink (*Mustela vison*) (Henttonen et al. 1987, Oksanen and Henttonen 1996, Ekerholm et al. 2001). In the light of the prevailing view that generalist mammalian predators have a stabilizing functional response (Andersson and Erlinge 1977, Erlinge et al.

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1983, Hanski et al. 1991, Turchin and Hanski 1997), the causal connection seemed straightforward. If increasing prevalence of generalists along the north-south gradient accounted for the spatial pattern from clearly cyclic to increasingly seasonal dynamics, then increasing numbers of an invading alien generalist looked like a natural candidate for explaining a corresponding temporal change. When fitting the pieces from different sources together, it seemed important to understand the mechanism generating the stabilizing functional response. This consideration led us to new questions and yielded unexpected results. While preparing this paper, P. Turchin (pers. comm.) pointed out another related issue where the connection between predator-prey theory and data is not so clear: the idea of multiple equilibria in boreal wolf-moose systems (Messier 1994). This idea was derived from the treatment of predators' numerical response in a way which is inconsistent with the operational definitions of predator-prey models.

Holling's (1959a, b) seminal work has had a major influence on studies of dynamics in boreal mammalian systems. Holling's work was, however, conducted before the development of modern optimal foraging theory (OFT; see e.g. Stephens and Krebs 1986), and the sufficiency of Holling's typology in describing the functional responses of optimal foragers is debatable (Abrams 1982, 1987). Moreover, Holling used the concept of numerical response when discussing the statistical connection between predator and prey numbers. The numerical response thus defined lacks obvious connection to predator-prey dynamics and is inconsistent with the meaning of the concept in predator-prey models, where numerical response of predators refers to the relation between prey density (or the combined density of prey and predators) and the rate of change of the predator population, deriving from the conceptual framework of Solomon (1949). The issue of numerical response is even connected to the dichotomy between the laissez-faire approach of Rosenzweig (1969, 1971, 1977), where predators are assumed to respond numerically to changes in predation success, related to absolute prey density, and the stacked logistic model of Leslie (1948) and May (1973), where the numerical response of predators is assumed to depend on the number of prey per predator. Both models can be regarded as simplifications of a more general model, which includes both prey dependence and direct density dependence, but the simplifications included in the two modeling approaches have very different consequences.

When pursuing the issues outlined above, we have followed two lines: the classical functional response approach, and an approach focusing on the consequences of differences in searching efficiency and costs of maintenance between small specialized predators, and the larger ones, traditionally referred to as generalists. In the former approach, we start from the connection between functional response and OFT. The scope of this part of the paper is not to propose new theoretical results but to re-evaluate the findings of OFT and to connect them to the specific issues outlined above (for formal analyses, see Murdoch and Oaten 1975, Abrams 1982, 1987, Krivan 1996). Thereafter, we will proceed by studying different ways how the generalist-specialist dimension can influence stability of predator-prey systems with folivorous mammals as prey, and whether and how the outcome can be influenced by density-dependent numerical response of predators. In the final sections, we will apply the results thus obtained to the empirical issues outlined above: whether and how the generalist-specialist dimension could account for the spatial and temporal patterns in dynamics of small, folivorous mammals and their predators and whether the concept of multiple stable states in large boreal predators and their prey is reasonable, given the available data and the generally accepted theoretical results. We will conclude by summarizing the expected patterns arising from the analyses.

Optimality, empiricism and Holling's typology of functional responses

Holling's typology and its applications to mammalian systems

When discussing the rate at which one predator kills prey, we usually rely on the three functional response types defined by Holling (1959a, b). The logic for the type I functional response was straightforward, and type II (Holling's famous disc equation) was mechanistically derived by considering the impacts of handling time. Unfortunately, no corresponding deduction of the type III functional response from type II was presented. Holling's biological motivation for the supposed prevalence of the type III functional responses in vertebrate predators is based on search image formation, although he used the term 'stimulus', as the term 'search image' had not yet been established in English language literature. A phenomenological mathematical model for the type III functional response was proposed by Murdoch and Oaten (1975). Even they regarded it as possible that search image formation could account for a type III functional response.

In a seminal paper, Andersson and Erlinge (1977) built on the studies of Holling (1959a, b) and a study by Ryszkowski and coworkers (1971) on e.g fox (*Vulpes vulpes*) and marten (*Martes foina*) and proposed that search image formation and/or switching to alternative prey is typical for mammalian and avian predators with a broad prey spectrum, referred to as generalists. Conversely, a type II functional response was proposed to be typical for specialized mammalian and avian predators. However, the proposition was not

deduced from a mechanistic analysis of the consequences of specialized and generalized feeding on functional response. The idea of Andersson and Erlinge was further developed by Hansson and Henttonen (1985), who argued that the importance of generalists decreases along the gradient from temperate to truly boreal areas, due to the lower abundance of alternative prey and the negative impact of deep snow on the searching efficiency of generalists.

Due to the fundamental importance of these arguments for analyses of stability conditions in northern systems with folivorous mammals as prey (summarized by Hanski et al. 2001), it is useful to derive the formula for type III functional response by explicitly including the consequences of search image formation and switching to the logical framework provided by type II functional response. The set of functional response types thus obtained is presented below:

$$F(N) = aN \quad \text{(type I or linear)}, \tag{1}$$

$$F(N) = \frac{aN}{1+ahN} \quad \text{(type II or Holling's disc equation)} \tag{2}$$

and

$$F(N) = \frac{p(N)aN}{1+p(N)ah(N)} \quad \text{(type III or sigmoid)} \tag{3}$$

where N stands for density of (primary) prey, $F(N)$ is the number of prey killed by predator per time unit, a is maximum searching efficiency of the predator, h is handling time per prey, $1/h$ is the asymptote of type II and III functional response curves. The impacts of switching and search image formation are incorporated in the function $p(N)$, obtaining values between 0 and 1 and thus representing the fraction of the maximal searching efficiency which the predator achieves at a given density of its primary prey. In order to yield the characteristic, sigmoid (type III) functional response, $p(N)$ must obtain very low values at low densities of primary prey. At moderate primary prey densities, the function must be increasingly accelerating so that it overrides the impacts of increasing handling time and makes the $F(N)$ function downwards convex. The arguments for and against the type III functional responses in generalists thus boil down to the question whether these properties are evolutionarily and empirically plausible consequences of generalized feeding habits.

Switching between prey types sharing the same habitat

According to OFT, predators should always attack the most profitable primary prey, no matter how low its abundance is. Alternative prey should be taken when encountered, as long as the density of the preferred prey is below a threshold. When the threshold is surpassed, the alternative prey should be ignored. The consequences of this 'zero-one rule' on functional response were studied by Abrams (1987; see also Persson and Diehl 1990), but the dramatic and unconventional functional response curves indicated by his graphs are derived from rather extreme parameter values. To clarify the situation, let us thus start by considering two suboptimally foraging predators: naive specialists, which always prey on primary prey only, and naive generalists, which always take both primary and alternative prey. In the former case, the functional response will follow eq. (2), and the gain rate will increase with increasing density of primary prey as shown by the solid line in Fig. 1A. In the latter case, functional response on the primary prey follows

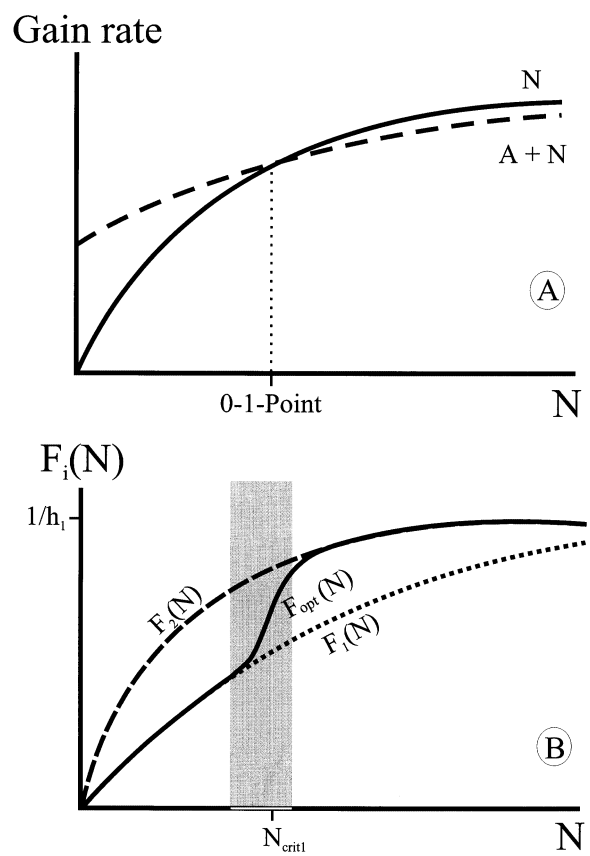

Fig. 1. Functional response of a generalist predator with primary and alternative prey in the same habitat to the density of its primary prey (N), assuming that the predator acts as a generalist ($F_1(N)$, dotted line), the predator acts as a specialist ($F_2(N)$, dashed line) and assuming semi-optimal behavior (attempt to forage optimally, slightly compromised by the need of sampling, $F_{opt}(N)$, solid line). N_{crit} represents the density of the primary prey where a perfectly optimal forager should switch from behaving as a generalist to behaving as a specialist. The white part of the N-axis represents the range of densities of primary prey where a functional response of semi-optimal forager is stabilizing. The functional response of a perfectly optimal forager is always destabilizing.

$$F(N) = \frac{aN}{1 + ahN + \alpha\eta A} \tag{4}$$

where A is the density of the alternative resource, α is the searching efficiency of the predator for this resource and η is the per item handling time of the alternative resource. Eq. (4) generates a type II functional response curve, but with lower slope. Even the gain rate curve (dashed line in Fig. 1A) has lower slope, but it starts above the origin, due to the energy provided by the alternative resource. As for the functional response curves (Fig. 1B), it is useful to let $N \to \infty$ in eqs (2) and (4). We see that both curves share the same asymptote $(1/h)$ and diverge only at moderate densities of primary prey. The dramatic divergence indicated by the graphs of Abrams (1987: Fig. 1) and Persson and Diehl (1990: Fig. 4) requires that the alternative prey is very abundant and very slow to handle, which is hardly a common situation in mammal-based predator-prey systems.

