AN EMPIRICALLY BASED MODEL FOR LATITUDINAL GRADIENT IN VOLE POPULATION DYNAMICS

Peter Turchin[1],* and Ilkka Hanski[2]

[1]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3042; [2]Department of Zoology, University of Helsinki, FIN-00014 Helsinki, Finland

Abstract.—Vole dynamics in northern Europe exhibit a well-defined geographical gradient, with oscillatory populations being confined to high latitudes. It has been proposed that oscillations in northern vole populations are driven by their interaction with specialist predators (weasels), while the more southern rodent populations are relatively stable because of regulation by generalist predators. We tested this generalist/specialist predation hypothesis by constructing an empirically based model for vole population dynamics, estimating its parameters, and makng predictions about the quantitative pattern of the latitudinal shift in vole dynamics. Our results indicated that the model accurately predicted the latitudinal shift in the amplitude and periodicity of population fluctuations. Moreover, the model predicted that vole dynamics should shift from stable to chaotic as latitude is increased, a result in agreement with nonlinear time-series analysis of the data. The striking success of the model at predicting the shifts in amplitude and stability along the geographical gradient in northern Europe provides strong support for the key role of specialist and generalist predators in vole population dynamics.

The role that predators play in vole population dynamics has been debated for decades. One view holds that predators exert a minimal impact on vole cycles (Chitty 1960; Krebs 1964; Krebs and Myers 1974; Chernyavsky and Tkachev 1982; Lomnicki 1995), another suggests that predators could stabilize vole oscillations (Erlinge et al. 1984; Korpimäki and Norrdahl 1991*a*), while a third maintains that predators actually destabilize vole dynamics by deepening and prolonging their population declines (Elton 1942; Pearson 1971; MacLean et al. 1974; Fitzgerald 1977). Theory suggests that the dynamical role of predators will depend on how closely predator numbers are linked to vole numbers. Predators may be divided into two broad groups: ''specialists,'' whose populations will increase when vole populations are abundant and decline when voles are scarce, and ''generalists,'' whose numbers are not affected by vole density (Hanski et al. 1991). Because specialists respond to changes in vole densities numerically, their response occurs with a time lag. Thus, an interaction between specialist predators and their prey typically leads to oscillations (Volterra 1931; May 1973). The dynamical role of generalist predators is more complex, but since many such predators are characterized by S-shaped functional responses

* E-mail: turchin@uconnvm.uconn.edu.

(Holling's [1965] Type III functional response), their effect will be stabilizing, as long as prey density is confined to the accelerating range of the functional response curve. The key issue is thus how fast predator-imposed mortality responds to changes in vole densities: if predators respond behaviorally (functionally), there is little or no lag, and their effect is expected to be stabilizing; if, on the other hand, they respond numerically, there is a lag and a tendency toward oscillations.

We enclosed *specialists* and *generalists* above in quotation marks because the predator community feeding on voles is more complex than would be suggested by this simple dichotomy. Andersson and Erlinge (1977) divided vole predators occurring in Fennoscandia into three groups, based on their degree of specialization and mobility. The first group is resident specialists, such as the least weasel (*Mustela nivalis nivalis*). Least weasels are the most specialized predators of voles: the proportion of small rodents in their diet is never <0.5 and is often close to 1 (King 1989). Because least weasels cannot switch to other prey and their mobility is low, weasel densities decrease drastically after a decline in density of small rodents (Korpimäki et al. 1991). It takes time for weasel populations to decline and increase; thus, these predators impose delayed density dependence on vole populations. The second group is nomadic specialists, such as kestrels (*Falco tinnunculus*) and short-eared owls (*Asio flammeus*). The diet of these predators also consists primarily of small rodents. Unlike weasels, however, these avian specialists are highly mobile and easily move from areas of low vole numbers to areas where voles are abundant. The predation rate imposed by avian specialists thus responds to changes in vole density on a fast timescale (Korpimäki 1994). The third group is generalists such as foxes (*Vulpes vulpes*), badgers (*Meles meles*), feral cats (*Felis catus*), and buzzards (*Buteo buteo*) that feed on many alternative prey. Population densities of these predators will be little affected by vole numbers, and their response to increased vole populations will occur on a fast timescale.

This classification of vole predators is not perfect. For example, it may also be useful to distinguish between migratory and overwintering predators (Korpimäki 1994). Additionally, the role of some predators depends on the locality (e.g., stoat *Mustela erminea* is considered a small rodent specialist in northern Fennoscandia but is a generalist in southern Fennoscandia where it has abundant sources of alternative prey; Korpimäki et al. 1991; Heikkilä et al. 1994; Hanski and Henttonen 1996). From the point of view of understanding microtine oscillations, however, the important distinction is between predators responding on a slow timescale (primarily, the least weasel) and predators responding on a fast timescale (nomadic specialists and nomadic or resident generalists). To avoid inventing new terminology, we will refer to these two categories as specialists and generalists, even though the latter one includes nomadic specialists.

Predation by both generalists and specialists appears to be the key factor in determining the dynamical patterns of vole populations in Europe. The generalist/specialist predation hypothesis (Hansson and Henttonen 1985, 1988; Han-

ski et al. 1991, 1993) explains the observed vole dynamics as follows. In the north (Fennoscandia north of 59°–61° N), the number of generalist predators is sparse, because there are few individuals and species of alternative prey (Hanski et al. 1991); this change in animal community appears to be related to the duration and depth of snow cover (Hansson and Henttonen 1985). Thus, vole dynamics are primarily determined by their interactions with the specialist predators, weasels. The result is multiannual, high-amplitude oscillations of the predator-prey type. In the south (Fennoscandia south of 59°–61° N, central Europe, and British Isles), the alternative prey and therefore generalist predators are numerous. Generalist predation exerts a powerful stabilizing influence on vole dynamics and possibly even on weasel populations (Korpimäki and Norrdahl 1989a, 1989b). As a result, vole populations exhibit erratic year-to-year fluctuations of small amplitude, although there is a systematic within-year, seasonal fluctuation pattern (Hansson and Henttonen 1988).

Previous theoretical investigation (Hanski et al. 1991) showed that a model for the generalist/specialist predation hypothesis yielded predictions in qualitative agreement with the observed dynamical patterns. In particular, the model suggested that increasing numbers of generalist predators should decrease the amplitude of weasel-vole oscillations and eventually stabilize them. Furthermore, the model predicted that there should be a positive correlation between the amplitude and period of oscillations. This prediction was found to be in agreement with the data. Further model development focused on the specialist predation component (Hanski et al. 1993; Hanski and Korpimäki 1995). We added seasonality to the model of weasel-vole interaction and estimated the model parameters using biological information and time-series data. For the plausible ranges of model parameters, the model exhibited dynamics closely resembling the 3–5-yr vole oscillations observed in northern Fennoscandia.

In this article, we extend our previous analyses in three directions. First, we parameterize the generalist predation component, which allows us to make predictions about not only the dynamical patterns that should be observed in the north but also the quantitative features of the north-south shift in vole dynamics. Second, we reserve time-series data for testing the model and estimate model parameters from independent data sources. This approach permits us to avoid circularity in comparisons between model predictions and observed dynamics. Finally, we add a stochastic (density-independent) component to the model. This allows us to compare directly and quantitatively the latitudinal shifts in amplitude, period, and stability predicted by the model with the patterns observed in time-series data.

This article is organized as follows. We begin by introducing the endogenous structure of the model, and then we add the two exogenous components: seasonality and environmental stochasticity. Next, we estimate model parameters, including both the median values and ranges. A numerical exploration of the parameter space is followed by quantitative comparisons between model-generated time series and the data on microtine population fluctuations in Europe. Finally, we discuss the implications of our results.

A MODEL FOR THE GENERALIST/SPECIALIST PREDATION HYPOTHESIS

Endogenous Structure of the Model

The starting point of our investigation is the following model (Hanski et al. 1991):

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{GN^2}{N^2 + H^2} - \frac{CNP}{N + D},$$

and (1)

$$\frac{dP}{dt} = sP\left(1 - Q\frac{P}{N}\right).$$

There are two dynamical variables in this model: the population density of *Microtus* voles, N, and the population density of the specialist predators (least weasels), P. The model is formulated as a system of ordinary differential equations in continuous time, because voles do not reproduce in discrete generations. However, the intensity of reproduction is affected by the seasonality (which will be added to the model later). The first term on the right side in the prey equation, $rN(1 - N/K)$, represents density-dependent growth of prey in the absence of both generalist and specialist predators. Parameter r is the prey's intrinsic rate of natural increase, and K is the carrying capacity. We do not interpret K as the ceiling on population density imposed by food availability, however. Instead, K is the equilibrium density reached by the population in the absence of predators, and it could be determined by a combination of food availability and social factors, such as territoriality or density-dependent maturation and dispersal rates. The effect of density on per capita rate of population change is assumed to be linear (i.e., the logistic growth). This assumption appears to be a reasonable approximation, at least for some vole species (Turchin and Ostfeld 1997).

