

Bank vole biology: Recent advances in the population biology of a model species

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PREDATION AND THE DYNAMICS OF THE BANK VOLE, *CLETHRIONOMYS GLAREOLUS*

ABSTRACT: Theoretical analyses and data suggest that the interaction between bank voles and their predators generates a locally stable equilibrium, regardless to the composition of the predator guild. The suggested primary proximate source for stability is female territoriality. Predation *per se* appears to be destabilizing. Whether or not predation regulates bank voles appears thus to be a semantic issue, depending on the operational definition of the concept of regulation. Confusion has arisen as different operational definitions have been tacitly used by different authors. The predicted intrinsic stability of bank vole-predator systems is most clearly displayed in the southern part of the boreal zone. Currently, even the dynamics of bank voles of taiga landscapes in Finnish Lapland are close to the predicted multiannual stability.

In those boreal areas, where grassy and productive *Microtus* habitats are relatively abundant, sustained, multiannual cycles appear to be generated by the interaction between small mustelids and *Microtus* spp. When densities of *Microtus* decline, fidelity to *Microtus* habitats becomes suboptimal for predators. Consequently, cyclicality seems to be externally imposed on bank voles, due to changing habitat preferences of predators during the course of the mustelid-*Microtus* cycle. In the temperate zone,

masting (seed crops of deciduous trees) increases the reproductive rate of bank voles and ameliorates female territoriality, initiating a transient increase in the numbers of bank voles and their predators. Before the system reaches its new equilibrium, the mast is over. Due to the combined effect of high predator numbers and normal reproductive performance, bank vole numbers then decline to the low level typical for post-mast years. Depending on the frequency of masting, the post-mast low can be followed by a stable phase or immediately by a new mast-triggered outbreak. Although fundamentally different mechanisms appear to account for multiannual density fluctuations in temperate and boreal bank vole populations, both phenomena can be interpreted as consequences of external perturbations upon intrinsically stable predator-prey systems.

KEY-WORDS: bank vole, *Microtus*, predators, boreal zone, temperate zone, modelling

1. INTRODUCTION

In the literature on population dynamics of microtine rodents, there is a long tradition of intense debates between schools emphasizing different factors, especially concern-

ing the role of predation (Norrdahl 1995, Korpimäki and Krebs 1996). In these debates, it has sometimes been difficult to distinguish differences in verbalization from conflicting views concerning biological issues, because the relationship between the implications of models and verbal concepts of regulation and limitation are not straight-forward. Moreover, the fact that predator-prey models are automatically multifactorial has been confusing for the advocates of a single factor approach. In all reasonable predator-prey models, the prey equation contains even a term for prompt density dependence, presumably generated proximately by social interactions, with the ultimate scope to ensure a sufficient resource basis for the prey (Stenseth 1986, L. Oksanen 1990, Hanski *et al.* 1991, in press). Even in model systems, so constructed that predation reduces average prey densities by orders of magnitude, relative predation rates (per cent of prey population removed in unit time) are often inversely density dependent in the neighbourhood of the equilibrium, and the local stability of the equilibrium depends on social interactions in prey.

The conceptual problems are especially pronounced for a widespread species such as the bank vole. The range of the bank vole covers a large part of the Palearctic region, extending from the northern fringes of the taiga to the southern limit of temperate deciduous forests. Along this geographical gradient, the diet of the species changes entirely, so does the reproductive behaviour of food plants and the composition of the predator guild. Our primary focus in this presentation is to study how predator-prey interactions contribute to the regulation of bank voles in different parts of its range. We approach the problem by constructing a simple predator-prey model, based on premises, which can be applied over the whole range of the species. We then relate model predictions to the extensive data sets on bank voles and their predators in boreal and temperate landscapes. Although our focus is on the bank vole in their typical forest habitats, especially our discussion of boreal dynamics includes excursions to systems where other rodent species prevail, because these subsystems are essential for understanding the landscape level dynamics of bank voles. As it is practical to proceed from the simple to the complex, we start with a somewhat hypothetical situation – bank voles inhabiting a northern taiga landscape, entirely consisting of relatively pro-

ductive coniferous forests. Moreover, we assume that the microtine community is totally dominated by the bank vole or by closely related and ecologically similar species (the red vole, *Clethrionomys rutilus* or by the American red back vole, *C. gapperi*) and the predator guild is dominated by a specialist predator, the least weasel *Mustela nivalis*.

2. THE THEORETICAL FRAMEWORK AND DYNAMICS IN A HOMOGENOUS NORTH BOREAL TAIGA LANDSCAPE

In theoretical studies concerning microtine dynamics the most frequently used approaches are the stacked logistic model (Leslie 1948, May 1973), used e.g. by Hanski *et al.* (1991, 1993) and laissez-faire models, developed by Rosenzweig (1971, 1977), used e.g. by Stenseth (1980; vole-plant interaction) and L. Oksanen (1990). The shared feature of both approaches is that density-dependent prey reproduction and different functional responses of predators are introduced to the framework of the classical Lotka-Volterra equations or their modifications. The logic in prey equation is identical in both models. In the absence of predation, the density of the prey increases at a rate determined by the product of its density (N), its reproductive potential (r), and a function $g(N, K)$, representing direct density-dependence of *per capita* reproductive output. The logistic equation, where $g(N, K) = 1 - N/K$, represents the most frequently used form of density-dependence in predator-prey models (Hanski *et al.* 1991, 1993, Turchin and Hanski 1997). This density-dependence is assumed to be linear and K stands for the prey density at which their population growth becomes zero in the absence of predation. The problem for this model is that it lacks a connection to the biology of microtine rodents. According to *Clethrionomys* specialists, density-dependence in *Clethrionomys* spp. is based on female territoriality (Bujalska 1970, Viitala 1977, Henttonen 1987, Löfgren 1995, Prévot-Julliard *et al.* 1999). This can be expressed by assuming $g(N, K) = \min(1, K/N)$, K standing for the density at which the density of reproducing females is equal to the maximum density of female territories. This assumption leads to much weaker density-dependence than in the logistic case. In the female territoriality

model, $N = K$ stands for the density at which population growth changes from exponential to linear and immature females start to accumulate. The difference between the two mechanisms of density-dependence is illustrated in Fig. 1. In spite of the entirely different biological foundations and different patterns in the intensity of density-dependence, it is not easy to distinguish between the two mechanisms by using real data which are likely to be noisy. The logistic model has technical advantages because prey dynamics can be expressed in a single, differentiable equation. In conceptual work, however, we regard the female territoriality model as preferable, because the parameter K is then derived from the biology of *Clethrionomys* spp. Both models share the same simplifying premise that the combination of predation and direct density-dependence together prevents the herbivorous prey from reaching so high densities that the forage basis would be severely depleted. (The interaction between prey and its forage includes time delays of its own and cannot thus normally be included in the density-dependent term of the prey equation.) Fortunately, bank voles are primarily found in relatively productive environments, where it would take enormous herbivore densities to destroy the vegetation. For these systems, the assumption that the basic food (dwarf shrubs, twigs, buds) is not depleted is not especially restrictive (Oksanen *et al.* 1981, Oksanen and Oksanen 2000).

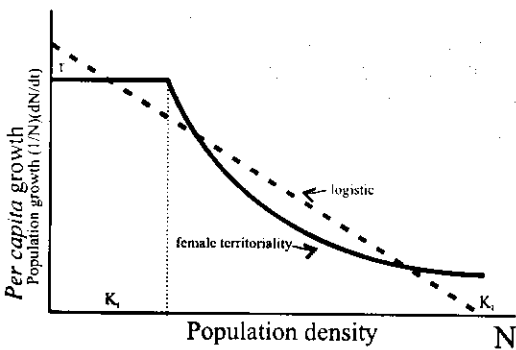


Fig. 1. The relation between population density (N) and per capita rate of population growth $(1/N)(dN/dt)$ in the absence of predation in systems where direct density-dependence is entirely caused by female territoriality, having no impact on the reproductive output of territory holders or on the survival of juveniles. A logistic function which approximates this form of density-dependence at low and moderate population densities is denoted with a dashed line, hitting the N -axis at $N = K_l$. K_t denotes the density at which female territoriality becomes limiting for the maturation of females

Encounters between predators and prey impose losses on the prey population. The absolute predation rate (number of prey removed in unit time) is determined by the product of prey density (N), predator density (C), searching efficiency of predators (a) and the fraction of the predator population which is actively searching for prey, $f(N)$, which can take values between 1 and 0. The product $af(N)N$ is thus the functional response of predators. In boreal systems, dominated by specialists, we can assume that resident predators have type II functional response (Hanski *et al.* 1991, 1993, Hanski and Korpimäki 1995, Turchin and Hanski 1997, see also below) where $f(N) = 1/(1 + ahN)$, h being the handling time per captured prey.