According to OFT, the less profitable prey is dropped when

$$\frac{\kappa}{\eta} < \frac{k}{h + \frac{1}{aN}} \tag{5}$$

where κ and k are the energetic values of the less and more profitable prey, respectively, the other parameters defined as in eqs (1)–(4). The ratio $1/(aN)$ represents the expected search time for the more profitable prey. Let us denote the switching threshold, at which $\kappa/\eta = k/(h + 1/(aN))$, as N_{crit1}. A perfectly optimally foraging predator should switch from behaving in accordance with eq. (4) to behaving in accordance with eq. (2) at $N = N_{\text{crit1}}$. Its functional response curve should thus be discontinuous, consisting of two pieces of the type II functional response with different slopes. As pointed out by Abrams (1987), predators must periodically sample the consequences of both behaviors when the density of the more profitable prey is close to N_{crit1}. Consequently, the 'jump' from eq. (2) to eq. (4) will in reality be replaced by a short, sigmoid section. Provided that the alternative prey are relatively abundant, their handling time is long, and N_{crit1} lies at moderate prey densities where the gap between the curves defined by eqs (2) and (4) is at its widest, the sigmoid section of the functional response curve of sampling optimal foragers can be empirically detectable (Fig. 1B). In other situations, the curve will be practically indistinguishable from the type II functional response. Even if a detectable sigmoid section existed, it covers such a short interval of the prey axis that the likelihood for the predator-prey equilibrium to lie in this range of prey densities must be regarded as small. Provided that switching is not accompanied by habitat change (see below), the type II functional response is thus a reasonable starting assumption in near equilibrium analyses of generalist dominated predator-prey systems.

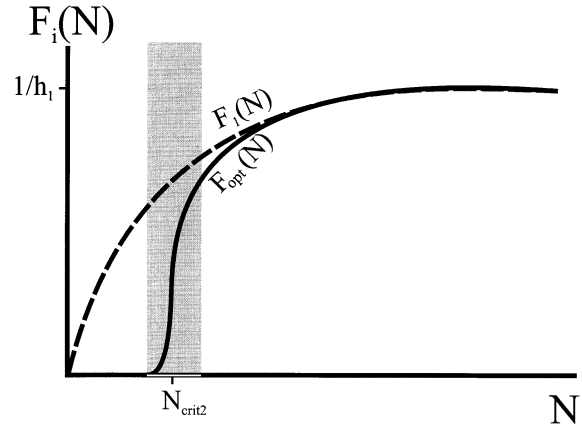

Fig. 2. Functional response of a generalist predator with primary and alternative prey in different habitats to the density of its primary prey (N), assuming that the predator forages in the habitat of the primary prey ($F_1(N)$, dashed line) and assuming semi-optimal foraging (optimality slightly compromised by sampling, $F_{\text{opt}}(N)$, solid line). N_{crit2} represents the density of the primary prey where a perfectly optimal forager should switch between the two habitats. The white part of the N-axis represents the range of densities of primary prey where the functional response of semi-optimal foragers is stabilizing, provided a donor-controlled interaction with alternative prey. If the interaction with the alternative prey is dynamical, functional response cannot be defined without explicit consideration of densities of both prey.

Switching between alternative prey in different habitats

If primary and alternative prey inhabit different habitats, the classical zero-one rule does not apply. For an optimally foraging predator, the criterion for choosing the habitat of primary prey should instead follow the rule

$$\frac{k}{\frac{1}{aN} + h} > \frac{\kappa}{\frac{1}{\alpha A} + \eta}. \tag{6}$$

In systems of this kind, $p(N)$ of eq. (3) can be interpreted as the fraction of total searching time spent by the predator in the habitat of the primary prey. If inequality (6) holds, then $p(N) = 1$ for an optimal forager. If the inequality is reversed, the predator should choose the habitat of the alternative prey, which yields $p(N) = 0$. The functional response of a perfect optimizer should jump abruptly from the prey axis to a curve generated by Holling's disc equation when the two sides of inequality (6) are equal. Let us denote the density of primary prey at which both habitats are equally profitable as N_{crit2}. In reality, again, the need for sampling should make the curve sigmoid in the neighborhood of N_{crit2}. The curve thus generated resembles Holling's type III (Fig. 2).

Notice, however, that predictable reaction to changes in the density of primary prey requires that the right

hand side of inequality (6) consists of constants only. Either the density of the alternative prey must be constant (and independent of predation) or movements between the habitats must be costly enough to prevent sampling and to force the predator to choose in accordance with expectations, based on past experience. If neither of these conditions is satisfied, the switching threshold varies in accordance with the density of the alternative prey, and functional response cannot be defined without knowledge of the density of the alternative prey. Obviously, such a functional response will be synchronizing but it cannot have stabilizing properties (Krivan 1996).

Empirical evidence for type III functional response

In discussions on the functional response of generalist predators, much attention has been paid to the classical studies reviewed by Murdoch and Oaten (1975), but citations have often been inaccurate. To repeat the main point, they regarded the empirical evidence for switching and search image formation as ambiguous. This conclusion was reached after reanalyzing the studies of Holling (1959a, b), Tinbergen (1960), and Mook et al. (1960), which dealt with visually hunting predators, exploiting passive or sluggish prey (resting moths, folivorous larvae, pupae, snails) – i.e. with situations where a search image is maximally likely to count. Moreover, Murdoch and Oaten reviewed in detail the nine experimental studies where predators had access to two different prey types. In five cases, Murdoch and Oaten did not find any evidence against the null hypothesis that differences in capture rates passively reflected differences in abundances of different prey types. In two cases, where different prey types occurred in different patches or habitats, Murdoch and Oaten found evidence for sigmoid (type III) functional response. Only in two studies, evidence for switching between coexisting prey was found. The results of these studies are reproduced in Fig. 3. In one of these (Fig. 3A), evidence for switching is weak. In the other case (Fig. 3B), switching occurs, but in a way more consistent with the zero-one rule of OFT (Stephens and Krebs 1986) than with a sigmoid (type III) functional response.

The results of Holling's (1959b) classical *Peromyscus* experiments are often cited as support for a sigmoid functional response in generalists. These experiments are presented by Holling replicate by replicate, which makes the detection of patterns difficult. We thus computed averages and standard errors for each density of primary prey. The results are reproduced in Fig. 4. The magnitude of switching is illustrated by the lines with the shallowest and steepest slope connecting some of the data points in the rising section of the functional response curve to the origin. Switching trajectories suggested by the data are presented as dashed lines. Even in these cases, switching amounts to specialization on the primary prey when its density is high, as predicted by the zero-one rule of OFT. Primary prey are detected even when rare. A seemingly more convincing case, reproduced even in textbooks, is provided by Holling's (1959b) estimate of the relationship between the density of pupae and numbers consumed by *Peromyscus* and

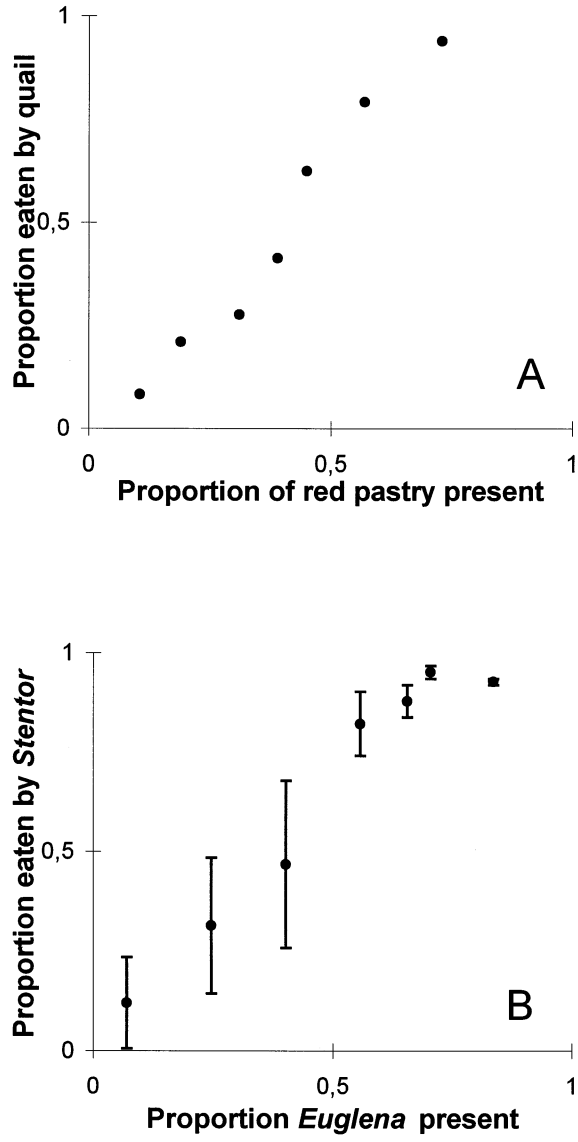

Fig. 3. Relation between the frequency of the focal prey in the prey community and the frequency at which the focal prey was attacked in the two experiments where Murdoch and Oaten (1975) found evidence for switching between co-occurring alternative prey types. A: Quails foraging on red pastry pieces in a habitat where red and blue pieces with identical quality were intermingled. B: *Stentor* preying on *Euglena* in a medium with both *Euglena* and *Chlamydomonas* (a less preferred unicellular alga).

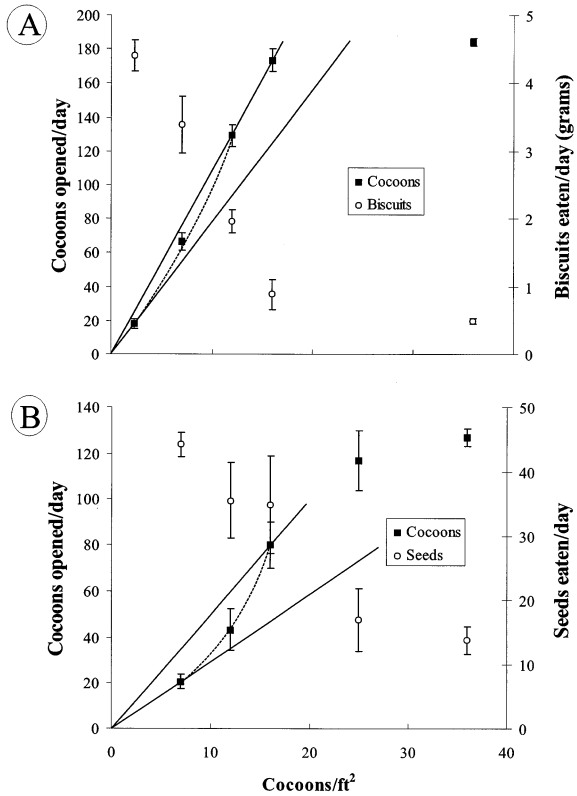

Fig. 4. Functional responses of *Peromyscus* on their preferred prey (cocoons) and alternative food items (dog biscuits in A, sunflower seeds in B.) in the classical experiments of Holling (1959b). The data are presented as averages and standard errors of the replicate runs. The slopes of the lines joining the extreme data points to the origin represent the lowest and highest attack rates (sensu Holt 1977) on the preferred prey. The dashed line represents the switching trajectory indicated by the data.