The second term on the right of the prey equation, $GN^2/(N^2 + H^2)$, reflects the action of generalist predators. We assume that generalist predation rate follows a sigmoid (Type III) functional response (Holling 1965). In other words, generalists switch from alternative prey to hunting voles when vole density increases over a certain threshold (or, in the case of avian specialists, aggregate where vole density is high). This assumption will be confronted with the data of Erlinge et al. (1983) and Korpimäki and Norrdahl (1989c, 1991a, 1991b) later. At very high population densities, the generalist predation rate will approach an asymptote, because all available generalists will be consuming voles at the highest possible rate. This saturation rate of generalist predation is given by G. The vole density at which the generalist predation rate is half of the maximum, H, is related to the vole density threshold at which generalists will switch over to voles.

The third term of the prey equation, $CNP/(N + D)$, reflects the impact of spe-

cialist predators. We have assumed that the predation rate of an individual specialist obeys the Type II (Michaelis-Menten) functional response with the maximum consumption rate C and the half-saturation constant D.

The equation for specialist predators is simply the logistic growth with carrying capacity proportional to prey density, N/Q. The parameter Q specifies the ratio of prey to predator densities at the equilibrium; that is, it indicates how many prey are necessary to support and replace each individual predator.

The logistic form of the predator equation (Leslie 1948; May 1973; Tanner 1975; Hanski et al. 1991; Berryman et al. 1995; also known as interferential—see Caughley and Lawton 1981) deserves a comment, since it is only one of several alternative functional forms that have been used for modeling predator-prey interactions. Another commonly used form is the laissez-faire predation (Caughley and Lawton 1981), in which the per capita growth rate of predators is determined by the balance between the rate of prey consumption and predator death rate. The assumption of a direct conversion of prey biomass into offspring, however, is inappropriate for a small mammalian predator that spends most of its energy intake on generating heat (King 1989). Furthermore, weasel dynamics should be better described by an interferential rather than a laissez-faire model, since they are territorial, especially at high rodent densities (Lockie 1966; King 1975). Parasitoid-host models (Nicholson and Bailey 1935; Hassell 1978) are inappropriate for our study system because they are discrete models and because they assume a direct conversion of parasitized prey into parasitoid offspring. Finally, a ratio-dependent model (e.g., Akcakaya 1992) was investigated (Hanski and Korpimäki 1995) and rejected because it does not reproduce certain features of the data (a positive correlation between amplitude and period of observed oscillations). Thus, we feel that among simple forms proposed for the predator equation, the logistic one is the most appropriate for the vole-weasel system.

Model (1) assumes homogeneous distribution in space and no age structure. Certain functional forms can be criticized as overly simplistic, such as our assumption that the predator growth rate is solely a function of the predator-prey ratio. This is probably not a bad assumption for high population densities of predators and prey but is certainly incorrect at low densities (see Hanski 1991). We acknowledge that the model is very simple and is, at best, a caricature of the real system. For an ecologist building an empirically based model tailored to a specific system, there is a temptation to make the model as biologically realistic as possible, including in it many different variables and parameters. Yet, complex models are more difficult to understand than simple ones, and they may add more confusion rather than clarify the critical issues. In addition, there is less opportunity for abuse in a simple model, such as tweaking various functional shapes and parameter values to prove whatever one wishes. Also, most parameters typically cannot be estimated precisely. As the number of parameters in the model is increased, more arbitrary decisions need to be made, which increases the uncertainty associated with model predictions. Finally, keeping the number of parameters to the absolute minimum is essential for an understanding

of how these parameters affect model dynamics. For these reasons, we have tried to keep the model as simple as possible.

Adding Exogenous Factors

Although model (1) may provide a useful approximation of the endogenous structure of the interaction between voles and their predators, it completely omits the effects of exogenous variables. The exogenous force has a periodic component (seasonality) and an irregular component (environmental stochasticity or dynamical noise). Seasonality has a profound effect on the rates of population growth in temperate and boreal population systems. Adding seasonality increases the dimensionality of the system and, as a result, expands the range of dynamical behaviors of which the model is capable to include chaos in addition to stable points and limit cycles. Dynamical noise (environmental stochasticity) should also be a key component of the model, because dynamical noise modifies the amplitude and period of oscillations and can shift the qualitative type of dynamics from the stable into the chaotic region and vice versa (Ellner and Turchin 1995). Thus, without explicitly including seasonality and noise into the model, we cannot directly and quantitatively compare model output with data.

In keeping with the general philosophy of this article, we add seasonality and noise to the model in the simplest possible manner. We assume that seasonality affects only the growth rate of populations:

$$\frac{dN}{dt} = r(1 - e \sin 2\pi t)N - \frac{rN^2}{K} - \frac{GN^2}{N^2 + H^2} - \frac{CPN}{N + D},$$

and   (2)

$$\frac{dP}{dt} = s(1 - e \sin 2\pi t)P - \frac{sQP^2}{N}.$$

Equation (2) assumes that the slope of density dependence does not vary with season. The consequence of this assumption is that both the intrinsic rate of natural increase and the carrying capacity oscillate with season (fig. 1) and can even become negative, if $e > 1$. This would imply that during the worst period of the year, the population always declines, even if population density is very low. Increased population density would further accelerate the rate of decline.

Instead of using the discontinuous seasonality function as we did previously (Hanski et al. 1993), here we model seasonality by a smooth sine wave. We do not claim that this is the most realistic functional form. However, empirical evidence does not contradict this assumption (Turchin and Ostfeld 1997). Additionally, a discontinuous seasonal shift causes difficulties for the numerical implementation of the model. Finally, model (2), excluding the generalist predation term, has fewer parameters (seven instead of 11) than does our original formulation (Hanski et al. 1993).

Dynamical noise was included by perturbing the model parameters. Details will be given later (see *Numerical Exploration of the Parameter Space*). In addi-
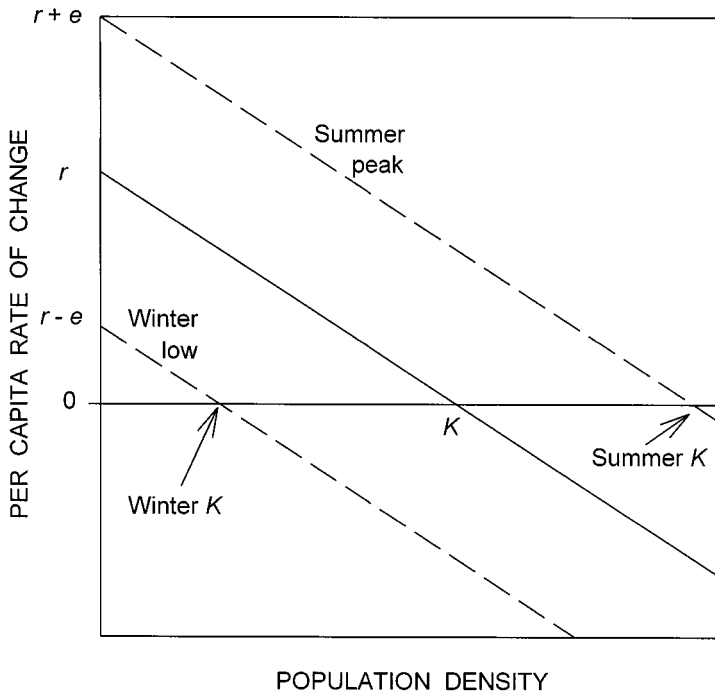
FIG. 1.—Effect of season and population density on the per capita rate of population change. The slope of density dependence is assumed to be constant, so that the whole line oscillates vertically as season changes. *Solid line,* the seasonally averaged relationship between per capita rate of change and density; *dashed lines,* the extreme bounds (achieved at the winter low and the summer peak).

tion to dynamical noise, real data are also typically affected to some degree by observation or measurement errors. Observation errors, unlike dynamical noise, do not affect the actual population trajectory, only the observed numbers. The measurement errors are often modeled as multiplicative, lognormally distributed random variables (e.g., Walters and Ludwig 1981). Accordingly, we assumed that observed values of vole density, $N'(t)$, are related to the actual, $N(t)$, as follows: $N'(t) = N(t) \exp(\sigma_{obs}X[t])$, where $X(t)$ is a random Gaussian variable with mean 0 and variance 1 and all autocorrelations between $X(t + \tau)$ and $X(t)$ are 0 for $\tau > 0$.