In order to cover the whole range of the bank vole, the model should incorporate the impacts of the variation in the abundance of high-quality food. When high-quality food abounds, female territories of *Clethrionomys* voles shrink (Ims 1987, Löfgren 1996, Prévot-Julliard *et al.* 1999) and the reproductive season gets longer (Secher Jensen 1982, H. Henttonen, pers. comm.). In the prey equation, we should thus index the parameter K as K_q and the parameter r as r_q to emphasize that the values of these parameters depend on the production of high-quality forage (the subindex q thus standing for the supply of high quality food). Moreover, abundant supply of high-quality forage allows the prey to spend less time foraging and to be more vigilant, which reduces the searching efficiency of predators. Hence, even the parameter a is indexed as a_q .

The above considerations lead to the following equation for prey dynamics:

$$dN/dt = r_q Ng(N, K_q) - a_q f(N)NC \quad (1)$$

Setting $dN/dt=0$, we obtain the equation for prey's (zero) isocline (the set of combinations of predator and prey densities, at which prey has zero rate of population growth) as:

$$C = (r_q/a_q)g(N, K_q)/f(N) \quad (2)$$

Given that density-dependence in prey is based on female territoriality and the dominating predators are resident specialists with type II functional response, equation (2) can be rewritten as:

$$C = (r_q/a_q)(1 + a_q hN) \text{ for } N < K_q \quad (3)$$

and

$$C = (r_q/a_q)(K_q/N)(1 + a_q h N) \text{ for } K_q < N \quad (4)$$

Thus, the prey isocline is a straight line with a positive slope for all $N < K_q$ i.e. when prey densities are so low that maturing females can find vacant territories. For higher prey densities the isocline is asymptotically decreasing function with $K_q a_q h$ as its lower asymptote. The dominating boreal specialists – least weasels – have short handling times, because their hunting behaviour typically consists of activity bouts when prey are searched, killed and cached, and are usually consumed later (Erlinge 1974, T. Oksanen 1990). Hence, the rising part of the prey isocline has a shallow slope, and the asymptote of the descending part lies close to the prey axis. The value of K_q can be estimated from the data of Prévot-Julliard *et al.* (1999, see also Henttonen *et al.* 1987). In northern taiga habitats, where bank voles largely depend on bilberry twigs, the maximum density of breeding females is about 5 per hectare, i.e. about 10 adult voles per ha. On a grid with plentiful high-quality food (oats), recruitment was observed even at the highest recorded density, 15 breeding females per hectare, indicating that the value of K_q exceeds 30 adult voles per ha in habitats where high-quality food abounds.

The equation for predator dynamics of laissez-faire and stacked logistic models are entirely different. In pure laissez-faire models, predators are assumed to search for prey independently of each other and their *per capita* dynamics are assumed to depend solely on the difference between energy needs and rates of prey capture. Due to the absence of direct density dependence in predators, the predator isocline generated by a laissez-faire model is vertical and meets the prey axis where prey density is just enough to sustain zero balance between energy losses and gains of a predator. In a pure stacked logistic model, in turn, there is no explicit connection between predator dynamics and the predation process. Prey density enters the model in the form of carrying capacity. The stacked logistic model creates predator isoclines with a positive slope, passing through the origin. As pointed out by P. Turchin (pers. comm.) the basic stacked logistic model corresponds to a situation where territoriality limits recruitment rate in predators, and territory sizes are adjusted to contain a fixed number of prey. Moreover, prey density is assumed to be so

high that the reproductive output of predators does not depend on the rate of prey capture. Dynamics at high predator and prey densities, where the above assumptions are reasonable, are crucial for the shape of the limit cycle, and the stacked logistic model has indeed been successful as a simulation tool (Hanski *et al.* 1991, 1993, Hanski and Henttonen 1996, Hanski and Korpimäki 1995, Turchin and Hanski 1997). Conversely, pure laissez-faire models tend to produce limit cycles with unrealistically high amplitude, especially if starvation of predators is modelled as exponential decrease (Gilpin 1975).

In studying the potential role of predation, it is essential to understand the stability properties of the bank vole – weasel model system. In this context, the conceptual strength of the laissez-faire model is obvious. The stability of the predator-prey equilibrium is determined by dynamics in the neighbourhood of the equilibrium – i.e. by dynamics at prey densities barely sufficient to allow an average predator to get its energy needs satisfied and at predator densities barely sufficient to create a balance between mortality and natality in this sparse prey population. Studies on small mustelids conducted under these conditions witness about broadly overlapping home ranges (Erlinge 1974, 1977, King 1975, 1989, Oksanen *et al.* 1992, Oksanen and Schneider 1995). Females show mutual avoidance during the reproductive season but evidence for territorial defense between reproducing females have only been observed at high weasel densities (Lockie 1966). Consequently, we have chosen to apply the laissez-faire approach, where the dynamics of predators are represented by a following differential equation:

$$dC/dt = -mC + ka_q f(N)NC \quad (5)$$

where m stands for the *per capita* maintenance costs of predators and their *per capita* rate of decline in the absence of prey and k is the assimilation efficiency of predators. Setting the growth rates of predators equal to zero, we obtain the equation for a laissez-faire predator isocline as:

$$N^* = m/(ka_q f(N^*)) \quad (6)$$

assuming type II functional response, equation (6) can be rewritten as

$$N^* = m/(a_q(k - mh)) \quad (7)$$

Equation (7) generates the typical vertical isocline of laissez-faire models. From equation (6) we see that the verticality of the predator isocline does not depend on functional response. Provided that $f(N)$ is a well-defined function, its value is uniquely determined by the value of its argument. Hence, $f(N^*)$ is a constant regardless to the shape of the $f(N)$ function, although we cannot determine the position of the predator isocline without specifying the functional response.

The potential of predator-prey systems to generate cyclic dynamics depends on the implicit time lag of these models. Increase in prey density increases the reproductive rate of predators, but the connection between reproductive rate and density is inevitably time delayed, whether or not the delay can be empirically detected. The stability analysis of laissez-faire models is simple because small changes in predator density have no immediate impacts on predator dynamics. In simple systems with type II functional response, small increases in prey density have two opposing impacts. First, predators spend a greater proportion of time handling already captured prey, which decreases the *per capita* predation risk for the prey (relative predation rate). Second, prey may experience direct density-dependence, which decreases their *per capita* reproductive output. In more complex systems (e.g. with type III functional response), the function $f(N)$ may even contain rising sections. Anyway, the net impact of these opposing forces is seen in the ratio $g(N, K_q)/f(N)$, which even determines the slope of the prey isocline (see equation (2)). If this ratio is a decreasing function of N in the neighbourhood of N^* , increased prey density leads to a negative rate of prey population growth, and, hence, to return towards the equilibrium. In the converse case, increased prey density leads to a positive rate of population growth, followed by predator-prey oscillations with increasing amplitude. Consequently, the equilibrium is locally unstable. Hence, a necessary and sufficient condition for a locally stable equilibrium in a laissez-faire model is that the slope of the prey isocline is negative at $N = N^*$ (see Rosenzweig 1971). If the slope is positive, Lyapunov's theorem tells that the system will have a cyclic attractor, referred to as a stable limit cycle. The assumption of pure laissez-faire dynamics can be relaxed by recalling that direct density-dependence is always stabilizing. Hence, the stacked logistic model can create a stable equilibrium

for parameter combinations which in laissez-faire models lead to cyclic dynamics, whereas the converse cannot happen.

Before we can combine the predator and prey equations for the bank vole - weasel system, we need information on the magnitude of N^* . According to Erlinge (1974) weasels are starving when densities of field voles are about 10 individuals per hectare. Bank voles are smaller and also more elusive. In the study area of King (1975), where the densities of bank voles and wood mice ranged from 20 to 40 individuals per hectare, least weasel reproduction was sporadic, and several disappearances of weasels were preceded by symptoms indicating starvation. It is thus safe to assume that N^* for systems with bank voles as the dominating prey and least weasels as the dominating predator is about 30 voles per hectare. Assuming an approximately even sex ratio, this implies that $N^* > 2K_q$ for boreal systems without large amounts of high-quality forage.