Sorex. In this data set, data points come partially from different field systems, which confounds the interpretation. Moreover, problems with estimating densities of *Sorex* create a degree of circularity in the work (see Holling 1959b: 299), and the curves are sensitive to non-linearities in the density index for small mammals. Holling's (1959b: 304) own conclusion is as follows: "Unfortunately, the data for any one functional response curve are not complete enough to establish a sigmoid relation". We agree.

In the studies cited by Andersson and Erlinge (1977) as evidence for type III functional response in generalists, we found no evidence against the null hypothesis that the observed diet changes passively reflect changing abundances of different prey types. The same conclusion emerges also from newer studies dealing with the same systems (Lindström 1989, 1992, 1994). Data on functional responses of two temperate generalists – tawny owl and pine marten – (Zalewski et al. 1995, Jêdrzejewski et al. 1996, Jêdrzejewska and Jêdrzejewski 1998), have been recently analyzed in Oksanen et al. (2000). These data indicate a type II functional response. The collective functional response of a generalist dominated predator guild in a temperate old field system (Erlinge et al. 1983) was analyzed by Turchin and Hanski (1997), who found evidence for the type III functional response. As no comparison to the type II functional response was presented, we reanalyzed the data set, using both Holling's disc equation and a sigmoid function with the same number of estimated parameters. The sigmoid function performed better ($R^2 = 0.822$) than Holling's disc equation ($R^2 = 0.738$), supporting the conclusions of Turchin and Hanski. The primary data (Erlinge et al. 1983) indicate that the sigmoid features are primarily a consequence of the tendency of wintering raptors to leave the area when vole numbers drop below a threshold, i.e. the source seems to be large-scale habitat change in mobile predators.

Integrating the generalist-specialist dimension to predator-prey dynamics

Laissez-faire or stacked logistic model?

In analyses of northern predator-prey systems two approaches have been frequently applied. Some authors (e.g. Andersson and Erlinge 1977, Oksanen 1990, Oksanen and Oksanen 2000) apply Rosenzweig's (1969, 1971, 1977) laissez-faire approach or its modifications, but in the context of small mammals, most analyses (e.g. Hanski et al. 1991, 1993, Hanski and Henttonen 1996, Hanski and Korpimäki 1995, Turchin and Hanski 1997) have been performed using the stacked logistic predator-prey model, developed by Leslie (1948) and May (1973). These two approaches appear to be derived from very different logical foundations. It is thus instructive to start with a model generalized enough to embrace both approaches as special cases.

Let us thus assume that the dynamics of prey (N) and predators (C) are governed by

$$\frac{dN}{dt} = rNg(N) - af(N)NC \tag{7}$$

and

$$\frac{dC}{dt} = -mC + kaf(N)NC - \frac{iC^2}{1 + tN} \tag{8}$$

where r is the intrinsic per capita growth rate of the prey, $g(N)$ stands for the density dependence in prey population growth, a is the searching efficiency of the predator, and $f(N)$ represents the relation between prey density and predators' motivation and ability to search for new prey. With the above definitions, functional response has thus the general form $F(N) = af(N)N$

while $af(N)$ is the attack rate sensu Holt (1977). The parameter m represents the energetic costs of maintenance of predators and their per capita death rates in the absence of resources, and the parameter k is the efficiency with which predators convert captured prey to energy for maintenance and reproduction. The parameter i stands for the maximum strength of direct, negative interactions between predators at infinitely low prey densities, and the parameter t represents the ameliorating impact of increasing prey density on these negative interactions.

The prey eq. (7) applies to all model types. The pure laissez-faire predator equation is obtained by setting $i = 0$ in eq. (8). Classical models with stereotypic self-limitation in predators can be obtained by setting $i > 0$ and $t = 0$. To obtain the predator equation of the stacked logistic model, we can first denote $(kaf(N)N - m) = \theta(N)$. Substituting this (8) and after some rearrangements, we obtain

$$\frac{dC}{dt} = \theta(N)C\left(1 - \frac{C}{(\theta(N)/i)(1 + tN)}\right). \tag{9}$$

Assuming that predators are reproducing at full capacity and their recruitment is limited by the availability of vacant territories, we can set $\theta(N) \equiv \rho$, where ρ represents the maximum per capita growth rate of the predator population. Substituting this (9) we obtain

$$\frac{dC}{dt} = \rho C\left(1 - \frac{C}{(\rho/i)(1 + tN)}\right) \tag{10}$$

which is a slightly modified version of the predator equation in the stacked logistic model, where the product $(\rho/i)(1 + tN)$ stands for the carrying capacity. The ratio ρ/i in the density-dependent term is a scaling factor. The only real difference as compared to the stacked logistic model in its classical form is the constant 1 in the denominator of the density-dependent term, which we included for the sake of flexibility and in order to remove a pathological feature of the classical model, where direct negative interactions are tacitly assumed to become infinitely strong when prey density approaches zero. The other pathological feature – that predators keep on reproducing at their maximal per capita rate even when prey density is low and that losses are entirely due to negative interactions between predators – has been removed in later versions of the model by assuming that there is a fixed threshold prey density below which no growth of the predator population can occur (Hanski and Korpimäki 1995, Hanski and Henttonen 1996, Turchin and Hanski 1997).

The choice between the two model types can be made with three different criteria. One possible goal is to be maximally realistic. If this is attempted, one should first ask whether direct density dependence among predators is significant and whether absolute prey densities are periodically so low that predators have problems finding enough food to reproduce and to support themselves. A negative answer to the first question makes the laissez-faire approach uncontroversial, while a negative answer to the second one implies that the premises of the stacked logistic model are fulfilled. If the answer to both questions is affirmative, the use of eq. (8) without short cuts is to be preferred. Second, the scope of the work may be to find necessary and sufficient conditions for limit cycles. Then, there is a point in using both model types in concert. The direct density dependence embedded in the stacked logistic model is stabilizing, whereas the total absence of direct density dependence in the laissez-faire model makes it maximally prone to create cyclic dynamics (Rosenzweig and MacArthur 1963, Tanner 1975). Thus, use of the laissez-faire model gives necessary conditions for cycles, whereas sufficient conditions can be derived from the stacked logistic model. Our scope in this paper is to study the impact of functional response and parameter values on stability conditions. In this context, the laissez-faire approach has clear advantages because the growth rate of the predator population is explicitly derived from the balance between the energy yielded by predation and the energetic costs of maintenance. Hence, the model allows us to study the dynamical consequences of changes in parameters influencing this balance. This is not possible in the stacked logistic model, due to the absence of a mechanistic connection between predation, energetic costs of living, and the numerical dynamics of predators.

Stabilizing and destabilizing aspects of functional response

As pointed out by Murdoch and Oaten (1975; see also Murdoch 1977); the intuitively derived statement that the type III functional response is stabilizing up to the inflection point of the curve is too restrictive. We will repeat their findings by connecting the issue to a maximally simple version of the laissez-faire model, where $g(N) \equiv 1$, i.e. the population growth of the prey in the absence of predation is exponential. Prey isocline thus follows

$$C = \frac{r}{af(N)}. \tag{11}$$

From eq. (11) we see that the slope of the prey isocline is negative if and only if $f(N)$ is an increasing function of N, i.e. if $f'(N) > 0$. Recall that $F(N) = af(N)N$. Thus, $f(N) = F(N)/aN$, and its first derivative $f'(N) = F'(N)/aN - F(N)/(aN^2)$. Consequently, the criterion for a stabilizing functional response can be written as

$$f'(N) > 0 \Leftrightarrow F'(N) > \frac{F(N)}{N}. \quad (12)$$

Thus, a sufficient and necessary condition for a stabilizing functional response is that the value of the derivative of the functional response curve exceeds the slope of the line drawn from the curve to the origin (Murdoch and Oaten 1975, Murdoch 1977). This criterion is thus even satisfied in the beginning of the upward convex parts of the curve, as illustrated by the white parts of the prey axis in Figs 1 and 2. The difference between the inflection point and the criterion (eq. 12) is especially pronounced if the functional response curve rises sharply from a very low level. Then, functional response can be stabilizing up to the vicinity of the asymptote. Switching between prey in different habitats (Fig. 2) can thus be strongly stabilizing, provided that the relatively restrictive conditions for a constant threshold density, discussed above, are satisfied.

Stability consequences of the specialist-generalist dimension mediated via searching efficiency (a), and energetic costs of maintenance (m)

As compared to specialists, generalists can be expected to have lower searching efficiency (a) by the principle that 'jack of all trades is master of none'. Moreover, a specialist need not be bigger than required for risk-free handling of primary prey, whereas generalists must be capable of handling other prey types, too, which often requires larger body size. Hence generalists are likely to have higher metabolic costs of maintenance (m) than specialists. Because the impacts of these parameters on stability are created via interaction with density dependence in prey, we now relax the assumption of exponential prey growth and assume that $g(0) = 1$, $g(N)$ is a decreasing function of prey density and there is a $K > 0$ such as $g(K) = 0$ (e.g. the logistic function, where $g(N) = 1 - N/K$, satisfies these criteria). The impact of searching efficiency is easiest to tackle, if we assume logistic density dependence in prey and type II functional response in predators. Substituting this eq (7) and letting $\mathrm{d}N/\mathrm{d}t = 0$, we obtain the equation for prey isocline as

$$C = \frac{r}{a} + \left(rh - \frac{r}{aK}\right)V - \frac{rh}{K}V^2. \quad (13)$$

Eq. (13) thus creates the familiar, parabola-like prey isocline (e.g. Rosenzweig 1969, 1971). Differentiating eq. (13) and setting the first derivative equal to zero, we see that the prey isocline has a 'hump' within the biologically relevant part of the phase space with positive predator and prey densities, if

$$\frac{1}{ah} < K. \quad (14)$$

Thus, the very existence of a section of prey isocline with positive slope is just as dependent on high searching efficiency as it is dependent on long handling time and high carrying capacity (see Rosenzweig 1973, Gilpin 1975). The specific criterion presented above depends on chosen forms of the functional response and prey's density dependence, but the principle can be generalized. Even in the formula for the type III functional response (eq. 3), handling time only appears in the product ahN. So it must be, because before a predator can start handling a prey, the prey must be detected.