Scaling Model Variables

Before a systematic exploration of the model's dynamical behavior, we need to reduce the number of parameters. We define new, scaled variables—$n = N/K$ and $p = KP/Q$—and rewrite model (2) as follows:

$$\frac{dn}{dt} = r(1 - e \sin 2\pi t)n - rn^2 - g\frac{n^2}{n^2 + h^2} - a\frac{np}{n + d},$$

and   (3)

$$\frac{dp}{dt} = s(1 - e\sin 2\pi t)p - s\frac{p^2}{n}.$$

Here the new parameter combinations are $g = G/K$, $h = H/K$, $d = D/K$, and $a = C/Q$. We now have four parameters describing the endogenous interactions between voles and specialist predators (r, s, a, and d), two parameters for the generalist predation component (g and h), and two parameters for the exogenous forcing (e and σ). The variance of observation noise is assumed to be fixed at $\sigma_{obs} = 0.15$ (see *Noise Parameters* under Parameter Estimates and Ranges).

<div align="center">PARAMETER ESTIMATES AND RANGES</div>

Parameters of Vole Population Growth

The intrinsic rate of vole population growth, r.—Microtine rodents are justly famous for their impressive powers of population increase. The intrinsic rate of natural increase for *Microtus pennsylvanicus* averaged over seasons within a year was estimated as 6.0 yr^{-1} (Turchin and Ostfeld 1997). Estimates of r for lemmings range even higher: 6.6–6.9 yr^{-1} for *Lemmus lemmus* (Koshkina 1970) and 7.2 yr^{-1} for *Lemmus sibiricus* (Batzli et al. 1980; see Turchin and Ostfeld 1997 for discussion). We will assume that $r = 6$ yr^{-1} but will also investigate the effect of varying r between 5 and 7 yr^{-1}. This estimate is higher than the seasonal average of $r = 4.05$ yr^{-1}, which we used previously (Hanski et al. 1993). However, our previous estimate was based on the maximum population increases observed in time-series data. This method underestimates the true r, because population growth of voles is so rapid that they quickly attain densities at which density-dependent forces slow down the rate of population increase.

The amplitude of seasonal forcing, e.—On the basis of the analysis of *M. pennsylvanicus* data and a literature survey, it has been suggested (Turchin and Ostfeld 1997) that e lies between 0.5 and 1. Since effects of seasonality should be especially extreme in boreal environments, we will assume that $e = 1$. Thus, at the seasonal peak the intrinsic rate of natural increase is 12 yr^{-1} (which agrees well with the maximum rates of population increase observed in *Microtus* rodents; see table 1 in Turchin and Ostfeld 1997), while at the seasonal low it is 0.

Since winter reproduction is probably rare or absent in least weasels, their intrinsic rate of natural increase should be negative for at least half the year. Thus, the value of $e = 1$ is an underestimate for the seasonal amplitude of variation in weasel reproduction. We are reluctant, however, to add another parameter to the model, especially because very little is known about winter mortality in weasels. We will, however, investigate numerically the effect of making weasels' $e > 1$.

Prey carrying capacity, K.—Peak densities typically observed in *Microtus agrestis* in old-field habitat are about 300 voles ha^{-1} (Myllymäki 1977). Assuming that the seasonal peak of carrying capacity is 300 voles ha^{-1} implies that K

= 150 voles ha^{-1}. The estimate of $K = 150$ voles ha^{-1} is higher than $K = 100$ used earlier (Hanski et al. 1993), because the previous estimate was based on peak vole densities observed at Alajoki, where the habitat is a mixture of culti-vated fields and ditches. Thus, Alajoki numbers probably underestimate the car-rying capacity of the optimal habitat.

The Specialist Predation Parameters

The intrinsic rate of weasel population growth, s.—Assuming that least wea-sels have only one generation per year, that under favorable conditions each fe-male can produce two litters (King 1989), and that the average number of births per litter is five (table 9.2 in King 1989), we have a theoretical maximum esti-mate (which does not include density-independent mortality) of $s = \ln(10/2) = 1.6$. We will assume that s can range from 1 to 1.5, with the median value of 1.25. This median value is close to our previous estimate (Hanski et al. 1993) of $s = 1.4$.

Maximum consumption per predator, C.—The parameter C reflects the maxi-mum number of voles that will be killed by a weasel in a year when voles are abundant and weasels are rare. Least weasels consume 0.6 g of food per gram of body mass per day (Gillingham 1984). The mean body mass of least weasels in Finland (Alajoki), averaged over both sexes, is 42 g, while the mass of *Mi-crotus* rodents is 25 g (Korpimäki et al. 1991). Thus, a weasel consumes approx-imately one vole per day. Pregnant and lactating stoat females consume three times as much food as do nonreproductive ones (Erlinge et al. 1983). Assuming that this value for least weasels leads to an estimate of least weasel consumption of approximately 400 voles per year. Additionally, ''surplus killing'' may amount to 50% of the food requirement (Jedrzejewska and Jedrzejewski 1989). Thus, C probably lies between 500 and 700 voles yr^{-1} weasel^{-1}, and we will assume that the median value is $C = 600$ (this is the same estimate used in Han-ski et al. 1993). Other, independent estimates of least weasel consumption are in good agreement with ours. Ternovsky (1977) estimated that one least weasel de-stroys 500 voles. On the basis of their extensive data on seasonal variation in the vole consumption of mustelids in the northwest Russia, Tumanov and Smelov (1980) estimated that a least weasel consumes 630 voles per year, on the average.

One weakness of our estimate is that it assumes that weasels only kill adult voles. Since weasels can easily penetrate vole burrows, weasel predation on nestlings should be a substantial source of mortality. Additionally, weasels can impose indirect mortality on immatures by killing lactating female voles. These considerations suggest that $C = 600$ voles yr^{-1} weasel^{-1} may be a conservative estimate.

The half-saturation constant, D.—The parameter D is the prey density (voles ha^{-1}) at which the predator consumption rate reaches one-half of the maximum, C. We have the following clue available for estimating this parameter. There is a critical minimum density of voles below which the weasel female is unable to reproduce (Erlinge 1974; Tapper 1979). This critical density was estimated by Erlinge (1974) as $N_{crit} = 10$ voles ha^{-1}. The estimate of Tapper (1979) was

slightly higher (14 voles ha^{-1}), but this is probably due to the larger size of common weasels that he studied. At prey density equal to N_{crit}, the consumption rate by an individual weasel is C_{crit}. Assuming that weasels need to consume a vole a day just to maintain themselves (see above) but without being able to reproduce, we have $C_{crit} = 365$. From this information, we can deduce D, since

$$C_{crit} = \frac{CN_{crit}}{N_{crit} + D},$$

or $D \approx 6$ voles ha^{-1}. This is close to the median value of $D = 5$ voles ha^{-1} previously assumed (Hanski et al. 1993).

A test of the assumed shape and the estimate of parameter D of the functional response is provided by data in Erlinge (1975). Erlinge (1975) reported the proportion of small rodents in weasel scats collected in two habitats (spruce plantation and replanted clearing) and two seasons (fall-winter and spring-summer). The rodent species were *M. agrestis, Apodemus flavicolis,* and *Clethrionomys glareolus.* We can add these three species together because they were not subjected to discriminate hunting by weasels (Erlinge 1975). If we assume that weasels would eat alternative foods (rabbits, water voles, shrews, and birds) only when they could not find small rodents, the proportion of small rodents in the weasel diet as a function of rodent density should be given by the functional response curve $f(N) = N/(N + D)$ (with the saturation level $= 1$). Plotting the proportion of small rodents in weasel scats against rodent density, we observe that the predicted relationship is in reasonable agreement with the data, suggesting that the Michaelis-Menten functional form with $D = 6$ voles ha^{-1} is an adequate description of the actual functional responses of weasels to the density of their prey (fig. 2).

Predator-prey ratio constant, Q.—The parameter Q, the ratio of equilibrium density of weasels to that of voles, is the most difficult quantity to estimate. The minimum bound on Q can be estimated as follows. Let us assume that at moderate vole population densities, a vole female will produce an average of two offspring every 20 d instead of five to seven offspring at low population densities (this reflects a lower proportion of females taking part in reproduction and lower than maximal litter sizes). Thus, a population of 20 voles, 10 of which are females, will produce 20 offspring every 20 d, enough to feed one weasel, or $Q = 20$ voles weasel^{-1}.

Explicit consideration of space leads to a similar estimate. A breeding female weasel will typically have a territory of approximately 2 ha in an optimal vole habitat (see table 8.1 in King 1989) and needs at least 10 voles ha^{-1} to reproduce (see above). Thus, the minimum number of voles per female is again 20.