Predator and prey isoclines corresponding to the above arguments and equations are presented in Fig. 2. The main message of the model is that in taiga areas with little or no high quality forage, with bank voles as the dominating prey and with least weasels as the dominating predator, the predator-prey equi-

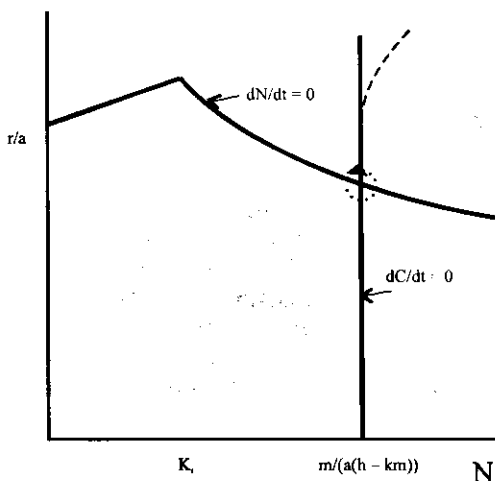


Fig. 2. An isocline model for a boreal predator (weasel) - prey (bank vole) system corresponding to equations (3), (4) and (7). The impact of direct density-dependence between predators at high density on the predator isocline is denoted by dashed lines. Due to the elusiveness of bank voles and the large size of their female territories in boreal systems without masting, the equilibrium point lies on the descending part of the prey isocline and is thus locally stable even in the absence of direct density dependence in predators

librium should be stable. Notice, that the model also illustrates the ambiguity of the concepts "to limit" and "to regulate". According to the model, the stability of the equilibrium is entirely caused by social interactions among bank voles, whereas predation rates are predicted to be inversely density-dependent in the neighbourhood of the equilibrium. However, the kind of social regulation included in the model is in itself insufficient to limit the population growth of bank voles. The model predicts that the removal of predators should lead to a population growth of prey at a constant rate, until factors not included in the model – such as destruction of the vegetation – enter the scene.

In spite of being based on premises, which are maximally unlikely to yield a stable equilibrium – pure laissez-faire dynamics in predators, total dominance of specialized residents (least weasels) in the predator guild, and only weak density-dependence in the prey – the above analysis leads to the same conclusion as obtained by Hanski and Henttonen (1996) with the stacked logistic model: predator-microtine systems dominated by bank voles should be characterized by multiannual stability. Sustained cycles can be imposed on intrinsically stable predator-prey systems by periodic changes in parameter values, e.g. due to masting (Kalela 1962, Tast and Kalela 1971, Sells 1997). However, the pronounced, synchronous pulses of flowering and fruit production, assumed by the above authors, have not been found in boreal data (Laine and Henttonen 1983, Oksanen and Ericson 1987). What little synchrony is observed seems to reflect the direct damage caused by vole peaks on dwarf shrubs (Ericson 1977). Moreover, if pronounced periodic masting were typical for boreal ground vegetation, then multiannual fluctuations of microtine rodents in northern taiga should be a robust phenomenon. This is not the case. In Finnish Forest Lapland, the classical vole cycles have been replaced by less regular fluctuations with strong seasonal component. This change of dynamics has, to our knowledge, not been accompanied by any dramatic changes in berry production whereas it has been associated with changes in the predator guild (increased abundance of stoats and minks, recovery of red foxes and decreased abundance of least weasels) and by increased predominance of bank voles in the vole guild (Haukisalml and Henttonen 1993, Hanski and Henttonen 1996, Ok-

sanen and Henttonen 1996, Prévot-Julliard *et al.* 1999). Although the causal connections can be complicated (Hanski and Henttonen 1996), the change in dynamics, coinciding with the emergence of bank voles as dominating prey species, corroborates the prediction that predator-prey dynamics in a northern taiga dominated by bank voles generates a stable equilibrium.

3. THE CONNECTION BETWEEN THE DYNAMICS OF *CLETHRIONOMYS* AND *MICROTUS* DYNAMICS IN THE BOREAL ZONE

The flat expanses of the Fennoscandian Shield landscape, typical for the Finnish Forest Lapland, are not far from the hypothetical homogeneous taiga, which formed the basis of the above analysis. Huge areas are occupied by forests with field layer dominated by dwarf shrubs, mosses and/or lichens, and most of the rest is covered by barren bogs. In the Pallasjärvi area, where the studies of H. Henttonen and his co-workers have been conducted (Henttonen *et al.* 1987, Haukisalml and Henttonen 1993, Prévot-Julliard *et al.* 1999), herb and grass-rich habitats only cover about one per cent of the landscape (Eronheimo *et al.* 1992, R. Virtanen, unpubl. data). Such homogeneity is, however, atypical for boreal Fennoscandia. Closer to the Scandinavian mountains, topographical variation increases and nutrient-rich rocks are frequently exposed. Thus, the abundance of habitats with herbaceous ground vegetation is higher in Scandinavia than in Finland (about 10% of the landscape along the fringes of the Scandinavian mountain chain, Anonymous 1975–1983). Moreover, the abundance of habitats with herbaceous ground vegetation increases considerably southwards within the boreal zone, as an increasing fraction of the landscape is occupied by man-made fields. Understanding bank vole dynamics in the habitat complexes of western and central parts boreal Fennoscandia thus requires a grasp of the dynamics generated in herb- and grass-rich habitats, where the vole guild is dominated by *Microtus* species.

There is an essential difference between the social systems of *Clethrionomys* spp. and *Microtus* spp. In *Microtus* spp, female territoriality is weak, and even colonial breeding has been observed (Myllymäki 1977, Viitala 1977, Henttonen 1987). Hence, sub-

stantial density-dependence in *Microtus* is only observed at high densities. Moreover, *Microtus* voles are easier to capture for a predator than bank voles (Erlinge 1974). Assuming laissez-faire interactions, the weasel isocline thus inevitably crosses the *Microtus* isocline in the section where its slope is positive, generating cyclic dynamics. Even the stacked logistic model, biased in the favor of a stable equilibrium (see above), predicts cyclic dynamics with parameter values realistic for field voles and least weasels (Hanski *et al.* 1991, 1993, Hanski and Korpimäki 1995, Hanski and Henttonen 1996, Turchin and Hanski 1997). Hence, the conclusion of predation-driven cyclic *Microtus* dynamics is robust.

All predator-prey limit cycles in homogeneous landscapes are characterized by periods of very low prey density and mass starvation of predators, especially so if direct density dependence in predators is weak or absent and habitat of the prey is productive (Gilpin 1975, Abrams and Roth 1994, Lundberg and Fryxell 1995). Optimally behaving predators in a habitat mosaic of forests and fields should thus specialize on typical *Microtus* habitats during periods of high *Microtus* density. Conversely, when the density of *Microtus* spp. decreases, there should be a point at which hunting becomes equally rewarding (or equally little rewarding) in habitats dominated by *Clethrionomys* spp. as in typical *Microtus* habitats. At this point, predators should become habitat generalists and remain so until the recovery of *Microtus* spp. makes again *Microtus* habitats more rewarding. The postulated changes in habitat selection are supported by data (Oksanen *et al.* 1992, 1999, Klemola *et al.* 1999). The dynamical consequences of changing habitat preferences in predators have been analyzed by M. Gyllenberg, L. Oksanen and T. Oksanen (unpubl. data). Their main result is that optimal habitat selection in predators reduces the amplitude of the cycle, especially in landscapes dominated by *Clethrionomys* habitats. Simultaneously, it imposes a degree of cyclicity on *Clethrionomys* dynamics, because vole densities in all habitats should be depressed to low levels in the late phases of *Microtus* declines. Via the change in the habitat use of predators, forests dominated by *Clethrionomys* spp. may thus play a major role in keeping the amplitude of the weasel-*Microtus* cycle reasonable. The postulated difference in the dynamics of sympatric *Microtus* and bank voles is seen in the exten-

sive trapping record by Hörnfeldt (1994): the fluctuations of field voles has a cyclic pattern, whereas the fluctuation of bank voles is intermediate between cyclic and seasonal.

The mechanism described above is illustrated by the dynamics of microtine rodents and their predators within northernmost widespread agricultural landscape in Fennoscandia: South Ostrobothnia, western Finland (approx. 63°N, 23°E), where the densities of *Microtus* voles (field vole *M. agrestis* and sibling vole *M. rossiaemeridionalis*, earlier *M. epiroticus*) oscillate with a dominant period of 3 years (Fig. 3, and Korpimäki 1993, Hanski *et al.* 1993). Within this landscape population fluctuations of bank voles closely reflect the oscillations in *Microtus* voles, but with a lower amplitude (Fig. 3 and Korpimäki and Norrdahl 1989a, 1991b), as implied by the above argument. In years with high vole abundance, *Microtus* voles are the most abundant small mammals in agricultural fields and grasslands whereas bank voles dominate in forests. At low vole densities, bank voles outnumber *Microtus* voles even in agricultural fields (Figs 3 and 4). These recurrent invasions of the elusive bank voles in agricultural fields further support the role of predation in the cycle. If the microtine cycles were driven by changes in the quality of forage, bank voles, whose food plants are uncommon on agricultural fields, should be totally eliminated from these habitats during population declines.