The impact of searching efficiency on the prey isocline is easiest to illustrate by assuming pure laissez-faire dynamics, i.e. setting $i = 0$ in eq. (8). The equation for predator isocline for the general case thus becomes

$$V^* = \frac{m}{ahf(V^*)} \quad (15)$$

and with the type II functional response it obtains the form

$$V^* = \frac{m}{a(k - mh)}. \quad (16)$$

Whether or not we assume the type II functional response, we thus find the searching efficiency in the denominator of the equation for the predator isocline. Hence, low searching efficiency has a dual stabilizing impact. Besides reducing the likelihood that the prey isocline has a 'hump', low searching efficiency is likely to move the predator isocline to the right side of the 'hump' if one exists (Rosenzweig 1973). If the generalist is larger than the specialist, its higher metabolic costs of maintenance enhances this effect, because the parameter m is in the numerator of the equation for the predator isocline (eq. 10). Thus, even high costs of maintenance are stabilizing. Notice that the stabilizing impacts of low searching efficiency and high costs of maintenance are maximal if the generalist has no alternative prey. Access to alternative prey creates an additional, positive term to eq. (8), which will appear as a negative term in the numerator of eqs (15) and (16), thus pulling the predator isocline to lower densities of primary prey, which is destabilizing, provided that the generalist has a destabilizing functional response (which should normally be the case; see above). If, however, cyclic dynamics are generated due to access to alternative prey, global stability of generalist dominated systems is still likely to be high, because specialization on the primary prey during outbreaks tends to reduce the amplitude of the limit cycle (Krivan 1996: Fig. 3C).

We can thus conclude that the relative inefficiency of generalists is a strongly stabilizing factor in predator-prey interactions, especially so if no alternative prey exist. The generalist can then break even only at relatively high densities of primary prey, and within this density range, the stabilizing impacts of density dependence in prey are likely to be strong. In a world with only competitive interactions between predators, such a system could indeed be invaded by the specialist, which would exclude the inefficient generalist. In the absence of significant alternative resources, the dominance of generalists is thus dependent on the existence of direct, negative impacts of generalists on specialists.

Intraguild predation: a potential mechanism for the persistence of inefficient generalists

An intriguing possibility for negative between-predator interactions is provided by the ability and tendency of generalists to prey upon the smaller specialists. The idea that intraguild predation might play a central role in small carnivores was proposed already by Rosenzweig (1966), while an explicit connection between the limiting impact of intraguild predation on small mammal dynamics was proposed by Korpimäki and Norrdahl (1989a, b) (see also Erlinge et al. 1983, Uttendörfer 1952: table on page 166). Moreover, the direct mortality imposed by intraguild predators probably underestimates their dynamical impacts, because threat of intraguild predation can influence habitat selection (King and Moors 1979, Erlinge and Sandell 1988) and lead to increased vigilance, thus reducing foraging efficiency (Brown 1992).

Consequences of intraguild predation in laissez-faire systems along productivity gradients were formally analyzed by Holt and Polis (1997). The only significant limitation of their analysis in the present context is that in the analysis of 'the food chain alternative' (with explicit prey dynamics) type I functional response is assumed. This approach excludes limit cycle dynamics and implies unlimited reproductive potential in predators. The more recent analysis of Krivan (2000) is even less suitable for our purposes, because it builds on the premise that the top predator population is dimorphic, consisting of obligate intraguild predators and individuals exploiting the primary prey, which is unrealistic for systems with folivorous mammals as primary prey. Thus, the arguments summarized below are primarily derived from the analysis of Holt and Polis (1997), qualified in response to our own analyses and computer simulations of systems with saturating functional responses (M. Aunapuu, L. Oksanen, T. Oksanen, K. Leonardsson, L. Persson and J. Löfgren unpubl.).

Assuming that specialists are more efficient in using the focal primary prey, unproductive systems will either have no predators at all or they will be specialist-dominated. In the model of Holt and Polis (1997), enrichment will always lead to invasion of generalists. With further enrichments, generalists will always take over. This result is, however, critically dependent on the assumption of linear functional response and unlimited capacity to convert captured prey to offspring. Assuming saturating functional response or limited reproductive potential in specialists, the collective density of primary prey and specialists will increase asymptotically. Moreover, if the specialist has a low conversion efficiency of captured prey to own population growth (as typical for small mammals), the contribution of the specialists to the over-all resource basis of generalists will remain marginal even in enriched systems. Instead of deterministically allowing generalists to enter, enrichment will lead to specialist-driven cycles. At some level of productivity, enrichment will lead to the emergence of an alternative, locally stable equilibrium point, where generalists prevail and specialists are excluded. If generalists have low searching efficiency as predators of specialists, the domain of attraction of the specialist-driven limit cycle is large and the system is likely to stay there. Conversely, high searching efficiency of generalists on specialists implies that the system easily moves to the domain of attraction of the generalist-primary prey equilibrium, if a few generalists invade the system during a primary prey peak.

Numerical response in large predators and the existence of multiple equilibria

For large specialist predators, such as wolves (*Canis lupus*), with strong tendency for between-pack territoriality (Mech 1966, Peterson and Page 1983, Messier 1994) direct density dependence can both stabilize the system and influence equilibrium densities of the prey. Messier (1994) argued that in these systems, density dependence in predators can be strong enough to shift the equilibrium to the vicinity of prey's carrying capacity or to create two stable, alternative equilibria-one where predators regulate the prey at a density well below carrying capacity, and one where prey is close to carrying capacity. If these two equilibria exist, there must even be a saddle point between them. The term 'predator pit' was introduced as a shorthand for the range of prey densities between the lower equilibrium and the saddle point, because in this density range, prey tends to 'fall down' towards the lower equilibrium.

The logic of the statement can be checked by substituting the equation for the type II functional response (eq. 3, see Messier 1994) to the generalized predator equation (eq. 8) and setting $t = 0$ (to match the assumption of stereotypic density dependence). With these premises the equation for the predator isocline will be

$$C = \frac{a(k - mh)N - m}{i(1 + ahN)}. \quad (17)$$

As N is in the same degree in denominator and numerator, the isocline thus created has a horizontal asymptote. With appropriate parameter values, we can produce a low density equilibrium (Fig. 5A), or a high density equilibrium (Fig. 5B). In order to get two alternative equilibria, we must choose a model structure where dynamics approximately follow the laissez-faire model at low and moderate predator densities, but higher up, there is 'ceiling', created by rigid territoriality (Fig. 5C). Even with this structure, we face the problem of local stability of the low density equilibrium. This can be solved by assuming type III functional response or a relative prey refugium (the dashed prey isocline in Fig. 5C). However, the result thus obtained is so dependent on a special model structure and a delicate balance between parameter values that the realism of the predator pit conjecture is debatable.

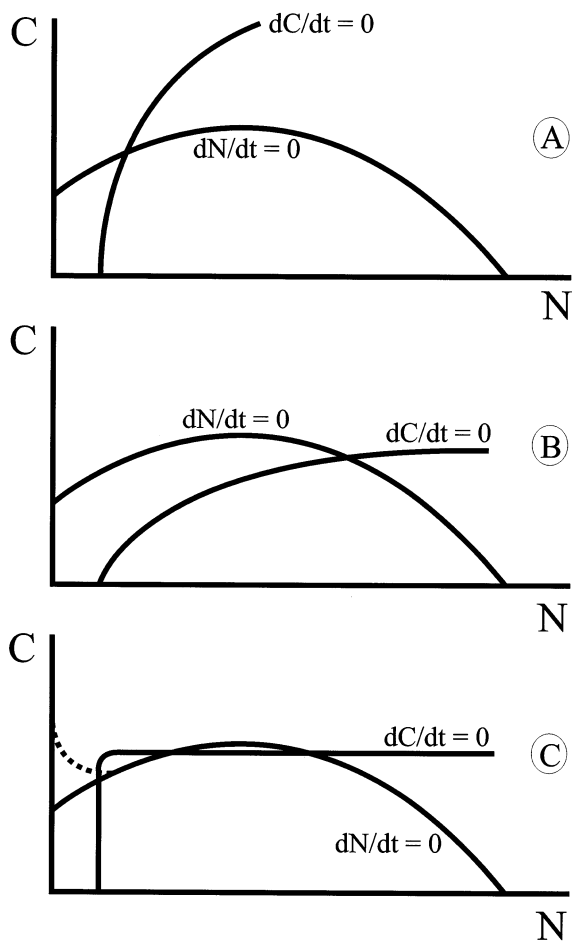

Fig. 5. Possible isoclines for wolf-moose systems with self-limitation in wolves. With weak or moderate degree of self-limitation in wolves (A), the equilibrium densities of moose are primarily controlled by predation. With strong self-limitation in wolves (B), moose are primarily resource-limited at equilibrium. The emergence of two alternative equilibria, separated by a saddle point (C) requires that wolves display almost pure laissez-faire dynamics at low densities and have a upper density limit, caused by strict density dependence. To be locally stable, the low density alternative must occur within the density range where moose have a relative refugium or wolves have a stabilizing functional response.