A more realistic estimate of Q, however, should also take into account the following factors: the interval between litters should be closer to 30 d, and there must be some vole surplus for both weasels and voles to replace themselves. Thus, it is more likely that $Q \approx 40$ voles weasel^{-1}. Additionally, weasels are preyed upon by generalist predators (Korpimäki and Norrdahl 1989a, 1989b). Since the numbers of generalist predators increase toward the south, we should
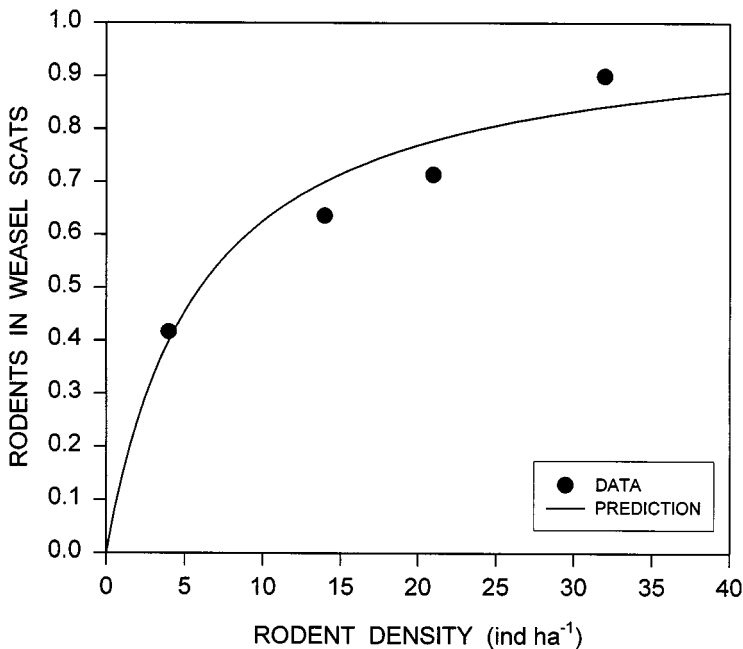
Fig. 2.—Predicted (*solid curve*) and observed (*points*) relationship between the proportion
of small rodents in weasel diet and rodent density (data from Erlinge 1975).

expect that equilibrium densities of weasels should decrease and Q would be-
come larger in the south (to keep the model simple, however, we do not model
this effect).

  Ranges of the composite parameters d *and* a.—Our estimate of the parameter
$d = D/K$ is $6/150 = 0.04$. Assuming that actual K lies between 100 and 200
voles ha^{-1} gives us a range of $d = 0.03–0.06$. The estimate of $a = C/Q$ is 15
yr^{-1}. This estimate is characterized by greater uncertainty, particularly because
there is little quantitative information to estimate Q. We will investigate the ef-
fect of varying a fourfold, between 7.5 and 30 yr^{-1}.

Generalist Predation Parameters

  The generalist predation function was estimated using the data collected by
Korpimäki and Norrdahl (1991*a*, 1991*b*) and Erlinge et al. (1983). Korpimäki
and Norrdahl (1991*a*, 1991*b*) studied the impact of nomadic avian predators on
vole populations during 1977–1987 in Alajoki, western Finland (63° N). They
recorded how the number of breeding pairs of European kestrels, short-eared
owls, and long-eared owls fluctuated in response to variable vole density. They
have also determined the proportion of voles in the diet of breeding predators.
From these data, they estimated the number of voles consumed per square kilo-
meter during each breeding season, approximately 100 d (table 2 in Korpimäki
and Norrdahl 1991*a*). We translated these numbers into units of voles consumed
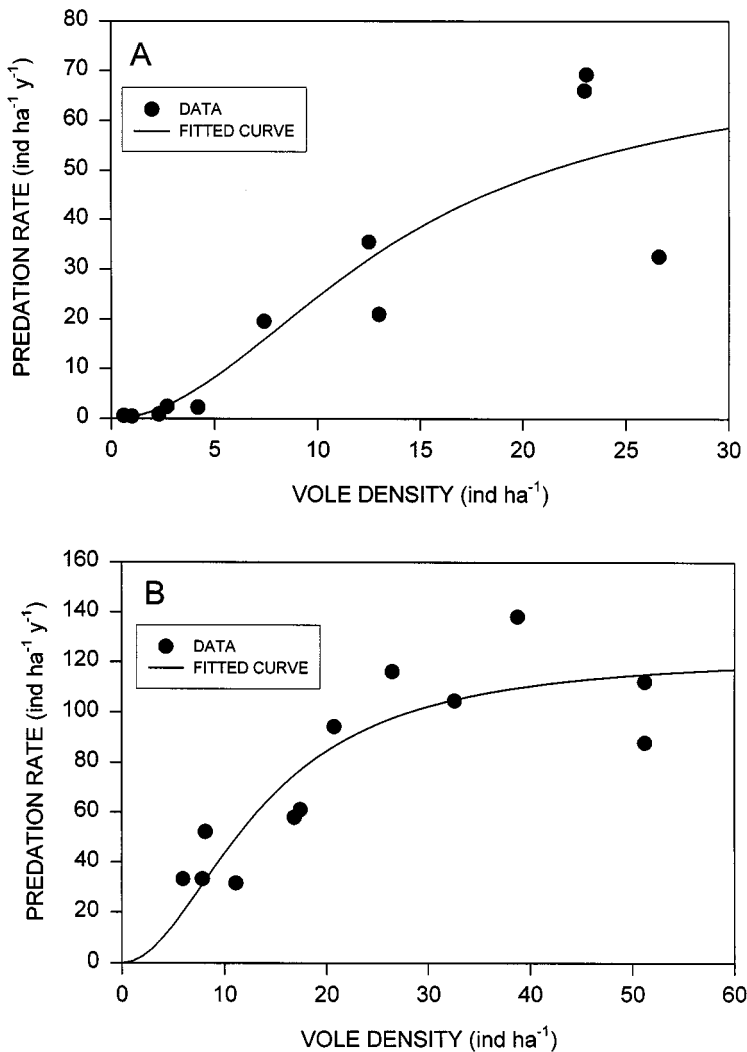
FIG. 3.—Relationship between the generalist predator pressure and vole density. *A,* Data from Korpimäki and Noordahl (1991*c*); *B,* data from Erlinge et al. (1983).

per year per hectare of farmland (the primary vole habitat at Korpimäki and Norrdahl's study site).

The breeding densities of the three predators, and therefore their predation rate on vole populations, were most closely correlated with the vole densities in the spring preceding the breeding season (Korpimäki 1994). Thus, the generalist predation was actually operating with a short lag, about 2 mo. To estimate the generalist predation function, we plotted the estimated predation rate against the spring density of voles in farmland (fig. 3*A*). The observed pattern supports

the hypothesis of a switching threshold postulated by the Type III response, since the generalist impact on vole population appears to be negligible when vole densities are less than approximately five individuals per hectare (fig. 3A). Fitting Type III response to these data by nonlinear least squares yielded the following estimates of the parameters: $G = 71$ voles ha^{-1} yr^{-1} and $H = 13.8$ voles ha^{-1}.

The Alajoki data set thus provides support for an S-shaped total response (functional response times predator numbers) by nomadic avian predators. Because vole density fluctuated extensively in Alajoki during the 11 yr of observation, this data set is particularly useful for estimating the switching threshold H. However, these data have two potential weaknesses: first, data are limited to only the avian predators; second, only summer predation is documented. These gaps are filled, at least partially, by data collected during a subsequent study of mortality factors in radio-collared voles (Norrdahl and Korpimäki 1995). First, Norrdahl and Korpimäki (1995) found that all observed predation events were due to either mustelids or avian predators. Second, the mortality rate did not change significantly between fall (September–October) and spring (April–June) during the increase phase of the vole cycle (when the effect of generalist predators is especially important, since few specialists are present). Taken together, these observations suggest that the generalist community in Alajoki was represented primarily by the avian predators and that there were no obvious seasonal changes in the generalist predation pressure.

More information on potential effects of seasonality on the generalist predation process is provided by the data collected by Erlinge et al. (1983), who studied vole predation by nine generalist species in Revinge, southern Sweden (56° N). They estimated predation pressure based on their data on food spectra, food requirements, and numbers of various predators present at different times of the year. Figure 2 in Erlinge et al. (1983) gives the data on the total number of voles consumed by all predator species during each month and the total number of voles estimated to be present in the study area. Similar to those at Alajoki, predators at Revinge tracked the densities of prey with a time lag of about 2 mo (figs. 2 and 4 in Erlinge et al. 1983). To express these data in units of voles per hectare per year, we translated the total vole numbers in figure 2 into vole densities per hectare, using the data in figure 1 of Erlinge et al. (1983), and multiplied by 12 the number of voles consumed per hectare per month. Then we plotted the estimated predation rate against vole density 2 mo before, to account for the lag in predator response (fig. 3B). Fitting the predator response function to these data, we obtained the following estimates: $G = 123$ voles ha^{-1} yr^{-1} and $H = 13.5$ individuals ha^{-1}. To summarize, the Revinge data suggest that most of variation in the generalist predation pressure can be explained by changes in vole density (fig. 3B). Thus, we decided not to include a seasonal component in the generalist predation term in our model. Additionally, the estimate of H from Revinge was very close to that from Alajoki. This result suggests that we may combine all species of generalist predators together (at least as a first approximation) and that there is no evidence that H changes systematically with latitude.