Table 1 shows a summary of the diet composition of most important avian and mammalian predators that use small mammals as their main prey in South Ostrobothnia. According to these data, which cover both good and poor vole years, the two *Mi-*

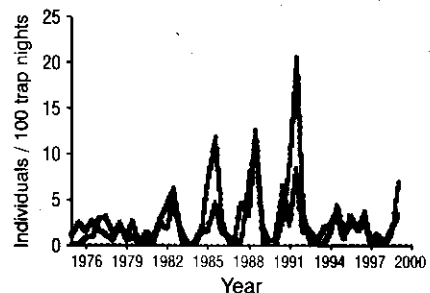


Fig. 3. The population oscillations of *Microtus* (red line) or bank voles (blue line) in the Kauhava region, western Finland. Data from regular snap-trappings performed every spring and autumn in agricultural fields and forests. For details, see Korpimäki and Norrdahl (1989)

crotus voles (field vole and sibling vole) are the main prey of most avian and mammalian predators. Bank voles are the main prey of only pygmy owls, *Glaucidium passerinum*, in both winter and spring, and of Tengmalm's owls, *Aegolius funereus* in spring. These owls are the only forest-dwelling species among predators listed in Table 1, and they also are able to hunt inside dense coniferous forests because of their small body size (Korpimäki 1992a). For example, Ural owls, *Strix uralensis*, eagle owls, *Bubo bubo*, common buzzards, *Buteo buteo* and red foxes, *Vulpes vulpes*, breed in coniferous forests, but probably are too large to effectively hunt bank voles in dense forests. In the data set collected annually during 1962 to 1971, the proportion of bank voles in the diet of breeding pygmy owls varied from 8 to 48% of prey items, whereas that of *Microtus* voles varied from 0 to 48% (Kellomäki 1977). Bank voles were the main prey in 8 of 10 years. In the long-term data set collected annually during 1966 to 1986, the proportion of bank voles in the food of breeding Tengmalm's owls varied from 3 to 45%, and that of *Microtus* voles from 6 to 61% (Korpimäki 1988). Bank voles were the main prey in 11 of 21 years.

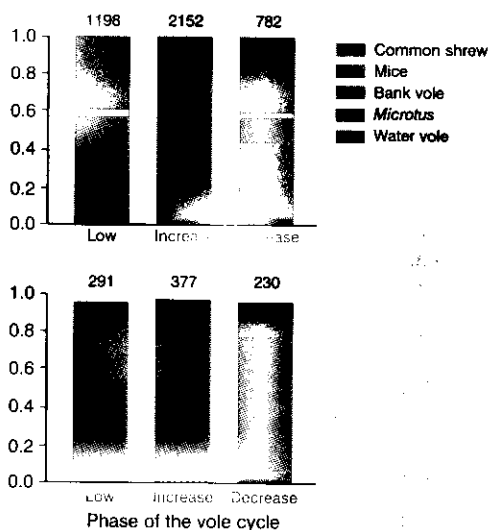


Fig. 4. The composition of small mammal assemblages in western Finland measured as the proportion of different species among snap-trapped individuals in agricultural fields (upper panel) and forests (lower panel) in years with low, increasing (high), or decreasing vole densities. Species, whose contribution to the total catch has consistently been less than 2%, have been omitted. Sample sizes are presented above bars. Snap traps were set in randomly chosen ditches or forest plots for two nights in April, June, August, and October. For more details see Norrdahl and Korpimäki (1995b)

According to radio telemetry studies made in agricultural fields in South Ostrobothnia, predation is the main cause of vole mortality (Norrdahl and Korpimäki 1995a, 1998). A majority of the voles studied were *Microtus*, but the mortality rate of bank voles appeared to be only slightly lower than that of *Microtus* voles (Table 2, and Norrdahl and Korpimäki 1995a). Both in *Microtus* and bank voles, small mustelids (the least weasel, *Mustela nivalis*, and the stoat, *M. erminea*) were responsible for 70% of kills whereas avian predators killed 16–28% of the voles studied (Table 2). The proportion of avian kills was higher in increasing than in decreasing populations of voles. Plots of relative predation rates against prey density or productivity can be used to examine whether mortality due to predation is dependent on prey density directly or with a time delay. Such plots have been constructed in order to find out whether predators have a potential to limit or regulate prey population densities (Sinclair 1989, Korpimäki 1993). Predation impact of breeding Tengmalm's owls on small mammals was studied in South Ostrobothnia during 11 years in an area dominated by spruce and pine forests (53% of the study area) but with high proportion of cultivated farmland (45%) (Korpimäki and Norrdahl 1989a). The relative predation rate (the percentage of prey items taken by breeding Tengmalm's owls out of the total number available in the study area) averaged 7% (S.D. = 5%) for *Microtus* voles and 6% (S.D. = 3%) for bank voles during 11 years (Korpimäki and Norrdahl 1989a). Tengmalm's owl predation impact on both *Microtus* and bank voles was directly dependent on prey density, i.e. a larger proportion of available voles was killed at high vole densities than at low ones. This was mainly because of two factors: breeding densities of owls were higher and owls produced larger broods in good vole years than in poor ones, and owls shifted to alternative prey when vole populations declined (Korpimäki and Norrdahl 1989a). Among these, shrews and small birds were most important.

Predation impact of three open-country birds of prey (the European kestrel, *Falco tinnunculus*, the short-eared owl, *Asio flammeus* and the long-eared owl, *A. otus*) on small mammals was studied in South Ostrobothnia during 11 years (Korpimäki and Norrdahl 1991a, 1991b). The mean predation rates of small mammals by these three birds of prey in the breeding season were 49% (S.D. = 27%)

Table 1. Diet composition of avian and mammalian predators in South Ostrobothnia, western Finland (% of prey items). N – number of prey items. Most of the data have been collected during three 3-year vole cycles (1983–1992) (see sources for further details)

Predator and season	<i>Microtus</i> spp.	Bank vole	Murids	Shrews	N	Source
Tengmalms' owl						
– winter	44.7	14.8	4.2	10.1	217	Korpimäki (1981)
– spring	26.8	24.2	3.0	33.1	12540	Korpimäki (1988)
Ural Owl						
– spring	31.1	11.4	2.8	11.9	1625	Korpimäki and Sulkava (1987)
Eagle owl						
– spring	24.6	1.3	31.0	0.5	2206	Korpimäki <i>et al.</i> (1990)
Long-eared owl						
– spring	70.8	10.2	4.4	11.6	3759	Korpimäki (1992)
Short-eared owl						
– spring	61.2	7.8	5.1	18.3	3626	Korpimäki and Norrdahl (1991b) and unpubl.
Pygmy owl						
– winter	15.3	22.3	1.0	17.2	215	Järvi (1986)
– spring	21.8	28.2	0.5	3.5	2240	Kellomäki (1977)
Hawk owl						
– spring	70.8	10.3	2.0	3.2	1207	Huhtala <i>et al.</i> (1987) and E. Korpimäki (unpubl.)
Kestrel						
– spring	36.4	8.4	6.7	11.9	2613	Korpimäki (1985)
Common buzzard						
– spring	21.9	4.1	0.7	6.7	868	E. Korpimäki (unpubl.)
Great-grey shrike						
– winter	51.2	6.5	24.4	14.3	168	Huhtala <i>et al.</i> (1977)
– spring	6.3	6.1	1.3	5.3	1840	Huhtala <i>et al.</i> (1977)
Stoat						
– winter	46.8	7.8	24.6	0.6	643	Korpimäki <i>et al.</i> (1991)
– summer	63.9	15.7	0.9	0	108	Korpimäki <i>et al.</i> (1991)
Least weasel						
– winter	68.3	8.9	13.3	1.3	158	Korpimäki <i>et al.</i> (1991)
– summer	67.9	10.7	0	0	28	Korpimäki <i>et al.</i> (1991)
Red fox						
– winter and summer	28.1	5.9	13.4	2.2	135	T. Laaksonen, M. Koivula, E. Korpimäki and K. Norrdahl (unpubl.)

for *Microtus* voles and 23% (S.D.=13%) for bank voles in good vole years, and 8% (S.D.=6%) and 4% (S.D.=4%), respectively, in poor vole years. The annual relative preda-

tion rates on *Microtus* and bank voles by breeding birds of prey were positively related to the spring density of voles (Korpimäki and Norrdahl 1991a), i.e. vole mortality by

Table 2. The proportion of radio-tracked *Microtus* and bank voles killed by small mustelids or avian predators in declining (years 1992, 1995) and increasing (years 1993, 1994) vole populations at Alajoki, western Finland. Each vole was tracked for 21 d or until it died. For details, see Norrdahl and Korpimäki (1995b, 1998)

Phase of vole cycle	Species	N	Killed	Proportion (%) killed by	
				mustelids	birds
Decrease	<i>Microtus</i>	49	25	84	16
Increase	<i>Microtus</i>	53	11	72	28
Increase	Bank vole	26	4	75	25

birds of prey depended directly on prey density in both voles. This was found despite the fact that bank voles are only the alternative prey for these open-country avian predators (Table 1; see also Korpimäki and Norrdahl 1991b). Direct density-dependence was attributable to fast numerical and functional responses of these birds of prey to fluctuating vole densities. Kestrels and two owls were even more mobile than Tengmalm's owls because both adult and young females and males showed low nest-site fidelity (Korpimäki 1994) which facilitated rapid immigration to and emigration from the area. In addition, birds of prey produced large broods in good vole years, and shifted to alternative prey when vole densities declined (Korpimäki and Norrdahl 1991b).