Speculative empirical connections – reshuffling pieces of empirical evidence

Outlines of the issues to be considered

The desire to understand mechanisms behind population cycles of northern small mammals has served as a continuous source of inspiration both for empirical surveys, experiments and theoretical analyses (Hansson and Henttonen 1985, Norrdahl 1995, Korpimäki and Krebs 1996, Stenseth 1999a). In systems where population densities vary with orders of magnitude, we should be able to see the action of feed-back mechanisms in a much more dramatic and obvious way than in systems where densities hover in the vicinity of the equilibrium. Moreover, the reasons why regulatory mechanisms sometimes lead to a stable equilibrium and sometimes to cyclic dynamics are intimately connected to the nature of the regulatory mechanisms. Thus, a thorough understanding of the mechanisms behind the bifurcation between limit cycles and stable dynamics is at this very moment one of the big issues in ecology (Turchin 2001). The other issue frequently discussed in the context of northern ecosystems is the eventual existence of multiple attractors. Even this issue is of profound theoretical significance, because the existence of multiple attractors would mean that two systems, described with an identical set of differential equations, might nevertheless display very different dynamics. We will thus focus on these two issues in the empirical section of the paper.

Relation to dynamics of small, folivorous mammals in northern Europe

Hansson and Henttonen (1985) and Hanski et al. (1991) pointed out that in northern Europe, the southern limit for winters with long-lasting, thick snow cover, coincides with the southern limit for genuine microtine cycles. Moreover, the change in environment and in rodent dynamics is associated with the transition between the boreal, specialist-dominated predator guild and the temperate, generalist-dominated one. According to their view, generalists with their supposedly stabilizing functional response were limited to low density in boreal areas because of the scantiness of alternative prey and because the deep snow reduced their efficiency as predators of microtines. Many facts con-

form to this interpretation. The boreal and low arctic cycles cover all habitats and have wide geographical and interspecific synchrony (Oksanen and Oksanen 1981, 1992, Henttonen et al. 1987, Oksanen 1990, Hanski et al. 1991, 1993, Hörnfeldt 1994, Norrdahl 1995). Small mustelids (the least weasel, *Mustela nivalis*, being more specialist compared to the stoat, *M. erminea*, and thus normally the key specialist; see Erlinge 1975, 1981, Jêdrzejewska and Jêdrzejewski 1989, Korpimäki et al. 1991) seem to be the key interactive predators, and *Microtus* voles with their ability to build dense local populations seem to be the pivotal prey (Oksanen and Oksanen 1981, Henttonen 1987, Henttonen et al. 1987, Hanski et al. 1991, 1993, Korpimäki et al. 1991, Oksanen et al. 1992, Korpimäki and Norrdahl 1998, Klemola et al. 2000a, b).

Pronounced and apparently cyclic fluctuations of microtine rodents have, however, even been documented in temperate systems (Schindler 1972, Birney et al. 1976, Tapper 1979, Taitt and Krebs 1985, Jêdrzejewski and Jêdrzejewska, 1996, Dyczkowski and Yalden 1998, Lambin et al. 1998, 2000). Moreover, idiosyncrasies of geography appear to sharpen the famous Fennoscandian gradient from violently cyclic to pronouncedly stable vole populations. A central source for a stabilizing guild-level functional response of predators in southernmost Sweden is provided by wintering raptors, which move across the Danish straits when microtine densities on the Swedish side have been reduced below a threshold value (Erlinge et al. 1983). The funnel-like shape of southern Sweden is likely to contribute to the high numbers of wintering raptors, and water barriers between Sweden and continental Europe create a situation, where the decision whether to stay or to move on must be based on a comparison between ambient gain rates in Sweden and expected gain rates on the continent. In our theoretical analysis, this was found to be one of the few mechanisms creating genuinely type III functional response in optimally foraging predators; this interpretation is supported by the data of Erlinge et al. (1983; see also Turchin and Hanski 1997). Even the details of the Fennoscandian gradient do not quite coincide with the supposed role of alternative prey. The transition from stable to cyclic dynamics in Fennoscandia takes place approximately at the so-called Limes Norrlandicus, where winters start to be snowy and last for several months (Hansson and Henttonen 1985, Hansson 1987), whereas the distribution limit of the rabbit, which, according to Erlinge et al. (1984) is the dominating alternative prey for predators of microtine rodents in southern Sweden, is at considerably lower latitudes (Siivonen 1975).

The general but imperfect trend from cyclic to relatively stable rodent dynamics along the gradient from northern to temperate Europe is consistent with the assumption that the primary role of generalists is to act as intraguild predators, thus marginalizing the role of the efficient specialists. During the largely snow-free temperate winters, small mustelids are exposed to predation by mammalian generalist predators, raptors and owls (Latham 1952, Uttendörfer 1952, Hamilton 1959, Cuthbert 1979, Chanin and Linn 1980, Chanin 1981, Korpimäki and Norrdahl 1989a, b). Thus, avian predators and larger predatory mammals take over and small mustelids become restricted to rare subhabitats with exceptionally good cover (e.g. stone fences, ditches; see Erlinge 1974, 1977). Avian predators and larger mammalian predators depend on exposed prey and are unable to enter vole holes. Moreover, larger predatory mammals weigh about 1–15 kg, i.e. one to two orders of magnitude more than small mustelids (Siivonen 1975, Erlinge et al. 1983, Görner and Hackethal 1988). Under these conditions, the lower searching efficiency and higher costs of maintenance of generalists may provide a sufficient stabilizing factor for predator-vole dynamics. In habitats with exceptionally good cover in the form of dense vegetation, small mustelids can prevail, generating local population cycles.

As for the mechanism behind the boreal and low arctic cycles, there is an apparent discrepancy between the advocates of Rosenzweig's (1971) laissez-faire approach (Oksanen 1990, Oksanen et al. 2000) and colleagues using the stacked logistic model (Hanski et al. 1991, 1993, Turchin and Hanski 1997). To some extent, the discrepancy is real. To our understanding, the premises of the stacked logistic model (strict territoriality in predators, prey easy to find) do not quite match with the biology of weasels and stoats. Even with relatively high vole densities in early winters, successful pursuits are normally separated by long stretches of searching tracks (own, unpublished data). Moreover, small mustelids have normally broadly overlapping home ranges, territoriality being restricted to mutual avoidance between reproducing females and to male-male competition for mates (Erlinge 1974, 1977, King 1975, 1989, Henttonen et al. 1987, Oksanen et al. 1992, 1997, Oksanen and Henttonen 1996, and unpublished data). True territoriality between females is only observed at very high population densities (Lockie 1966).

When the two modeling approaches are modified to embrace the consequences of the above empirical evidence, the difference between them decreases. The absolute prey density threshold for predator reproduction, incorporated in modern works based on the stacked logistic model tradition, creates a vertical segment to the predator isocline (Fig. 6A), which corresponds to the vertical predator isocline of laissez-faire models. Conversely, it is reasonable to assume direct density dependence at high specialist densities. Even the direct and indirect impacts of intraguild predation, which is common even in northern areas during the peak phase of the cycle (Korpimäki and Norrdahl 1989b); could be incorporated in the specialist equation as a negative higher order term, if the larger predators are not explic-

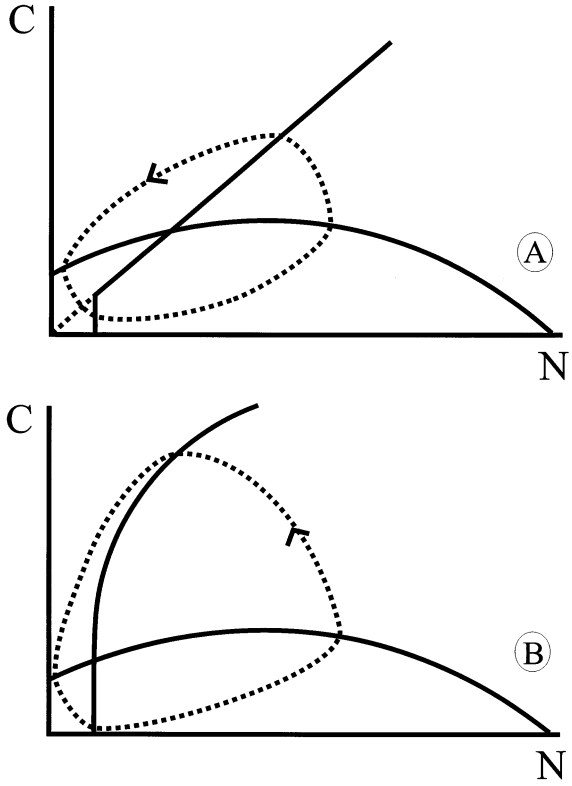

Fig. 6. Predator and prey isoclines and outlines of limit cycles in specialist-dominated northern small mammal system according to the modified stacked logistic model, with absolute prey density threshold for predator reproduction (A) and according to a modified laissez-faire model, including direct density dependence in predators at high densities (B).

itly included in the model. With these sources of density dependence included in the predator equation, the predator isocline will get a positive slope at high predator densities (Fig. 6B), although we do not yet have enough empirical evidence to firmly conclude whether this positive slope exists at biologically relevant predator densities. If it does, then the difference between models derived from the two approaches is quantitative rather than qualitative, the modified laissez-faire model implying cycles with higher amplitude than the modified stacked logistic model.

The case of boreal North America and the impact of snow quality

A striking feature in cross-Atlantic comparisons, as pointed out by Hansson and Henttonen (1985), is that while voles are cyclic in boreal Europe, boreal North America is characterized by cyclic populations of snowshoe hares (*Lepus americanus*) (Krebs et al. 1992). Even these cycles give way to relative stability at the boreal-temperate interface (Buehler and Keith 1982). From the results obtained in the model part (that cyclic dynamics are generated when the efficient specialists are protected against intraguild predation), and the observation discussed above (that the occurrence of boreal population cycles is restricted in areas with thick, long-lasting snow cover), we can infer that the cycles should be found in systems where specialists can take maximal advantage of snow conditions. In this respect, the two continents are quite different. In northern Eurasia, the western coast has only low mountains, and Atlantic warm fronts penetrate deep into the continent, being the main source of winter precipitation. Consequently, snowfall is normally associated with rising temperatures. Recurrent melting of the top snow creates the typical European 'ski snows' with several crusty layers embedded in the snow pack. Snow of this kind provides excellent protection for weasels against larger predators. In North America, the impact of corresponding Pacific warm fronts is restricted to the western mountains, where weasel-vole cycles do occur (Fitzgerald 1977). In the rest of the continent, winter precipitation is primarily generated when arctic cold fronts meet moisture-laden Atlantic and Caribbean air masses. Thus, snowfall is normally associated with sinking temperatures, creating the deep, powdery 'snowshoe snow' typical for North America east of the Rockies. This kind of snow can be penetrated by owls (Mebs and Scherzinger 2000) and provides thus little protection for weasels. On the other hand, deep powder snow efficiently protects the light-footed lynxes (*Lynx canadensis*) against predation by wolves (*Canis lupus*). Thus, the release of lynxes from intraguild predation may account for the North American hare-lynx cycles. Consistent with our interpretation, patterns in spatial synchrony of the hare-lynx cycle correspond to climatic regions (Stenseth 1999b), which correlate with snow quality.