The estimate $G = 123$ individuals ha^{-1} yr^{-1} is probably an underestimate of

TABLE 1

Effect of Latitude on Generalist Predation Pressure, G

		Generalist Density	G		
Locality	Latitude		Estimated	Expected	Assumed
Revinge	56	10	140	140	140
Grimsö	59	2.5	. . .	35	110
Alajoki	63	. . .	70	. . .	70
Kilpisjärvi	69	.9	. . .	13	10

Note.—Generalist density is the pooled density of avian predators and generalist mammalian predators (individuals per square kilometers). Estimated G is derived using quantitative data of Erlinge et al. (1984) and Korpimäki and Norrdahl (1991*a*, 1991*b*). Expected G is calculated by decreasing G from the value observed in Revinge in proportion to the density of generalist predators. Assumed G is the relationship between G and latitude assumed in the model ($G = 70° − 10 × L$).

the true value of this parameter, since Erlinge et al. (1983) stated that predation rates calculated for cats and buzzards were probably in the low range. To correct for this bias, we will use the value $G = 140$ for Revinge. Now, if we assume a linear decline of G with latitude, the values of G estimated for Revinge and Alajoki (140 and 70, respectively) suggest the following relationship between generalist pressure and latitude, L: $G = 70° − 10 × L$. This formula implies that G decreases from 200 to 0 vole ha^{-1} yr^{-1} as latitude increases from 50° to 70° N. An independent check of this assumption is provided by the information on pooled density of generalist predators cited elsewhere (table 1 of Hanski et al. 1991). Assuming that G is directly proportional to the density of generalist predators and using Revinge as the reference point, we calculated the expected G for Grimsö and Kilpisjärvi areas (table 1). The expected G for Kilpisjärvi agreed very closely with the value assumed by our model (13 vs. 10; see table 1). For Grimsö, however, the expected G was much lower than the assumed value (35 vs. 110; see table 1). We will return to this discrepancy in the Discussion.

In summary, our model simulates the latitudinal gradient in generalist predation pressure by linearly varying G from a high value in the south to 0 in the far north. Using the jargon of the dynamical system theory, we may say that G is our "bifurcation" parameter, because, according to the generalist/specialist predation hypothesis, it is decreasing G from a high value to 0 that brings about a bifurcation in vole population dynamics from stability to oscillations.

Noise Parameters

The parameter σ was added to the model in a purely phenomenological fashion and thus cannot be estimated directly using biological reasoning. To obtain an indirect estimate, we have to break our rule against using time-series data in parameter estimation. Specifically, we used the information that the amplitude (measured by the standard deviation of log-transformed numbers, S) of vole fluctuations in southern Fennoscandia is characterized by $S \approx 0.3$ (thus, we will not be able to use this datum in testing the model output). Numerical experi-

ments with the model using median values of other parameters and G estimated for Revinge generated fluctuations with the same S for $\sigma = 0.12$, which is our estimate for this parameter.

Most of the time-series data that we will use for model testing were collected using snap trapping. Snap-trapping data had previously been compared with results from an intensive live-trapping study (Hanski et al. 1994; see fig. 1 there, based on data collected by H. Henttonen). If we assume that live trapping gives the actual density of rodents, these data suggest that the standard deviation between the snap-trapping estimate and the true density is 0.17 on the log-transformed scale. We assumed a somewhat lower value of $\sigma_{obs} = 0.15$, since live-trapping estimates also have some observation error.

CHARACTERIZING DYNAMICAL BEHAVIORS OF THE MODEL

The model was solved numerically using a fourth-order Runge-Kutta routine (Burden et al. 1981). The solution was started in the ''fall''—that is, when the seasonally varying intrinsic rate of increase $r(1 - e \sin 2\pi t)$ started to decrease from its average value (thus the minus sign in front of the sine). The model was solved in time steps equal to 0.02 yr, so that after 50 steps the solution was brought to the end of the year. Stochasticity was implemented by assuming that each parameter changed randomly and independently of other parameters according to the general formula $p_i = p(1 + N[0, \sigma^2])$, where p_i stands for the value of the parameter ($r, s, d, a, e, g,$ or h) chosen for year i, p is the mean value of the parameter, and $N(0, \sigma^2)$ is a normally distributed random variable with mean 0 and variance σ^2 (same for all parameters). Thus, the actual system of equations solved by the Runge-Kutta routine was

$$\frac{dn}{dt} = r_i(1 - e_i \sin 2\pi t)n - r_i n^2 - g_i \frac{n^2}{n^2 + h_i^2} - a_i \frac{np}{n + d_i},$$

and   (4)

$$\frac{dp}{dt} = s_i(1 - e_i \sin 2\pi t)p - s_i \frac{p^2}{n}.$$

This system was solved for 1-yr i, from fall to fall ($t = i + 0.02, i + 0.04, \ldots, i + 1$), then the parameter values were updated for year $i + 1$, and the whole process was repeated.

Since we are concerned with multiannual oscillations rather than with within-year seasonal dynamics, we sampled the model output once per year (apart from some limited comparisons; see below). The model trajectory was sampled in the fall (i.e., at integer values of $t = 1, 2, \ldots$), because the field data on microtine population fluctuations that we will use to test the model were collected in late summer or early fall (see below).

By sampling the model output once per year, we are left with an essentially discrete population system of the general form

$$\mathbf{X}_{t+1} = f(\mathbf{X}_t, \mathbf{U}_t), \tag{5}$$

where $\mathbf{X}_t$ is a two-component vector of vole and weasel population densities and $\mathbf{U}_t$ is a vector of exogenous variables (density-independent random forcing). As discussed elsewhere (Turchin 1995, p. 34), periodicity and sensitive dependence on initial conditions are two separate attributes of complex dynamics affected by exogenous noise. Accordingly, we used the following measures when characterizing the dynamics of the vole-weasel model for various values of parameters: the dominant Lyapunov exponent (Λ) that quantifies the endogenous stability of the system or, alternatively, the sensitive dependence on initial conditions (Ellner and Turchin 1995); the dominant period T and the strength of periodicity from the estimated autocorrelation function (ACF); and a measure of the amplitude of population fluctuations, the standard deviation of log-transformed population densities, S (Lewontin 1966; Stenseth and Framstad 1980). This latter measure has been widely used in the microtine literature; unfortunately, it is often referred to as the cyclicity index (Stenseth and Ims 1993), although it measures amplitude rather then periodicity of oscillations.

MODEL PREDICTIONS AND DATA

Numerical Exploration of the Parameter Space

Effect of parameter values on the predicted behavior in the north.—Before we can begin comparing the dynamics predicted by the model with the data patterns, we need to understand how much the uncertainty in parameter estimates affects the precision of the model predictions. Accordingly, we have performed an extensive numerical exploration of the parameter space of the model. We solved the model for all combinations of the following values of the biological parameters: $r = 5, 6, 7$; $s = 1, 1.25, 1.5$; $d = 0.03, 0.04, 0.06$; and $a = 7.5, 10, 15, 20, 30$. For each parameter, the median value is our best estimate, and the high and low values represent the possible extremes. We used five values for a, because our estimate of this parameter is characterized by the greatest degree of uncertainty. The other parameters were fixed at $e = 1$, $\sigma = 0.12$, and $\sigma_{obs} = 0.15$. For each combination of the four parameters, we simulated the model three times, starting from random initial conditions. The model was solved for 1,100 yr, and the first 100 yr were discarded to allow the transients to die out. The quantitative dynamics of each simulated time series were characterized by Λ, S, T, and ACF(T). To quantify the effects of parameters on the model dynamics, the values of these measures were analyzed by univariate ANOVAs.