Predation impact by least weasels and stoats on voles was studied during six winters in South Ostrobothnia (Korpimäki *et al.* 1991). Relative predation rates on *Microtus* voles by least weasels in winter were positively correlated with the prey density in the preceding spring (9-month lag), but direct density-dependence was not found. The same delayed density-dependent relationship for the stoat remained non-significant (Korpimäki 1993). No direct or delayed density dependence was detected for bank voles, but both least weasels and stoats preyed on bank voles only at a low rate (Korpimäki *et al.* 1991). *Microtus* voles were their main prey, and mice (in particular harvest mouse *Micromys minutus*) was their most important alternative prey (Table 1). In addition, stoats killed high numbers of water voles *Arvicola terrestris* at low densities of their main prey (Korpimäki *et al.* 1991).

The above studies suggest that the boreal predator guild consists of two main compo-

nents with different functional responses. Small mustelids constitute one subguild, least weasels being more strict vole specialists than stoats. However, both species can be assumed to have type II functional response to voles, because the alternative prey of stoats by and large share the habitat of *Microtus* voles. Regardless of vole densities, stoats thus remain a threat for the surviving voles. (The impact of switching in the sense of the optimal foraging theory, i.e. dropping alternative prey when the density of voles is high, appears to be insufficient to have a detectable impact on functional response; see next section.) Predation by the small mustelid guild should thus be destabilizing, producing *Mustela-Microtus* cycles, to which bank voles are drawn as an alternative prey due to predator movements into bank vole habitats during periods of low *Microtus* densities as proposed by Henttonen (1987). The postulated changes in habitat selection of small mustelids are supported by data (Klemola *et al.* 1999).

The other subguild consists of avian predators, switching between voles and avian prey and/or reacting to changes in vole density with extensive movements. Change in habitat use influences the likelihood of predators to encounter voles in a given area – either *via* the fraction of predators choosing this area or *via* hunting at different heights from ground level. Hence, both these two behavioural mechanisms have a similar impact on the $f(N)$ function, which can be written as

$$f(N) = p(N)(a_q/(1 + a_qhN)) \quad (8)$$

where $p(N)$, getting values from 0 to 1, represents the fraction of the predator population hunting in the vole habitat and being a threat to voles. If the $p(N)$ function is sigmoid,

which is a plausible consequence of optimal foraging and the need to sample different habitats and hunting techniques, a stabilizing type III functional response will be generated (T. Oksanen *et al.*, in press). The threshold vole density for the invasion of avian predators and for the switching from avian to mammalian prey by resident avian predators is fairly high (Korpimäki *et al.* 1987, Korpimäki 1993). Hence, near-equilibrium dynamics of the system will be determined by the interaction between voles and small mustelids. The avian predators in turn, will reduce the amplitude of the limit cycle by imposing additional, density-dependent mortality on voles (see above) and on weasels (Korpimäki and Norrdahl 1989a, 1989 b).

Ultimately, all hypotheses are to be tested experimentally. Manipulations of densities of vole-eating predators have been performed in fences and islands, and in unfenced mainland areas. The message of fence and island experiments is clear indeed. Whether the scale of the experimental system is a greenhouse table, where a single vole represents an enormous density (Moën *et al.* 1993), fenced plots of hayfield (Klemola *et al.* 2000a, 2000b) or islands (Hambäck and Ekerholm 1997, L. Lingren, P. Ekerholm, G. Lopez, L. Oksanen, T. Oksanen and O. Suominen, unpubl. data), absence of predators consistently leads to sustained, very high vole densities and to total destruction of the vegetation. However, fences and water around islands prevent even normal movements of voles and their predators. Hence, manipulations of predator densities in large unfenced areas with sufficient replication in space and time should serve as a final test of the specialist predation hypothesis (Korpimäki and Krebs 1996). The effects of reduction of breeding avian predators (mainly European kestrels and Tengmalm's owls) on voles were studied during 1989–1992 (Norrdahl and Korpimäki 1995b). Potential breeding sites of birds of prey were removed from 5 unfenced farmland areas (3 km² each) in South Ostrobothnia, whereas control farmland areas had nest-boxes in addition to natural cavities and stick-nests. The distance between manipulation and control areas was 4 to 15 km. In all the four years, removal of nest sites resulted in lower breeding densities of birds of prey in manipulated areas than in control areas, but in densities of hunting raptors the difference between reduction and control areas was significant only in two

years. (Birds of prey may hunt far from their nests, and in other two years they might have aggregated to manipulation areas.) Reduction of breeding birds of prey caused short-term changes in the main prey (*Microtus* voles) dynamics but not in the alternative prey (bank vole) dynamics. Also, no long-term differences in vole densities between manipulated and control areas were found, possibly because least weasel densities tended to increase in manipulation areas, and increased weasel predation on voles might compensate for decreased avian predation losses.

Experiments along the same line were performed by Korpimäki and Norrdahl (1998) in two crash phases (1992 and 1995) of the three-year cycle of voles in South Ostrobothnia. They replicated the treatments sufficiently so that an area, rather than a rodent individual living in an area, could be used as an independent observation unit in statistical tests (Korpimäki *et al.* 1994, Korpimäki and Krebs 1996). In this experiment, densities of small mustelids (the least weasel and the stoat) and avian predators (mainly the European kestrel and Tengmalm's owl) were reduced in 6 different areas (2–3 km² each) (three areas both in 1992 and 1995) for approximately three months (late March to June). In areas with least weasel reduction and in control areas without predator manipulation, densities of *Microtus* voles continued to decline in the subsequent summer (June to August) both in 1992 and 1995, whereas the reduction of all main mammalian and avian predators resulted in an increase of densities of these voles in the course of the subsequent summer. In these areas, the densities of *Microtus* voles were 3-fold higher compared to control areas during June to August. The effects of predator reduction on bank voles were not that obvious, and the initial density in early spring, before the manipulation, significantly explained the inter-areal variation of bank vole densities in late summer. That a significant treatment effect for bank voles was not found was not unexpected, because all main predators reduced in this experiment (apart from Tengmalm's owl) shift to bank voles only at low densities of their main prey, *Microtus* voles (Korpimäki and Norrdahl 1989a, 1991a, 1991b, Korpimäki *et al.* 1991).

In these six predator manipulation areas, the mean proportion of pregnant *Microtus* vole females was 68.7% in late June to August, whereas the corresponding proportion was significantly lower (only 28.1%) for

control areas (Klemola *et al.* 1997a). There was no obvious difference in the proportion of pregnant females between manipulation and control areas before the start of the experiment, and body condition of females was not affected by the manipulation. In an earlier replicated predator manipulation made in large unfenced areas, reduction of small mustelids increased the proportion of pregnant bank vole females (90.1% in reduction areas and 24.7% in control areas) in the crash phase of the vole cycle (Korpimäki *et al.* 1994). The most plausible explanation of these results is that selective killing of female voles, in particular pregnant females, by small mustelids, slows down a population growth of voles, which then causes a summer crash, although environmental conditions are favorable for breeding voles and high-quality food is abundant in summer (Klemola *et al.* 1997b). That female voles are more vulnerable to small mustelid predation is also supported by the data from radio-collared voles (Norrdahl and Korpimäki 1998).

The experimental data summarized above corroborate the idea that sustained cyclic fluctuations in boreal populations of bank voles are driven by a *Mustela-Microtus* cycle, generated in productive habitats with herbaceous ground vegetation. The predation hypothesis also accounts for the geographical synchrony of small rodent cycles. Nomadic predators aggregate to patches of high prey density, reducing local densities close to the average density of a larger area (Ydenberg 1987, Korpimäki and Norrdahl 1989a). In the 5 areas with bird of prey reduction and 5 control areas in agricultural fields in South Ostrobothnia, hunting avian predators aggregated at high prey density areas in the early breeding season (April) and after their breeding season (August), but not during the late breeding season (June) when they were required to feed their young in the nest (Norrdahl and Korpimäki 1996). The reduction of breeding birds of prey increased variation in small rodent density (including *Microtus*, bank and water voles, and mice) among areas but not within areas. The difference in variation between manipulation and control areas was largest in the late breeding season of birds of prey (June), and decreased rapidly after the breeding season (August). With due respect to the potential synchronizing impact of climatic factors (Sinclair *et al.* 1993), the results summarized above suggest that the synchronizing potential of nomadic predators is strong. Predation and climatic factors ap-

parently are complementary, rather than exclusive, and contribute to the geographical synchrony in small rodent cycles (Norrdahl and Korpimäki 1996).