The American mink: possible impacts of a boreal generalist on stability

In spite of similar snow conditions, there is a clear difference between the classical microtine cycles of Fennoscandia, which were synchronous over enormous areas (Hanski et al. 1993) and strong enough to spread to *Clethrionomys*-dominated habitats where local dynamics would probably have created a stable equilibrium (Henttonen 1987, Hanski and Henttonen 1996, Oksanen et al. 1999, 2000), and the more local cycles on the western mountains of North America (Fitzgerald 1977). A difference in the predator guild may account for this contrast. The North American predator guild includes a fairly abundant generalist, the American mink, capable of switching between terrestrial and aquatic prey (Cahalane 1947, Chanin and Linn 1980, Pulliainen 1984, Niemimaa and Pokki 1990), but prob-

ably unable to significantly influence densities of aquatic prey, due to the refugia provided by larger bodies of water. Just such a situation, where the predator has alternative prey in another system and the interaction there is donor-controlled, was found to be maximally likely to create a stabilizing, type III functional response. Moreover, minks prey upon smaller mustelids (Hamilton 1959, Cuthbert 1979, Chanin and Linn 1980, Chanin 1981). Their impact is thus stabilizing in two ways, and this should be felt especially strongly in northern areas without large agricultural habitats, because the natural habitats of *Microtus* spp. normally occur as narrow strands along creeks, which should make the pivotal weasel-*Microtus* subsystem (Henttonen 1987, Hanski and Henttonen 1996) vulnerable to the impact of minks.

The recent changes in the dynamics of North Fennoscandian vole populations (Hanski et al. 1993) are consistent with this interpretation. In our study area in northernmost Norway, tracks of the American mink were first observed in 1984, and by 1990, mink had become a major component of the mustelid guild (Bevanger and Ålbu 1986, Oksanen and Oksanen 1992, Bevanger and Henriksen 1995, Oksanen et al. 1997, and unpubl.). Since 1991, vole dynamics have been much more seasonal than before, and a clear cycle has only prevailed in an area with exceptionally large chunks of *Microtus* habitat, not associated with running water (Oksanen et al. 1999, Ekerholm et al. 2001). In the outbacks of Finnish Lapland, the invasion of the mink occurred about a decade earlier (Kauhala 1996), so did the change to more seasonal dynamics in *Clethrionomys* habitats (Henttonen et al. 1987, Oksanen and Henttonen 1996, Prévot-Julliard et al. 1999). At Pallasjärvi, we recorded widespread mink activity in 1982–1983, when the change was going on (Oksanen and Henttonen 1996, T. Oksanen, unpubl.). Hanski and Henttonen (1996) explained the change in vole dynamics as a consequence of the tension between the upland subsystem, where the more generalized stoat would have a stable equilibrium with *Clethrionomys* spp. (see also Oksanen et al. 1999, 2000) and the riparian subsystem, where the strictly specialized weasels tend to have limit cycle dynamics with *Microtus* spp. As the two subsystems interact, alternative attractors can emerge (see also Hansen et al. 1999). While this may be a part of the explanation, we regard it as unlikely that the changes in the two areas had just by chance coincided with the invasion of the American mink.

Even another generalist – the red fox – has recently increased due to its recovery from the sarcoptic mange (Hörnfeldt 1991, Haukisalmi and Henttonen 1993). W. Svendsen (pers. comm.) pointed out that the red fox population of Finnmark, Norway, did not only recover but overshot its normal level, due to the build-up of high hare densities during the virtual absence of foxes. This may indeed have contributed to the changes in vole dynamics, but if this were the only reason, the phase of primarily seasonal density changes should have been short-lived. Recent data from Pallasjärvi, Finnish Lapland (Prévot-Julliard et al. 1999) are in conflict with this interpretation, as vole dynamics have remained primarily seasonal for a decade. Moreover, the alternative prey of red foxes – mountain hares – are primarily found in the best *Microtus* habitats (riparian willow thickets), which should make the functional response of red fox destabilizing (see above). When both spatial differences (the contrast between Fennoscandia and western North America) and temporal changes are considered, we thus find it likely that mink is the main cause for relative stability in those boreal areas, where it is present and where *Microtus* habitats are intimately associated with running water. In this case, stabilization is probably primarily caused by a sigmoid functional response, conforming to the reasoning of Hanski et al. (1991).

Multiple equilibria in boreal wolf-moose systems?

In the section on numerical response, we analyzed possibilities for having multiple equilibria in systems with big mammalian predators and prey. In the empirical argument for the existence of two locally stable alternative equilibria (Boutin 1992, Messier 1994, Eberhardt and Peterson 1999, Marshal and Boutin 1999, Eberhardt 2000, Hayes et al. 2000, Messier and Joly 2000), numerical response of wolves has been inferred by plotting densities of wolves against densities of moose (*Alces alces*). Recall that in analyses of predator-prey dynamics, the numerical response of the predator is defined in the spirit of Solomon (1949), as the relation between prey density (or the combination of prey and predator densities) and the instantaneous rate of change of the predator population. Plotting predator densities against prey densities is hence not an appropriate way to infer numerical response of predators from data. The relevant information consists of observations of density combinations of predator and prey, accompanied by data on rates of change in predator density.

We know only one source of such information, representing an area with an undisturbed wolf population: the long-term record from Isle Royale (Peterson and Page 1983, McLaren and Peterson 1994). During the period covered by the data, the moose population displayed two fluctuations which are presented as a phase space plot in Fig. 7. In one of these, moose densities moved back and forth, while wolf densities remained low. The data of McLaren and Peterson on fir sapling growth demonstrate that during this fluctuation, moose acted dynamically as predators of fir saplings, not as prey of wolves. Apparently, wolves suffered from some problem caused by the limited

space and low absolute numbers (for us, breakdown of the big pack to units too small to kill adult moose, appears the most probable cause) and, thus, failed to respond to the increase in moose numbers. In the other fluctuation, the time trajectory moves counterclockwise in the phase space, as it should do in an interactive wolf-moose system. The moose density at which the numerical trend in wolf numbers changes its sign, is similar in the top and bottom phases of the wolf cycle, which is consistent with the predictions of pure laissez-faire models. The case of Isle Royale thus does not provide any indications for the kind of strong, direct density dependence in wolves, which would be essential for the existence of two alternative equilibria.

There are even other reasons to suspect that the high-density equilibrium does not exist, unless we include systems where wolves are regulated by hunting. Crête (1999) recently reviewed geographical patterns in ungulate densities in North America. The main conclusion of his study was that wherever wolves had been relatively free from human persecution at the time scale of decades, ungulate densities were low. Conversely, in areas where wolves are absent or only starting to recover, ungulate densities correlated with evapotranspiration, which governs large-scale patterns in terrestrial primary productivity. The high-density 'equilibrium' appears to reflect the latter situation, whereas in truly interactive wolf-ungulate systems, only the low-density equilibrium appears to exist.

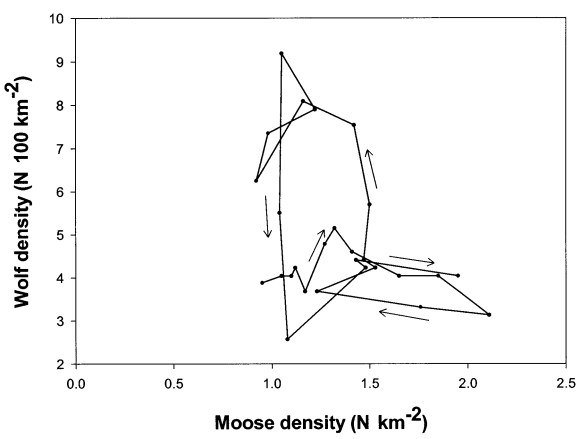

Fig. 7. A phase space plot of wolf and moose fluctuations on Isle Royale, based on the corrected density estimates of Messier (1991). One of the fluctuations cannot represent an interactive wolf-moose system (as wolves do not even respond to changes in moose density), while the other fluctuation is consistent with the dynamics in a coupled predator-prey system. The maxima and minima of wolf numbers are obtained at the same moose density, which is consistent with the predictions of a pure laissez-faire model and indicates that direct density dependence in wolves is not significant within the density range represented in the data.

Conclusions

The current body of predator-prey models predicts that all along the gradient from temperate fields and forests to low arctic scrublands, the interaction between folivorous mammals and their predators normally creates a single attractor, where folivore populations are regulated by predation (Oksanen 1990, Hanski et al. 1991, 1993, Oksanen and Oksanen 2000). In less productive arctic and high alpine areas the pivotal predator-prey interaction is probably between herbivores and plants (Crête and Manseau 1996, Oksanen and Oksanen 2000, Turchin et al. 2000; but see Stenseth 1999a). A possible underlying cause is a sufficiently high primary productivity, creating a situation where densities of folivorous prey can get well above the level required for predators to break even and still be sustained by the annual production of the vegetation (Oksanen and Oksanen 2000). However, proper understanding of dynamics of small predators and their prey in northern areas obviously requires more specific assumptions on snow cover (Hansson and Henttonen 1985) and its impact on parameter values.