ANOVA suggested that most variance in model stability, as measured by Λ, is explained primarily by variation in s, d, and a. Just the main effects of these three parameters explained 76% of variance in Λ. Similarly, these three parameters explained 82% of the variance in the amplitude of fluctuations, S. Since r had only a slight effect on Λ and S (and to avoid an unwieldy table), we present the results of parameter space exploration only for the median value of $r = 6$ (table 2). As could be expected, the Lyapunov exponent and fluctuation amplitude were positively related (see table 2; correlation coefficient = 0.82). By far

TABLE 2

RESULTS OF EXPLORATION OF PARAMETER SPACE

s AND d	MEASURES	a				
		7.5	10	15	20	30
1.00:						
.03	Λ	.05	.13	.12	.16	.15
	S	.65	.73	.84	.90	.97
	$T(\mathrm{ACF}[T])$	5(.4)	5(.4)	5(.5)	5(.5)	5(.5)
.04	Λ	.00	.10	.17	.16	.15
	S	.58	.69	.79	.86	.94
	$T(\mathrm{ACF}[T])$	4(.3)	5(.4)	5(.4)	4(.4)	5(.4)
.06	Λ	−.09	.02	.12	.17	.19
	S	.46	.57	.68	.76	.85
	$T(\mathrm{ACF}[T])$	4(.4)	4(.5)	4(.5)	4(.4)	4(.5)
1.25:						
.03	Λ	−.05	.09	.12	.12	.12
	S	.62	.71	.82	.89	.96
	$T(\mathrm{ACF}[T])$	4(.5)	4(.5)	4(.5)	4(.5)	4(.5)
.04	Λ	−.07	.04	.12	.11	.15
	S	.54	.64	.76	.82	.91
	$T(\mathrm{ACF}[T])$	4(.4)	4(.5)	4(.5)	4(.5)	4(.5)
.06	Λ	−.20	−.05	.08	.13	.15
	S	.42	.52	.66	.74	.82
	$T(\mathrm{ACF}[T])$	4(.3)	4(.3)	4(.4)	4(.5)	4(.5)
1.50:						
.03	Λ	−.12	−.01	.05	.09	.11
	S	.56	.67	.78	.86	.93
	$T(\mathrm{ACF}[T])$	3(.3)	4(.3)	4(.4)	4(.3)	4(.3)
.04	Λ	−.18	−.02	.05	.10	.15
	S	.50	.59	.70	.79	.85
	$T(\mathrm{ACF}[T])$	3(.4)	3(.3)	3(.3)	3(.3)	3(.2)
.06	Λ	−.31	−.12	.02	.07	.11
	S	.38	.48	.62	.69	.77
	$T(\mathrm{ACF}[T])$	3(.3)	3(.4)	3(.3)	3(.4)	3(.3)

the greatest effect on these two dynamical measures was due to the parameter *a,* which by itself explained more than half of the variance in both Λ and S.

By contrast, the primary determinants of the period were the intrinsic rates of increase of prey and predators, consistent with the analysis of model (1) (Hanski et al. 1991). The main effects and the interaction term between these two parameters explained 75% of the variance in T. Oscillations were characterized by 5-yr periodicity for low values of these parameters ($r = 5$ and $s = 1$) and by 3-yr periodicity for high values ($r = 7$ and $s = 1.5$). The dominant period for the median values of all parameters was $T \approx 4$ yr.

Although dynamics for all combination of parameters were characterized by statistical periodicities of 3–5 yr, the periodicity was not very strong (table 2). The autocorrelation at the dominant period for the median values of parameters was approximately 0.5 and varied between 0.6 and 0.2.

The Lyapunov exponent was positive for most combinations of parameter values (including the median ones), indicating that the dynamics of vole-weasel in-

teractions are probably chaotic. This result suggests that the irregularity in the model-predicted dynamics is due to both exogenous noise and nonlinear endogenous dynamics. To illustrate this point, we ran the model for the median values of parameters but with the noise level (σ) set to 0. The model-generated dynamics had both a periodic and an irregular, chaotic component (fig. 4*A, B*). Plotting the trajectory in the phase space suggested that this dynamical behavior of this system is governed by a strange attractor (fig. 4*C*). However, the system is not strongly chaotic, as evidenced by the presence of a significant periodic component and by values of Λ not greatly exceeding 0 (table 2).

Effect of alternative seasonality functions.—One unrealistic assumption of the model is that seasonality affects predator and prey rates of population growth in a similar way. To explore the possible effect of this assumption, we solved a variant of model (3) in which the seasonal forcing in the predator equation (e_p) was varied independently of the prey's seasonal forcing (e). Varying e_p from 0.6 to 2 and e from 0.6 to 1.4 (while keeping other parameters at their median values), we found that e_p had very little effect on the amplitude, the average period, and the strength of periodicity. Increasing e_p, however, tended to make the Lyapunov exponent more positive. Increasing e of the prey had the same effect on the stability and, in addition, decreased the strength of periodicity.

We also investigated the effect of smoothness in the seasonal transitions between summer and winter. This was done by replacing $\sin 2\pi t$ in equation (2) with

$$\frac{\sin 2\pi t}{|\sin 2\pi t|}|\sin 2\pi t|^{\theta}.$$

In this formulation, the smoothness of seasonal transitions is controlled by θ. For $\theta = 1$ we recover model (2), while as θ approaches 0, the transition approaches the step function assumed previously (Hanski et al. 1993). Solving the model for $\theta = 0.2$ (intermediate smoothness) and for $\theta = 0.04$ (almost a step function), we found that decreasing smoothness tended to make dynamics more chaotic but had no effect on the amplitude and the period of resulting oscillations.

Effect of generalist predation pressure on model dynamics.—To simulate the latitudinal gradient in vole dynamics, we systematically varied the generalist predation pressure G from 0 to 200 voles ha^{-1} yr^{-1}, while keeping all the other parameters at their median values. The model predicts that as G increases, the amplitude of fluctuations decreases (fig. 5). The average period shifts from 4 to 3 yr, while the strength of periodicity decreases, so that eventually fluctuations are aperiodic (fig. 5*E*). This result is consistent with previously obtained predictions based on the model lacking exogenous forcing (Hanski et al. 1991).

Comparison of Model Predictions with Data

Time-series data.—The database for testing model predictions consisted of time-series data documenting fluctuations in the pooled numbers of all microtine rodents (primarily *Microtus* and *Clethrionomys* voles). We used all the data sets that we know, with two restrictions: the data were collected at a European loca-
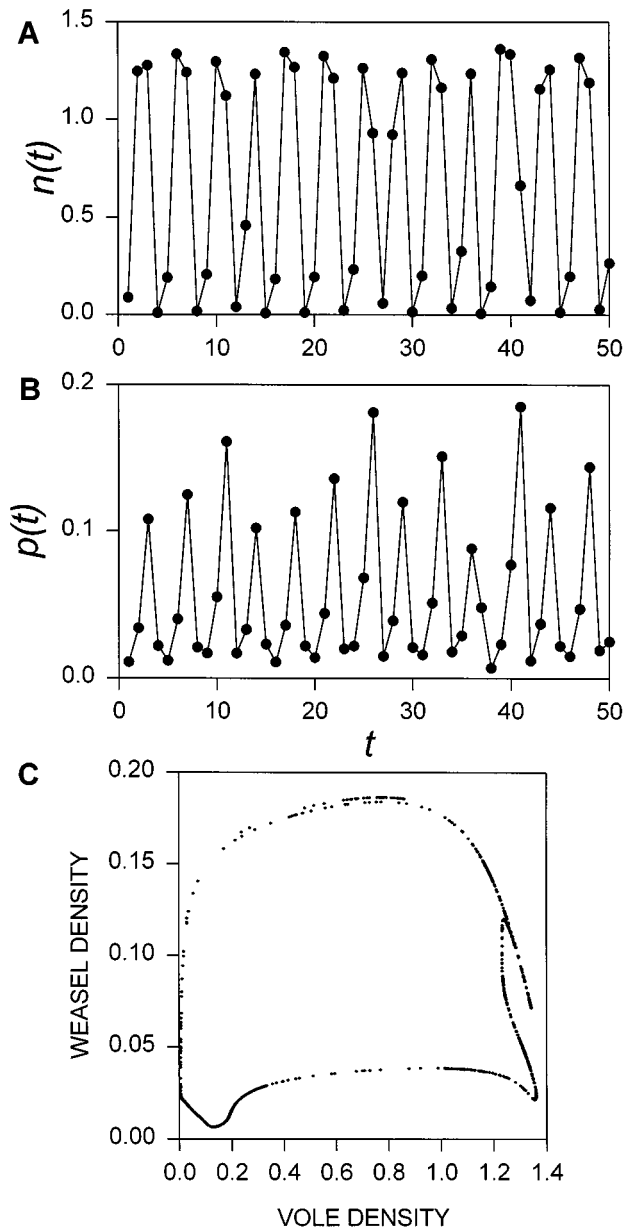
FIG. 4.—A sample trajectory generated by the model with $\sigma = 0$ and $G = 0$ and the median values of other parameters. A, Fluctuations of vole numbers. B, Fluctuations of predator numbers. C, 1,000 points plotted in the $n(t) - p(t)$ phase space.
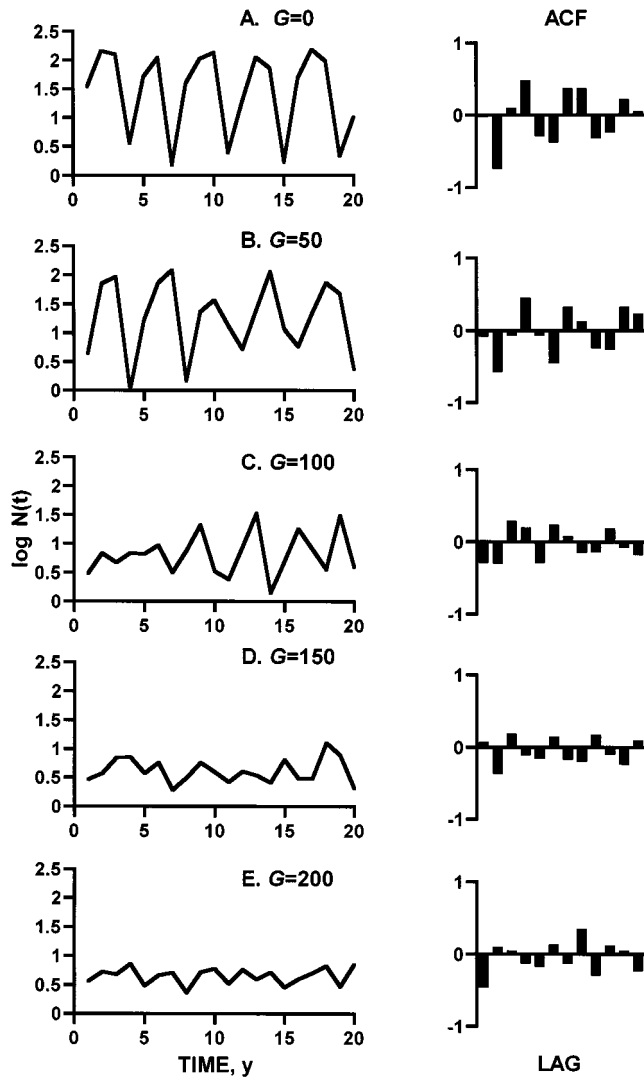
FIG. 5.—The dynamical shift in vole population dynamics predicted by the model. *Left graphs,* sample trajectories for five values of *G* and median values of other parameters. *Right graphs,* autocorrelation functions for each trajectory.