4. PREDATION AND THE DYNAMICS OF BANK VOLES IN EUROPE'S TEMPERATE FORESTS

The role and importance of predation for temperate vole populations is currently intensely debated. According to the Nordic school, violent *Microtus* cycles, characterized by deep lows when bank vole habitats are invaded by starving predators, disappear in the southern part of the boreal zone (Erlinge *et al.* 1983, Hansson and Henttonen 1985, Hanski *et al.* 1991), the suggested cause being the stabilizing impact of generalist predators and wintering avian predators. On the other hand, the 'cyclicality indices' (indices of multiannual variability) summarized by Hansson and Henttonen show large variation between different temperate populations, and clear cycles have been demonstrated from the temperate zone, too (Jędrzejewski and Jędrzejewska 1996, Lambin *et al.* 1998). However, *Microtus* cycles in the temperate zone are less synchronous and characterized by essentially higher vole densities than their boreal counterparts, and the difference is especially pronounced in the crash phase (Jędrzejewski and Jędrzejewska 1996, Lambin *et al.* 1998). In the habitat mosaics, where forest patches are small compared with the surrounding open landscape with cyclic *Microtus*, boreal-type invasions of hungry predators occur in temperate forests, too, suppressing densities of forest rodents but not being able to change their predominantly seasonal dynamics into cycles (Ryszkowski *et al.* 1973). Thus, externally imposed, predation driven cycles in temperate bank voles have not been recorded.

Another central difference concerns the food supply. In the temperate zone, in turn, forest floor in deciduous forests mainly harbor spring and summer herbs. This food supply is periodically supplemented by massive masting, to which bank voles respond by changing their territorial behavioural and reproductive effort (Secher Jensen 1982, Pucek *et al.* 1993, see also review by Hansson *et al.* 2000, this volume). In years when superabundant seed crops were produced during two subsequent years (e.g. oak and

hornbeam in 1995 and 1996 in Białowieża, see Fig. 6 in Hansson *et al.* 2000, in this volume), the result was an extended bank vole peak. The crucial role of high quality resources in temperate forests is further corroborated by two experiments with food addition for bank voles: (1) on a Crabapple Island in Bełdany Lake (NE Poland) (Andrzejewski 1975, Bujalska 1975, Banach 1986), and (2) in the Kampinos National Park, Central Poland (Andrzejewski 1975), resulting to 4–5-fold higher densities of bank voles in both winter and summer, as compared to controls. Just as in the case of masting, addition of high quality food caused winter breeding and improved survival of voles. The above data indicate that massive production or supplementation of high quality food does not only initiate transient dynamics but has even considerable impact on the value of the parameter a_q , influencing equilibrium prey density, as even indicated by supplemental feeding experiments in the boreal zone (see previous sections).

In order to understand the interaction between masting and predation on bank vole dynamics in temperate forests, it is essential to look at the results of detailed predation studies. Predation on bank voles in the deciduous and mixed forests of Europe has been studied in depth in three localities: (1) Turew, western Poland (Ryszkowski *et al.* 1973, Goszczyński 1977), (2) Wytham Wood, southern England (King 1980, Southern and Lowe 1982), and (3) Białowieża National Park, eastern Poland (Jędrzejewski *et al.* 1995, 1996; Zalewski *et al.* 1995, Jędrzejewski and Jędrzejewska 1993, 1996, Jędrzejewska and Jędrzejewski 1998). Turew and Wytham Wood are representative for small 'islands' of forest surrounded by unforested, agricultural landscape. Both places are characterized by impoverished communities of predators (<10 species present). By contrast, Białowieża is part of a large and well preserved woodland and it harbours very rich community of predators (totally over 30 species of carnivores and birds of prey).

The studies in Wytham Wood covered two species of predators, the tawny owl, *Strix aluco*, and the least weasel *Mustela nivalis*. Weasels exploited, on average, 8–10% of bank vole population per month (King 1980, 1985), and tawny owls removed 20–30% of bank vole standing crop per 2-monthly periods (Southern and Lowe 1982). In Turew, all predators (6–8 species) removed 28–56%

of forest rodents present throughout autumn and winter (non-breeding season of rodents) and 18% in spring-summer (breeding season; data combined for bank voles, yellow-necked mice, and field striped mice, but bank voles constituted, on average, 67% of all forest rodents). Predation contributed by 33–75% to the whole recorded mortality of forest rodents (Ryszkowski *et al.* 1973). Most important predators were pine martens (*Martes martes*, 34% of the total predation impact), red foxes (24%), common buzzards (19%), and tawny owls (18%).

In the pristine forests of Białowieża National Park, population dynamics of bank voles are characterized by 4–7 years of moderate densities with seasonal fluctuations and outbreak-crash sequences lasting two years, triggered by masting (usually synchronous in oak, hornbeam, and maple; Pucek *et al.* 1993, Hansson *et al.* 2000). The relation between the impact of predation and population density of prey can be studied by a detailed analysis of the whole predator community. In Białowieża Forest, bank voles constitute, on average, 53% of forest rodent numbers, and yellow-necked mice 26% (Jędrzejewska and Jędrzejewski 1998). Bank voles fell as prey to 20 species of carnivores and birds of prey out of 27 species of forest predators with known diet composition (i.e. nearly 75%). However, in six species only, bank voles were an important component of diet (Table 3). Three species, the Tengmalm's owl, the pine marten and the pygmy owl (all of boreal or boreal-nemoral distribution) preferred bank voles (Table 3). The roles of various predators in the total predation on bank voles were estimated combining information on diet composition, densities and food requirements of predators. In Białowieża Forest, tawny owls, weasels, common buzzards, and pine martens dominated in the predator community (Jędrzejewska and Jędrzejewski 1998). In effect, tawny owls appeared the single most important predator of bank voles; they consumed nearly half of bank vole numbers taken annually by all predators. In years of moderate density of bank voles, predators removed 60–90% of autumn numbers of rodents during the subsequent winter and were responsible for the whole winter mortality. In spring and summer (breeding season for rodents), predators removed an equivalent to 30–60% of the estimated seasonal increase in the numbers of bank voles. In outbreak years, the absolute predation rate (number of bank voles removed by predators) increased

Table 3. Predation on bank voles in deciduous and mixed forests of Białowieża Primeval Forest (E Poland), data for 1985–1994. * predators positively selecting bank voles from the available community of forest rodents. + denotes values <0.05 . Boldfaced are three most important predators of bank voles. Total annual predation amounted to 46.2 bank voles from an average hectare of the forest. Combined contribution of all other predators to the total annual predation on bank voles (blank spaces in the right column) is 1.8%. Source: Jędrzejewska and Jędrzejewski (1998, and unpubl.)

Species of predator	Bank vole in predator diet (% biomass)	Contribution of a predator to the total annual predation on bank voles
Tengmalm's owl <i>Aegolius funereus</i>	42.8*	
Pine marten <i>Martes martes</i>	34.5*	22.5
Pygmy owl <i>Glaucidium passerinum</i>	31.2*	1.8
Stoat <i>Mustela erminea</i>	31.0	
Weasel <i>Mustela nivalis</i>	21.9	9.6
Tawny owl <i>Strix aluco</i>	19.0	47.6
Red fox <i>Vulpes vulpes</i>	7.8	6.8
Raccoon dog <i>Nyctereutes procyonoides</i>	4.3	1.7
Common buzzard <i>Buteo buteo</i>	4.3	6.7
Long-eared owl <i>Asio otus</i>	3.6	
Polecat <i>Mustela putorius</i>	2.7	1.5
American mink <i>Mustela vison</i>	2.2	
Sparrowhawk <i>Accipiter nisus</i>	2.1	
Lesser spotted eagle <i>Aquila pomarina</i>	1.4	
Goshawk <i>Accipiter gentilis</i>	0.4	
Hobby <i>Falco subbuteo</i>	0.4	
Badger <i>Meles meles</i>	0.2	
River otter <i>Lutra lutra</i>	+	
Wolf <i>Canis lupus</i>	+	
Eurasian lynx <i>Lynx lynx</i>	+	

slightly, but relative predation rate (per cent consumption of bank vole population) declined to 10–30%. During the crash year, total number of bank voles removed by predators declined, but relative predation rates were high and the predation impact was particularly heavy (Jędrzejewski and Jędrzejewska 1993, Jędrzejewska and Jędrzejewski 1998).