A series of analyses and simulations performed by Hanski, Turchin and coworkers (Hanski et al. 1991, 1993, Hanski and Korpimäki 1995, Turchin and Hanski 1997) penetrated the problem, and applied an analytical approach which decidedly improved our comprehension of spatial patterns in small mammal dynamics. When searching for a mechanism for the recent changes in small mammal dynamics, we initially took their premises as a point of departure and focused on the question whether changed generalist to specialist ratios could account for patterns in time, too. However, we agree with Rosenzweig (1969, 1971, 1977) that the laissez-faire approach, based on the idea that the balance between capture rates and energy needs is of fundamental importance for predators, is a more fertile point of departure than the stacked logistic model, where no explicit connection exists between predation and predator dynamics. The parameters of laissez-faire models provided additional clues to the problem of cyclic vs stable dynamics, as they highlighted the destabilizing impacts of high searching efficiency and low costs of maintenance, typical for specialists. Conversely, the conjecture of a stabilizing functional response in generalists appeared to have a narrower range of applicability than previously thought. In the new framework thus emerging, the primary importance of deep and long-lasting snow cover was to protect efficient but vulnerable specialists against intraguild predation by larger generalists. The impact of snow on the searching efficiency of generalists as predators of primary prey turned out to be less important: if the generalists manage to exclude the specialists and the habitat is sufficiently productive to sustain large densities of primary prey, their densities will increase until the generalists

are able to break even. The results obtained with this approach are in some parts inconsistent with the views of Hanski and his co-workers. The main predictions of our conjectures are presented below.

Concerning ungulates and big predators, we expect that where ever full re-establishment of big predators is allowed, ungulates will be driven to same relatively low level (biomass < 100 kg km^{-2}) as typical for the Canadian taiga today (Crête 1999). As for the dynamics of boreal small mammals, the critical prediction differentiating between our interpretation and ideas focusing on the type of functional response of generalists (e.g. Hanski et al. 1991) lies in the role of shelter and alternative resources. In the contexts of wintering raptors in southern Sweden, changing habitat at a large spatial scale, and minks in Lapland, switching between terrestrial and aquatic prey, the idea of generalists having a stabilizing type III functional response is plausible. However, even in these cases, direct mortality, inflicted by generalists on specialists, may contribute to the stabilizing impact of generalists. We predict that cyclic vole dynamics could be generated in the temperate zone by manipulating the habitat so that specialists have good cover. In northern areas with specialist-driven cycles, providing predators with an alternative food source in a *Microtus* habitat should not stop cycles. Conversely, according to the interpretation of Hanski et al. (1991) access to alternative food should be able to stabilize northern systems, whereas providing cover for small mustelids should not destabilize temperate ones. As for the intriguing connection between the American mink and boreal to low arctic vole cycles, we can look forward to obtaining critical evidence soon. The success of the mink on the low arctic tundra represented the overshooting phase of the invasion and was thus short-lived. Only few observations have been obtained in our study area during the last five years. If the mink has a central role for the recent changes in vole dynamics in northern Fennoscandia, the good old cycles should be restored in Fennoscandian low arctic landscapes, whereas in forested areas, where minks have been established, dynamics should remain comparable to those found in the western mountains of North America: local cycles should occur in large meadow areas, but dynamics in the forests should remain predominately seasonal.

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References

Abrams, P. A. 1982. Functional responses of optimal foragers. – Am. Nat. 120: 382–390.

Abrams, P. A. 1987. The functional responses of adaptive consumers of two resources. – Theor. Popul. Biol. 32: 262–288.

Andersson, M. and Erlinge, S. 1977. Influence of predation on rodent populations. – Oikos 29: 591–597.

Bevanger, K. and Ålbu, Ö. 1986. Mink, *Mustela vison*, i Norge. (Mink, *Mustela vison*, in Norway.). – Ökoforsk utredninger 6: 1–73.

Bevanger, K. and Henriksen, G. 1995. The distributional history and present status of the American mink, *Mustela vison* Schreber, 1777) in Norway. – Ann. Zool. Fenn. 32: 11–14.

Birney, E. C., Grant, W. E. and Baird, D. D. 1976. Importance of vegetative cover for the cycles of *Microtus* populations. – Ecology 57: 1043–1051.

Boutin, S. 1992. Predation and moose population dynamics: a critique. – J. Wildl. Manage. 56: 116–127.

Brown, J. S. 1992. Patch use under predation risk: I. Models and predictions. – Ann. Zool. Fenn. 29: 179–182.

Buehler, D. A. and Keith, L. B. 1982. Snowshoe hare distribution and habitat use in Wisconsin. – Can. Field-Nat. 96: 19–29.

Cahalane, V. H. 1947. Mammals of North America. – Macmillan.

Chanin, P. 1981. The diet of the otter and its relations with the feral mink in two areas in southwest England. – Acta Theriol. 26: 83–95.

Chanin, P. and Linn, I. J. 1980. The diet of the feral mink (*Mustela vison*) in southwest Britain. – J. Zool. Lond. 192: 205–223.

Crête, M. 1999. The distribution of deer biomass supports the hypothesis of exploitation ecosystems. – Ecol. Letters 2: 223–227.

Crête, M. and Manseau, M. 1996. Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. – Evol. Ecol. 10: 51–62.

Cuthbert, J. H. 1979. Food studies of feral mink (*Mustela vison*) in Scotland. – Fish. Manage. 10: 17–25.

Dyczkowski, J. and Yalden, D. W. 1998. An estimate of the impact of predators on the British field vole *Microtus agrestis* population. – Mammal. Rev. 28: 165–184.

Eberhardt, L. L. 2000. Reply: predator-prey ratio dependence and regulation of moose populations. – Can. J. Zool. 78: 511–513.

Eberhardt, L. L. and Peterson, R. O. 1999. Predicting the wolf-prey equilibrium point. – Can. J. Zool. 77: 494–498.

Ekerholm, P., Oksanen, L. and Oksanen, T. 2001. Long-term dynamics of voles and lemmings in low arctic tundra and above the willow limit as test of theories on trophic interactions. – Ecography (in press).

Erlinge, S. 1974. Distribution, territoriality, and numbers of the least weasel, *Mustela nivalis*, in relation to prey abundance. – Oikos 25: 308–314.

Erlinge, S. 1975. Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. – Oikos 26: 378–384.

Erlinge, S. 1977. Spacing strategy in stoat, *Mustela erminea*. – Oikos 28: 32–42.

Erlinge, S. 1981. Food preference, optimal diet and reproductive output in Swedish stoats *Mustela erminea*. – Oikos 36: 303–315.

Erlinge, S. and Sandell, M. 1988. Coexistence of stoat, *Mustela erminea*, and weasel, *M. nivalis*: social dominance, scent communication, and reciprocal distribution. – Oikos 53: 242–264.

Erlinge, S., Göransson, G., Hansson, L. et al. 1983. Predation as regulating factor on small rodent populations in southernmost Sweden. – Oikos 40: 36–52.

Erlinge, S., Göransson, G., Högstedt, G. et al. 1984. Can vertebrate regulate their prey? – Am. Nat. 123: 125–133.

Fitzgerald, B. M. 1977. Weasel predation on cyclic populations of the montane vole (*Microtus montanus*) in California. – J. Anim. Ecol. 46: 376–397.
Gilpin, M. E. 1975. Group selection in predator-prey communities. – Princeton Univ. Press.
Görner, M. and Hackethal, H. 1988. Säugetiere Europas. – Deutscher Taschenbuch Verlag and Ferdinand Enke Verlag.
Hamilton, W. D. 1959. Food of mink in New York. – New York Fish Game 6: 77–85.
Hansen, T. F., Stenseth, N. C., Henttonen, H. and Tast, J. 1999. Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. – Proc. Natl. Acad. Sci. USA 96: 986–991.
Hanski, I. and Korpimäki, E. 1995. Microtine rodent dynamics in northern Europe: parameterized models for predator-prey interaction. – Ecology 76: 840–850.
Hanski, I. and Henttonen, H. 1996. Predation on competing rodent species: a simple explanation of complex patterns. – J. Anim. Ecol. 65: 220–232.
Hanski, I., Hansson, L. and Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – J. Anim. Ecol. 60: 353–367.
Hanski, I., Turchin, P., Korpimäki, E. and Henttonen, H. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. – Nature 364: 232–235.
Hanski, I., Henttonen, H., Korpimäki, E. et al. 2001. Small rodent dynamics and predation. – Ecology (in press).
Hansson, L. 1987. An interpretation of rodent dynamics as due to trophic interactions. – Oikos 50: 308–318.
Hansson, L. and Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. – Oecologia 67: 394–402.
Haukisalmi, V. and Henttonen, H. 1993. Population dynamics of *Taenia polyacantha* metacestodes in the bank vole *Clethrionomys glareolus*. – Ann. Zool. Fenn. 30: 81–84.
Hayes, R. D., Baer, A. M., Wotschikowsky, U. and Harestad, A. S. 2000. Kill rate by wolves on moose in the Yukon. – Can. J. Zool. 78: 49–59.
Henttonen, H. 1987. The impact of spacing behaviour in microtine rodents on the dynamics of least weasels, *Mustela nivalis* – a hypothesis. – Oikos 50: 366–370.
Henttonen, H., Oksanen, T., Jortikka, A. and Haukisalmi, V. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? – Oikos 50: 353–365.
Holling, C. S. 1959a. Some characteristics of simple types of predation and parasitism. – Can. Entomol. 91: 385–398.
Holling, C. S. 1959b. The components of predation as revealed by a study of small-mammal predation on the European pine sawfly. – Can. Entomol. 91: 293–320.
Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. – Theor. Popul. Biol. 12: 276–290.
Holt, R. D. and Polis, G. A. 1997. Theoretical framework for intraguild predation. – Am. Nat. 149: 745–764.
Hörnfeldt, B. 1991. Cycles of voles, predators, and alternative prey in boreal Sweden. – Doctoral dissertation, Umeå Univ., Umeå.
Hörnfeldt, B. 1994. Delayed density dependence as a determinant of vole cycles. – Ecology 75: 791–806.
Jêdrzejewska, B. and Jêdrzejewski, W. 1989. Seasonal surplus killing as hunting strategy of the weasel *Mustela nivalis* – Test of a hypothesis. – Acta Theriol. 34: 347–359.
Jêdrzejewski, W. and Jêdrzejewska, B. 1996. Rodent cycles in relation to biomass and productivity of ground vegetation and prediction in the Palearctic. – Acta Theriol. 41: 1–34.
Jêdrzejewska, B. and Jêdrzejewski, W. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study – Springer-Verlag.
Jêdrzejewski, W., Jêdrzejewska, B., Szymura, A. and Zub, K. 1996. Tawny owl (*Strix aluco*) predation in a pristine deciduous forest (Białowieża National Park, Poland). – J. Anim. Ecol. 65: 105–120.
Kauhala, K. 1996. Distributional history of the American mink (*Mustela vison*) in Finland with special reference to the trends in otter (*Lutra lutra*) populations. – Ann. Zool. Fenn. 33: 282–291.
King, C. M. 1975. The home range of the weasel (*Mustela nivalis*) in an English woodland. – J. Anim. Ecol. 44: 639–668.
King, C. M. 1989. The natural history of weasels and stoats. – Christopher Helm.
King, C. M. and Moors, P. J. 1979. On co-existence, foraging strategy and the biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. – Oecologia 39: 129–150.
Klemola, T., Korpimäki, E. and Norrdahl, K. 2000a. Do delayed effects of overgrazing explain population cycles in voles? – Oikos 90: 509–516.
Klemola, T., Koivula, M., Korpimäki, E. and Norrdahl, K. 2000b. Experimental tests of predation and food hypotheses for population cycles of voles. – Proc. R. Soc. Lond. B 267: 351–356.
Korpimäki, E. and Norrdahl, K. 1989a. Avian predation on mustelids in Europe 2: impact on small mustelids and microtine dynamics – a hypothesis. – Oikos 55: 273–276.
Korpimäki, E. and Norrdahl, K. 1989b. Avian predation on mustelids in Europe 1: occurrence and effects on body size variation and life traits. – Oikos 55: 205–215.
Korpimäki, E. and Krebs, C. J. 1996. Predation and population cycles of small mammals. – BioScience 46: 754–764.
Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small mammal cycles. – Ecology 79: 2448–2455.
Korpimäki, E., Norrdahl, K. and Rinta-Jaskari, T. 1991. Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? – Oecologia 88: 552–561.
Krebs, C. J., Boonstra, R., Boutin, S. et al. 1992. What drives the snowshoe hare cycle in Canada's Yukon? – In: McCullough, D. R. and Barrett, R. H. (eds), Wildlife 2001: populations. Elsevier, pp. 886–896.
Krivan, V. 1996. Optimal foraging and predator-prey dynamics. – Theor. Popul. Biol. 49: 265–290.
Krivan, V. 2000. Optimal intraguild foraging and population stability. – Theor. Popul. Biol. 58: 79–94.
Lambin, X., Eston, D. A., Petty, S. J. and MacKinnon, J. L. 1998. Spatial asynchrony and traveling waves in cyclic populations of field voles. – Proc. R. Soc. Lond. B 265: 1491–1496.
Lambin, X., Eston, D. A., Petty, S. J. and MacKinnon, J. L. 2000. Cyclic dynamics in field populations and generalist predation. – J. Anim. Ecol. 69: 106–118.
Latham, R. M. 1952. The fox as a factor in the control of weasel populations. – J. Wildl. Manage. 16: 516–517.
Leslie, P. 1948. Some further notes on the use of matrices in population dynamics. – Biometrika 35: 213–245.
Lindström, E. 1989. Food limitation and social regulation in a red fox (*Vulpes vulpes*) population. – Holarct. Ecol. 12: 70–79.
Lindström, E. 1992. Diet and deomography of the red fox (*Vulpes vulpes*) in relation to population density. – In: McCullough, D. R. and Barrett, R. H (eds), Wildlife 2001: populations. Elsevier, pp. 922–931.
Lindström, E. 1994. Vole cycles, snow depth and fox predation. – Oikos 70: 156–160.
Lockie, J. D. 1966. Territoriality in small carnivores. – Symp. Zool. Soc. Lond. 18: 143–165.
Marshal, J. P. and Boutin, S. 1999. Power analysis of wolf-moose functional responses. – J. Wildl. Manage. 63: 396–402.
May, R. M. 1973. Stability and complexity in model ecosystems. – Princeton Univ. Press.