tion, and they had at least 16 yr of uninterrupted annual censuses. Although some data sets contain both spring and fall estimates of vole densities, we only used the latter, since the fall numbers are measured with a greater degree of accuracy (see fig. 1 in Hanski et al. 1994) and better reflect the differences in the observed dynamical patterns between northern and southern populations (Henttonen et al. 1985). We found 16 data sets that fit our criteria, ranging in latitude from 51° N to 69° N (table 2). One long data set (Kilpisjärvi) was split into two

TABLE 3

SUMMARY OF TIME-SERIES ANALYSES OF EUROPEAN VOLE DATA

Locality	Years	Latitude (° N)	S	T	ACF(T)	Λ
Kilpisjärvi 1	1949–70	69	.58	5	.24	.12
Kilpisjärvi 2	1971–92	69	.68	5	.44*	.12
Pallasjärvi	1970–92	68	.73	4	.41*	1.36
Kola	1946–64	67	.79	. . .	. . .	.70
Umeå	1971–94	64	.52	4	.51*	.12
Sotkamo	1966–92	64	.49	4	.51*	.21
Ruotsala	1973–92	63	.65	3	.61*	.87
Alajoki	1977–92	63	.77	3	.41	1.63
Loppi	1972–92	61	.27	. . .	. . .	−2.06
Karelia	1957–77	61	.35	. . .	. . .	−.62
Grimsö	1973–94	59	.48	3	.38	.03
Zvenigorod	1956–86	57	.34	3	.36*	−.18
Tataria	1936–58	56	.34	4	.20	−2.69
Serpukhov	1951–75	55	.26	. . .	. . .	−.52
Tula	1949–76	54	.32	3	.24	−.46
Białowieża	1971–91	52	.42	. . .	. . .	−1.02
Wytham Wood	1948–69	51	.27	. . .	. . .	−.79

NOTE.—Abbreviations: S = the standard deviation of log-transformed vole numbers, T = the average period (periods shown only if ACF[T] > 1 SE of ACF), ACF(T) = the estimated autocorrelation at lag T (an asterisk indicates that ACF[T] > 2 SE), and Λ = the estimated Lyapunov exponent. Sources of data: Kilpisjärvi, Laine and Henttonen 1983 and Hanski et al. 1993; Pallasjärvi, Henttonen et al. 1987; Kola, Koshkina 1966; Umeå, Hörnfeldt 1994; Sotkamo and Loppi, Hanski et al. 1993 (data collected by A. Kaikusalo); Ruotsala and Alajoki, Korpimäki and Norrdahl 1991b and Korpimäki 1994; Karelia, Tataria, Serpukhov, and Tula, Ivanter 1981; Grimsö, Lindström et al. 1994; Zvenigorod, Ivankina 1987; Białowieża, Pucek et al. 1993; and Wytham Wood, Southern 1979.

pieces to compensate for nonstationarity. For each data set we calculated the amplitude S, the average period T, and ACF(T); the Lyapunov exponent was estimated by the methodology described elsewhere (Turchin 1993, 1997) (table 3).

Qualitative features of the dynamical gradient predicted by the model (fig. 5) were in close agreement with the patterns observed in the time-series data (fig. 6). The model correctly predicted an increase in amplitude with increased latitude and a shift from aperiodic dynamics to dynamics dominated by approximately 4-yr periodicity. The model also correctly predicted that the average period in the transitional zone will be approximately 3 yr (see figs. 5C and 6C) and that the period will increase with latitude. However, while in the data the period of the northern-most location is approximately 5 yr, the model predicted 4-yr periodicity for $H = 0$ (figs. 5A and 6A). The observed range of periodicity strength in northern data (0.24–0.61; see table 3) was in close agreement with the predicted range of 0.2–0.6 (see above).

A quantitative comparison between model predictions and data patterns was performed as follows. For each value of $G = 0, 10, 20, \ldots 200$ and the median values of other parameters (including both the dynamical and observation noise), we generated 500 time series, each 22 yr long (because the average length of time-series data was 22 yr). Each model-generated time series was analyzed in
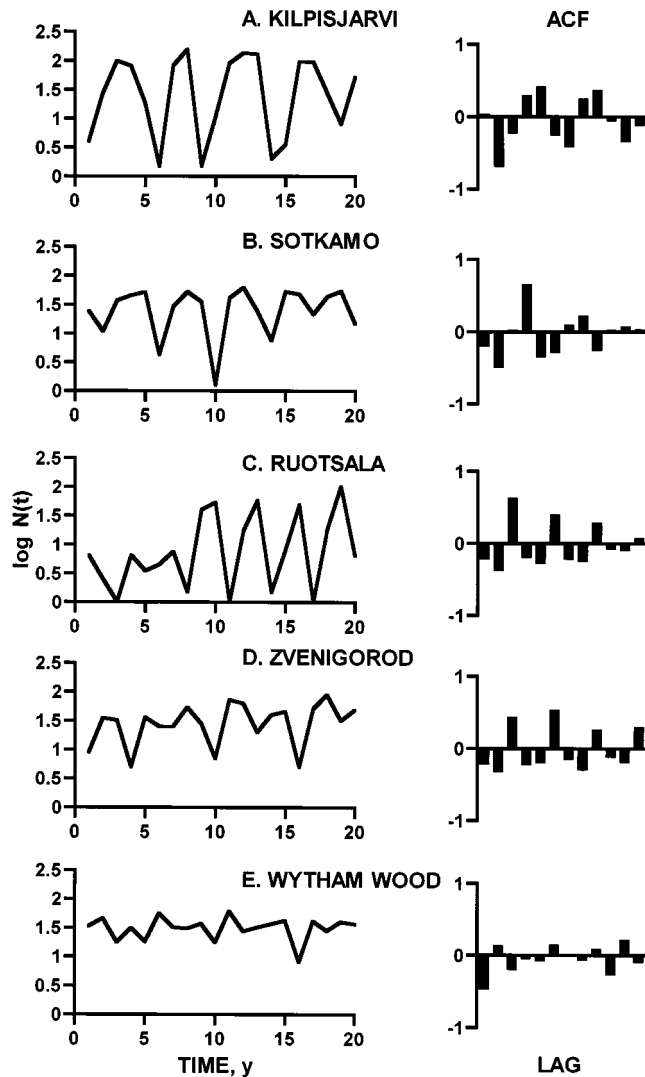
FIG. 6.—The dynamical shift in vole population dynamics in the data. *Left graphs,* time-series data from five locations. All data are plotted using identical *X* and *Y* scales (only the first 20 points are shown). *Right graphs,* autocorrelation functions for each trajectory.