The combined impact of three species (tawny owl, pine marten, and weasel) accounted for 80% of the total predation (Table 3). Thus the mechanisms of predation may be elucidated by close examination of these three species of predators. A crucial constraint on the predation impact is the fact that birth and growth of young in temperate predators takes place in spring and summer only. Due to the ability of tawny owls and pine martens to utilize alternative food resources, their densities are fairly stable (Jędrzejewski *et al.* 1995, 1996, Zalewski

et al. 1995). Production of young is far more variable, with complete failures in years of very low numbers of rodents (Southern 1970, Jędrzejewski *et al.* 1996). In both winter and summer, numerical responses of tawny owls to changes in rodent numbers were of logarithmic type (Fig. 5). Due to their fast reproduction rate least weasels traced the increase in rodent abundance quickly. However, when rodents declined, least weasel numbers declined deeply as well. The numerical response of least weasels to fluctuations in rodent numbers was immediate (with no detectable time lag) and of logarithmic type (Fig. 5). Year-to-year variations in pine marten numbers were predominantly influenced by changes in forest rodent abundance, to which pine martens responded with one year lag. Pine marten has a pregnancy with delayed implantation, so mating in July–August results in young born in March–April of the following year. Thus, the highest den-

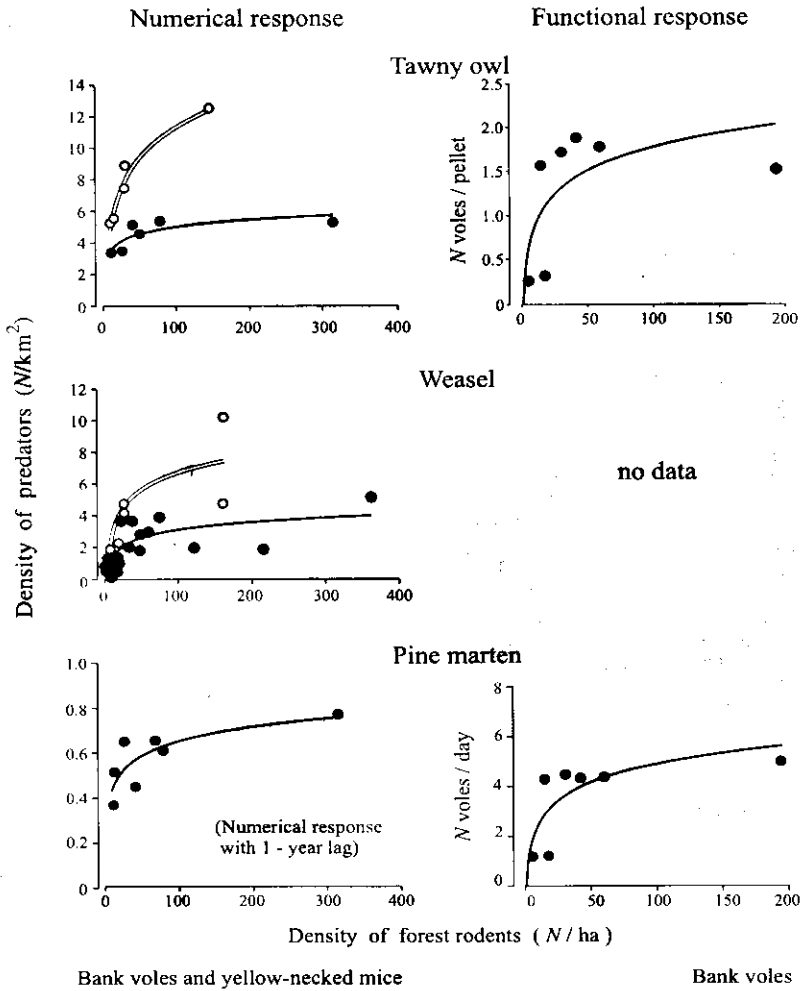


Fig. 5. Left graphs: Numerical responses of predators to changes in densities of forest rodents (bank voles and yellow-necked mice combined) in the pristine deciduous and mixed forests of Białowieża National Park, E Poland. Black points – non-breeding season: autumn-winter densities of owls plotted against autumn density of voles, and autumn, winter, and spring densities of weasels plotted against densities of vole in the same seasons. In the pine marten (a species with delayed implantation), autumn-winter densities correlated with rodent abundance in autumn of the previous year. Open points – breeding season: summer densities of owls and weasels plotted against rodent densities in the same summer. No data were available for martens. Right graphs: functional response of tawny owls and martens in autumn-winter to variation in autumn densities of bank voles (data from diet analysis: each point = one autumn-winter season). Sources: Jędrzejewski *et al.* (1995, 1996), Zalewski *et al.* (1995), Jędrzejewska and Jędrzejewski (1998)

sities of pine martens were observed a year after the rodent outbreak, and the lowest ones a year after the rodent crash (Fig. 5).

In contrast to the predator guilds of south boreal forests and temperate fields, the predator guild of temperate deciduous forests does not include either nomadic avian predators, which could concentrate to areas with rodent outbreak, or overwintering migrants, which could use the forests as long as rodent density exceeds a threshold. Hence, there are no

predators for which equation (8), producing a stabilizing type III functional response, would apply. In the Białowieża study, the rate of tawny owl hunting on bank voles (expressed as number of voles per pellet which is legitimate as no variation in total pellet production was detected; Fig. 6) increased deceleratingly with increasing vole density. Similarly, owls strongly responded to fluctuations of yellow-necked mice, their preferred prey (Jędrzejewski *et al.* 1994). In their feeding

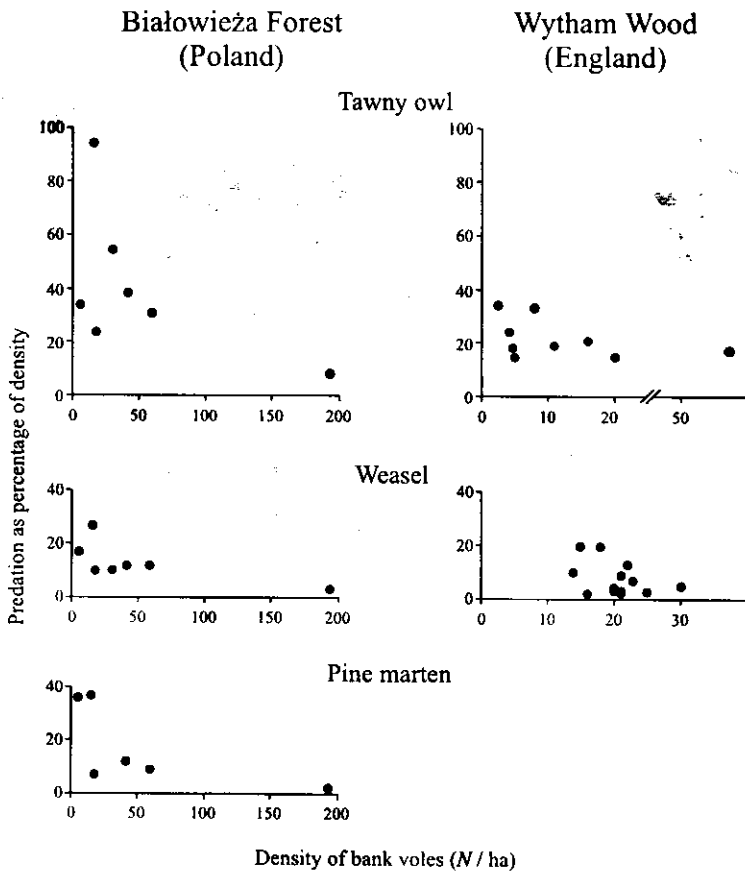


Fig. 6. Predation on bank voles as percentage of their density in the deciduous and mixed forests in Europe. Data from Białowieża Forest: Autumn-winter predation by tawny owls, weasels, and pine martens expressed as percentages of autumn densities of bank voles and plotted against their autumn densities; each point = one year. Data from Wytham Wood: Bimonthly predation rates by tawny owls, and monthly predation rates by weasels plotted against densities of vole. Sources: King (1980, 1985), Southern and Lowe (1982), Jędrzejewski *et al.* (1995, 1996) and Zalewski *et al.* (1995)

habits, tawny owls were able to buffer the changes in rodent abundance by utilization of three other food resources, used in parallel: birds, shrews, and frogs. This allowed the resident owls to maintain fairly stable densities of despite strong fluctuations of rodent numbers. Even the functional response of pine martens on bank voles numbers was an asymptotic (Fig. 6). Pine martens compensated for the scarcity of rodents by increased consumption of buffer resources: birds and fruit in spring-summer, and insectivorous mammals and ungulate carcasses in autumn-winter (Jędrzejewski *et al.* 1993), but the changes in diet breadth was not accompanied by changes in habitat use. The data for tawny owls and pine martens indicates that the increase in searching time, obtained by concentrating on rodents during outbreaks, was not sufficient to have detectable impact on functional response which is destabilizing type II

for both species. No data on year-to-year variation in weasel diet composition from Białowieża are available, but studies conducted in other parts of Europe (King 1980, Korpimäki *et al.* 1991) documented that weasels are specialized on rodents and continue to hunt for them even when rodents are scarce (see above), which indicates destabilizing type II functional response for weasels, too. Consequently, relative predation rates imposed by tawny owls, pine martens, and weasels on bank voles decline rapidly with growing numbers of voles (Fig. 7).