McLaren, B. E. and Peterson, R. O. 1994. Wolves, moose and tree rings on Isle Royale. – Science 266: 1555–1557.
Mebs, T. and Scherzinger, W. 2000. Die Eulen Europas. – Franckh-Kosmos.
Mech, L. D. 1966. The wolves on Isle Royale. – Fauna of the National Parks of the United States Fauna Series 7, Washington.
Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white tailed deer. – J. Anim. Ecol. 60: 377–393.
Messier, F. 1994. Ungulate population models with predation: a case study with the North American Moose. – Ecology 75: 478–488.
Messier, F. and Joly, D. O. 2000. Comment: regulation of moose populations by wolf predation. – Can. J. Zool. 78: 506–510.
Mook, J. H., Mook, I. J. and Heikens, H. S. 1960. Further evidence for the role of 'search images' in the hunting behavior of titmice. – Arch. Néerl. Zool. 13: 448–465.
Murdoch, W. W. 1977. Stabilizing effects of spatial heterogeneity in predator-prey systems. – Theor. Popul. Biol. 11: 252–273.
Murdoch, W. W. and Oaten, A. 1975. Predation and population stability. – Adv. Ecol. Res. 9: 1–131.
Niemimaa, J. and Pokki, J. 1990. Minkin ravinnosta Suomenlahden ulkosaaristossa. – Suomen Riista 36: 18–30 (with English summary).
Norrdahl, K. 1995. Population cycles in northern small mammals. – Biol. Rev. 70: 621–637.
Oksanen, L. 1990. Exploitation ecosystems in seasonal environments. – Oikos 57: 14–24.
Oksanen, L. and Oksanen, T. 2000. Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarksvidda, northern Norway. – Rep. Kevo Subarct. Res. Stn. 17: 7–31.
Oksanen, L. and Oksanen, T. 1992. Long-term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. – Ecography 15: 226–236.
Oksanen, L. and Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. – Am. Nat. 155: 703–723.
Oksanen, L., Aunapuu, M., Oksanen, T. et al. 1997. Outlines of food webs in a low arctic tundra landscape in relation to three theories on trophic dynamics. – In: Gange, A. C. and Brown, V. K. (eds), Multitrophic interactions in terrestrial systems. Blackwell Science, pp. 351–373.
Oksanen, T. and Henttonen, H. 1996. Dynamics of voles and small mustelids in the taiga landscape of northern Fennoscandia in relation to habitat quality. – Ecography 19: 432–443.
Oksanen, T., Oksanen, L. and Norberg, M. 1992. Habitat use of small mustelids in a tundra landscape: a test of the hypothesis of patchy exploitation systems. – Ecography 15: 237–244.
Oksanen, T., Schneider, M., Rammul, Ü. et al. 1999. Population fluctuations of voles in North Fennoscandian tundra: contrasting dynamics in adjacent areas with different habitat composition. – Oikos 86: 463–478.
Oksanen, T., Oksanen, L., Jêdrzejewski, W. et al. 2000. Predation and the dynamics of the bank vole, *Clethrionomys glareolus*. – In: Bujalska, G. and Hansson, L. (eds), The bank vole: a study in population dynamics. Pol. J. Ecol. (Suppl.) 48: 197–217.
Persson, L. and Diehl, S. 1990. Mechanistic individual-based approaches in the population/community ecology of fish. – Ann. Zool. Fenn. 27: 165–182.
Peterson, R. O. and Page, R. E. 1983. Wolf-moose fluctuations at Isle Royale National Park, Michigan, U.S.A. – Acta Zool. Fenn. 174: 251–253.
Prévot-Julliard, A.-C., Henttonen, H., Yoccoz, N. G. and Stenseth, N. C. 1999. Delayed maturation in female bank voles: optimal decision or social constraint? – J. Anim. Ecol. 68: 684–697.
Pulliainen, E. 1984. Pohjois-Suomen minkkien ravinnon koostumuksesta runsaan pikkujyrsijäkannan oloissa. – Suomen Riista 31: 43–46 (with English summary).
Rosenzweig, M. L. 1966. Community structure in sympatric carnivora. – J. Mammal. 47: 602–612.
Rosenzweig, M. L. 1969. Why the curve has a hump? – Am. Nat. 103: 81–87.
Rosenzweig, M. L. 1971. Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. – Science 171: 385–387.
Rosenzweig, M. L. 1973. Evolution of the predator isocline. – Evolution 27: 84–94.
Rosenzweig, M. L. 1977. Aspects of biological exploitation. – Q. Rev. Biol. 52: 371–380.
Rosenzweig, M. L. and MacArthur, R. H. 1963. Graphical representation and stability conditions of predator-prey interactions. – Am. Nat. 97: 209–223.
Ryszkowski, L., Wagner, C. K., Goszczynski, J. and Truszkowski, J. 1971. Operation of predators in a forest and cultivated fields. – Ann. Zool. Fenn. 8: 160–169.
Schindler, U. 1972. Massenwechsel der Erdmaus, (*Microtus agrestis* L.) in Süd-Niedersachsen 152-71. – Z. Angew. Zool. 59: 189–203.
Siivonen, L. 1975. Pohjolan nisäkkäät. – Otava, Keuruu.
Solomon, M. E. 1949. The natural control of animal populations. – J. Anim. Ecol. 18: 1–35.
Stenseth, N. C. 1999a. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. – Oikos 87: 427–461.
Stenseth, N. C. 1999b. Common dynamic structure of Canada lynx populations within three climatic regions. – Science 285: 1071–1073.
Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton Univ. Press.
Taitt, M. J. and Krebs, C. J. 1985. Population dynamics and cycles. – In: Tamarin, R. H. (ed.), Biology of New World *Microtus*. American Society of Mammalogists, Shippens, PA, pp. 567–620.
Tanner, J. T. 1975. The stability and intrinsic growth rates of prey and predator populations. – Ecology 56: 855–867.
Tapper, S. 1979. The effect of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland. – J. Anim. Ecol. 48: 603–617.
Tinbergen, L. 1960. The natural control of insects in pine woods. I Factors influencing the intensity of predation by songbirds. – Arch. Néerl. Zool. 13: 265–343.
Turchin, P. 2001. Does population ecology have general laws? – Oikos 94: 17–26.
Turchin, P. and Hanski, I. 1997. An empirically based model for latitudinal gradient in vole population dynamics. – Am. Nat. 149: 842–874.
Turchin, P., Oksanen, L., Ekerholm, P. et al. 2000. Are lemmings prey or predators? – Nature 405: 562–564.
Uttendörfer, O. 1952. Neue Ergebnisse über die Ernährung der Greifvögel und Eulen. – Eugen Ulmer.
Zalewski, A., Jêdrzejewski, W. and Jêdrzejewska, B. 1995. Pine marten home ranges, numbers and predation on vertebrates in a deciduous forest (Białowieża National Park, Poland). – Ann. Zool. Fenn. 32: 131–144.