We can thus conclude that, predation on bank voles in temperate forests does not normally act in a density-dependent way. Hence, it can hardly be a regulatory, stabilizing factor. The degree to which predators limited bank vole numbers beyond the level which would prevail in the absence of predators is still an open question, to be answered by

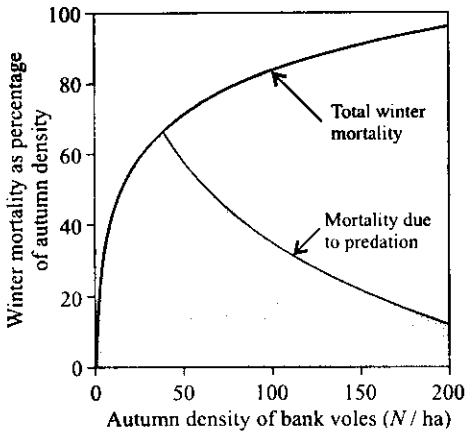


Fig. 7. Relationships between overwinter mortality of bank vole, percentage predation on voles in autumn-winter, and their autumn densities: based on data from Białowieża National Park in 1985–1992 (Pucek *et al.* 1993, Jędrzejewska and Jędrzejewski 1998, and unpubl.)

predator removal experiments. What can be concluded with currently available evidence is that in addition to a_q , even the parameters r_q and K_q in equations (1) and (2) for temperate forest populations of bank voles are profoundly influenced by masting, which prolongs the reproductive season of bank voles and reduces the sizes of female territories. Moreover, snow in winter influences the activities of temperate predators, in concordance to the argument of Hansson and Henttonen (1985). In Białowieża Forest, Poland, mean percentage occurrence of bank vole remains in owl pellets declined from 82%, when there was no snow, to 47% when snow was 30–40 cm deep (Jędrzejewski *et al.* 1994). In the cold season of 1995/96, when bank voles grew numerous after heavy crop of hornbeam seeds, the population of tawny owls underwent a mass deaths from starvation: snow cover exceeding 0.5 m persisted for several weeks. In spring 1996, mere 20–25% of the previous-year pairs of owls was recorded. Similarly, pine martens hunting success for bank voles was dependent on snow depth. In winter, the mean dry weight of bank vole remains per one scat dropped from 0.31 g when snow was 1–10 cm deep to 0.04 g when the thickness of snow cover exceeded 40 cm (Jędrzejewski *et al.* 1993). In continental and relatively northern parts of the temperate zone, variation in winter conditions further reduces the potential of predators to efficiently track rodent densities and play a regulatory role. The step from Białowieża to boreal landscapes where the impact of predation is primarily destabilizing (see above) is not a long one.

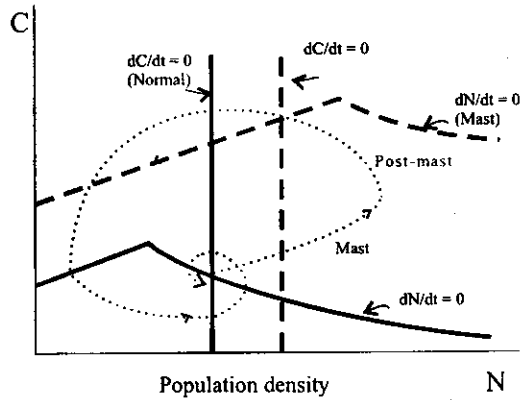


Fig. 8. An isocline model for predator-prey systems of temperate forests, with bank voles as prey and with a predator guild dominated by species with high degree of habitat fidelity. The solid lines refer to isoclines in a non-mast situation, which correspond to isoclines for homogeneous taiga area (Fig. 2) and create a stable equilibrium point. The dashed isoclines refer to a mast situation, with small female territories, high reproductive output and good possibilities for voles to spend most of their time hiding. The dotted line with arrows refer to transient dynamics caused by masting

Our conjecture on the causal background of bank vole dynamics in the deciduous and mixed forests of western Europe, where snowy winters seldom occur, is summarized in the phase diagram of Fig. 8. In normal years, the constellation of predator and prey isoclines is basically similar to the constellation of isoclines in the northern taiga. Predators do not regulate voles, if regulation is operationally defined as generation of prompt density-dependence, but predators are nevertheless crucial in keeping the vole population at its observed density range. Masting lifts the prey isocline to entirely different part of the phase space *via* decreasing a_q and increasing r_q and K_q . Masting thus initiates transient dynamics, where the first thing to happen is a massive increase in densities of bank voles. If masting would last, the new equilibrium point would probably turn out to be locally unstable. However, the 1–2 years of masting which are observed in nature, are too short a period for generating cyclic dynamics. When the mast ends, the parameter values change back, and the isoclines return to their previous positions. Consequently, the predator densities are now way above the prey isocline, while the prey densities are to the right of the predator isocline, i.e. vole densities start to decline while predator densities continue to rise. The post-mast depression in vole densities are a consequence of this numerical unbalance.

5. OVERVIEW OF BANK VOLE DYNAMICS IN EUROPE

The feeding habits of bank voles make it likely that their populations are normally characterized by strong density-dependence already at relatively modest population densities. Their specialization on high quality food, which can be regarded as an adaptation to intense predation (Oksanen 1992), makes them elusive as prey, which pushes the predator isocline to relatively high prey densities in systems with bank voles as the dominating prey. This tends to create a stable equilibrium. Hence, sustained multiannual density fluctuations in bank voles are probably primarily generated by external factors. In the boreal zone, bank voles are alternative prey for small mustelids, which appear to be locked in a stable limit cycle with their primary prey – *Microtus* spp. The two prey types occur primarily in different habitats, but they co-occur within the spatial scale defined by the territories or home ranges of small mustelids. Hence, small mustelids can be expected to change their habitat use during the course of the *Mustela-Microtus* cycle. When *Microtus* peaks, its habitats are more profitable than the habitats of bank voles. Hence, predation on bank voles is relaxed and bank vole densities increase. Conversely, when the *Microtus* populations decline, there will be a point when both habitat categories are equally profitable. When this happens, small mustelids become habitat generalists, and bank voles are drawn in a guild-level decline of microtine rodents. The amplitude of the cycle will be influenced by abundance relationships between *Microtus* and *Clethrionomys* habitats and by the abundance of avian predators and by mammalian generalists, which can reduce the amplitude of the cycle by preying on voles and small mustelids when their densities are at their highest.

In the southern part of the boreal zone, synchronous *Microtus* cycles disappear, probably due to the stabilizing impact of avian predators and mammalian generalists (Erlinge *et al.* 1983, Hansson and Henttonen 1985, see also Zablotskaya 1971, Koshkina and Korotkov 1975), although cycles do occur locally in habitats where food and cover abound, and these cycles are locally reflected in bank vole dynamics, too (see above). Masting constitutes the dominating external cause for multiannual bank vole fluctuations in the temperate zone. In terms of

predator-prey models, these fluctuations can be regarded as recurrent transient dynamics. Social factors, ultimately determined by the supply of high quality food, play a pivotal role in the regulation of bank voles. Except for the profound impacts of predators supported by *Microtus* spp., the degree to which predation limits bank voles is still by and large an open question, to be settled by predator removal experiments.

6. CONCLUSIONS

1. Due to their feeding habits and social system, bank vole populations are characterized by sufficiently strong density-dependence to stabilize predator-prey systems with bank voles as the dominating prey.

2. In the absence of destabilizing external impacts, bank vole populations thus show primarily seasonal density fluctuations, reflecting seasonal changes in reproductive rates, ultimately controlled by changes in food production. Such dynamics are typical for the southern part of the boreal zone.

3. In more northern areas with sustained *Mustela-Microtus* cycles, bank voles are drawn in the cycles as alternative prey.

4. In the temperate zone, masting results to changes in reproductive rates of bank voles and in other parameters relevant for predator-prey dynamics. This initiates periodic transient dynamics, seen as outbreak-crash sequences in time series.

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