exactly the same way as the actual data to derive estimates of *S* and Λ. The distribution of these statistics for each value of *G* was summarized by its mean and 90% confidence interval (obtained by discarding 5% of the highest and 5% of the lowest values). Next, we plotted the mean and the confidence interval as a function of ''latitude'' (assuming that *G* increases linearly from 0 at 70° N to 200 at 50° N) together with the data-derived values (fig. 7). An additional test of the model is provided by a comparison between the predicted shift in *S* and
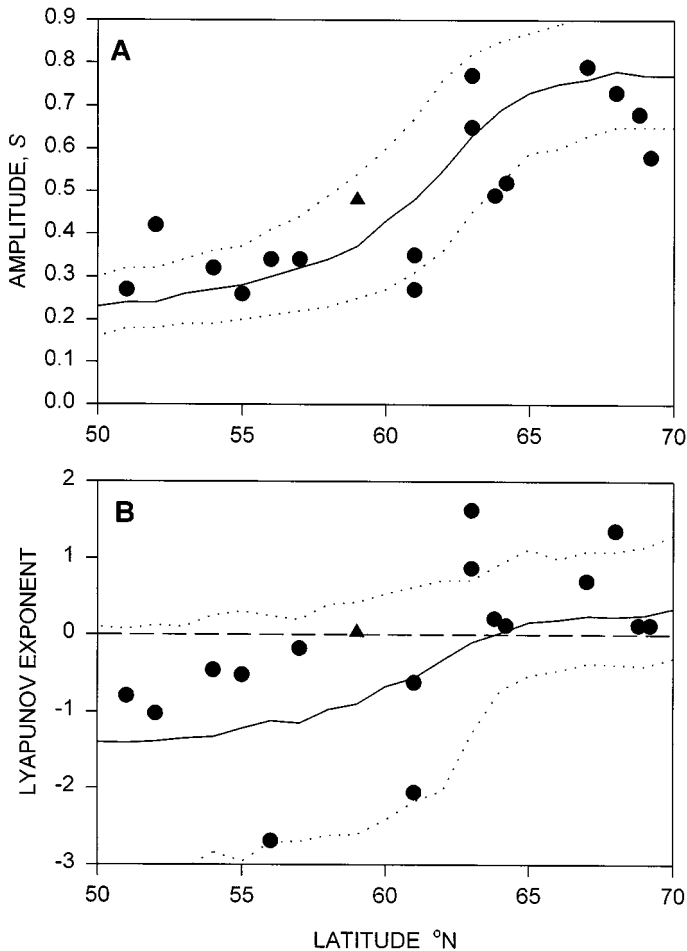
Fig. 7.—Predicted (*solid lines*) and observed (*points*) relationship between latitude and (*A*) the amplitude of fluctuations and (*B*) the trajectory stability. The solid triangles indicate the estimates for the Grimsö area. Dotted lines indicate 90% confidence intervals.

the S values for *Clethrionomys* and *Microtus* populations reported by Hansson and Henttonen (1985, apps. A and B) (fig. 8).

Not all details in the data patterns were correctly predicted by the model (see figs. 7 and 8). In particular, there appears to be more scatter than expected around the predicted S curve (fig. 7*A*). Additionally, at northern sites the data-based estimates of Λ are more positive than are the predicted ones, suggesting that the dynamics of northern populations may be more chaotic than those predicted by the model. Despite these minor deviations, the degree of match between the model and the data is striking. What is especially interesting is that the model predicts a rather abrupt shift from stable, low-amplitude dynamics to chaotic, high-amplitude dynamics, even though the "tuning" parameter G is
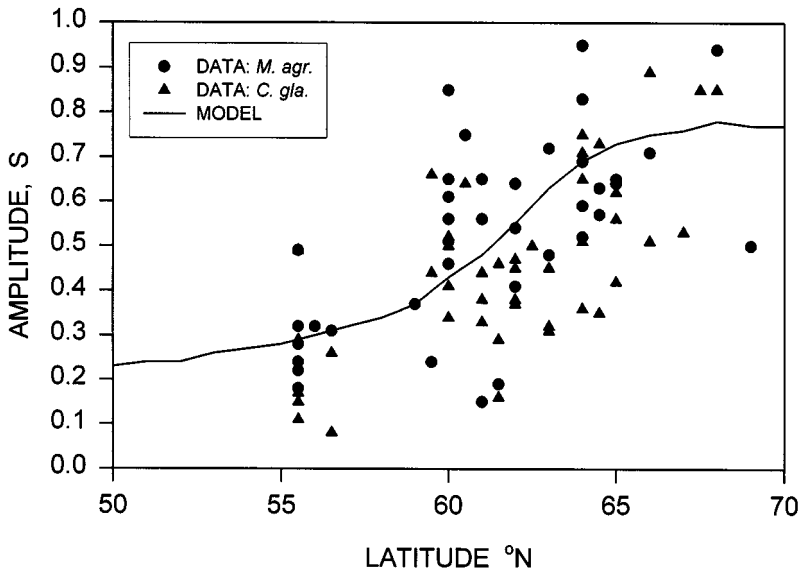
FIG. 8.—Predicted and observed relationship between latitude and the amplitude of fluctuations (data from Hansson and Henttonen 1985).

changed gradually. It is even more interesting that the data appear to bear out this prediction (see fig. 7*A, B*). Finally, both the model and the data exhibit a shift from stable to chaotic dynamics at the same latitude, around 63° N (fig. 7*B*).

<center>DISCUSSION</center>

Hansson and Henttonen (1985) established conclusively that there is a well-defined geographical gradient in rodent dynamics in northern Europe, with cyclic rodent populations being confined to high latitudes. Several workers had previously conjectured that the more southern rodent populations are relatively stable because of regulation by generalist predators (Hansson 1971; Andersson and Erlinge 1977; Erlinge et al. 1983), but it was the combination of the latter idea with the geographical gradient documented by Hansson and Henttonen (1985) that steered the field forward. Other studies (Hanski et al. 1991) showed that the density of generalist predators increases by an order of magnitude from north (69° N) to south (56° N) in Fennoscandia, and it was shown with model (1) that an increased impact of generalist predators may account for the observed decrease in the amplitude and the period of rodent oscillations from north to south. A subsequent parameterization of the vole-weasel part of the model successfully predicted the observed rodent dynamics in the north, where the impact of generalist predators is relatively weak (Hanski et al. 1993; Hanski and Korpimäki 1995). In this article, we have brought this line of research to its logical conclusion, by parameterizing also the generalist predator component in the

model. We have also refined the procedures of parameter estimation, using earlier results (Erlinge 1975; Erlinge et al. 1983; Korpimäki and Norrdahl 1991*a*, 1991*b*; Turchin and Ostfeld 1997). Finally, we used the parameterized model to predict the observed quantitative patterns in time-series data. We have shown that the model predicts correctly the latitudinal shift in rodent dynamics in northern Europe.

Though we are well aware of the pitfalls in the modeling approach used here (and will discuss potential difficulties later), the strikingly successful predictions of the amplitude and stability of rodent dynamics along the entire geographical gradient in northern Europe (figs. 5–8) speak for themselves. A great advantage of our model is that its structure and assumptions are simple and transparent, so that the predicted dynamical behavior is easily verified by others. The estimation of model parameters includes no hidden assumptions, and our estimates are clearly laid out for possible challenges. We believe that if the alternative hypotheses explaining rodent oscillations (as listed in, e.g., Stenseth and Ims 1994) would be developed in the same spirit as the predation hypothesis, the prospects for arriving at some consensus on the 70-yr-old puzzle of rodent dynamics (Elton 1924) would be closer.

Assumptions about Values of Critical Parameters

In the process of parameterizing our model, we made several assumptions about parameter values that are critical for model behavior. In the following section, we comment in turn on the estimation of the intrinsic rate of vole population increase and the vole carrying capacity, the vole-weasel ratio, the seasonality in the reproduction of voles and weasels, and the latitudinal decline in the rate of predation by generalist predators.

The estimate of the intrinsic rate of population increase (r) used in this article was based on the detailed analysis of experimental data for *Microtus pennsylvanicus* (Turchin and Ostfeld 1997). The yearly average (i.e., average over all seasons within a year) obtained for *M. pennsylvanicus* is substantially greater ($r = 6$) than the one used by us previously ($r = 4.05$; Hanski et al. 1993). Our previous estimate was based on maximum rates of increase observed in time-series data during summer and winter. Given the generally high rate of increase, our previous estimates are likely to be affected by density dependence and hence to be underestimates. Another factor that should bias the r estimate downward is predation by generalist predators. On the other hand, the estimate obtained from enclosed populations of *M. pennsylvanicus* in high-quality habitat may overestimate r in *Microtus* populations at the higher latitudes in northern Europe. Our numerical results (see above) indicated that variation in r had little effect on the stability and amplitude of population oscillations but a substantial effect on the predicted people in the north, with $r = 5$ producing the best match with the data (see fig. 9). Thus, it appears that our two estimates of $r = 4$ (Hanski et al. 1993) and $r = 6$ (this study) most likely bracket the actual r for *Microtus* in Fennoscandia.

One of the most problematic parameters in the model (with the possible exception of Q) is K, the prey's equilibrium population size in the absence of pred-
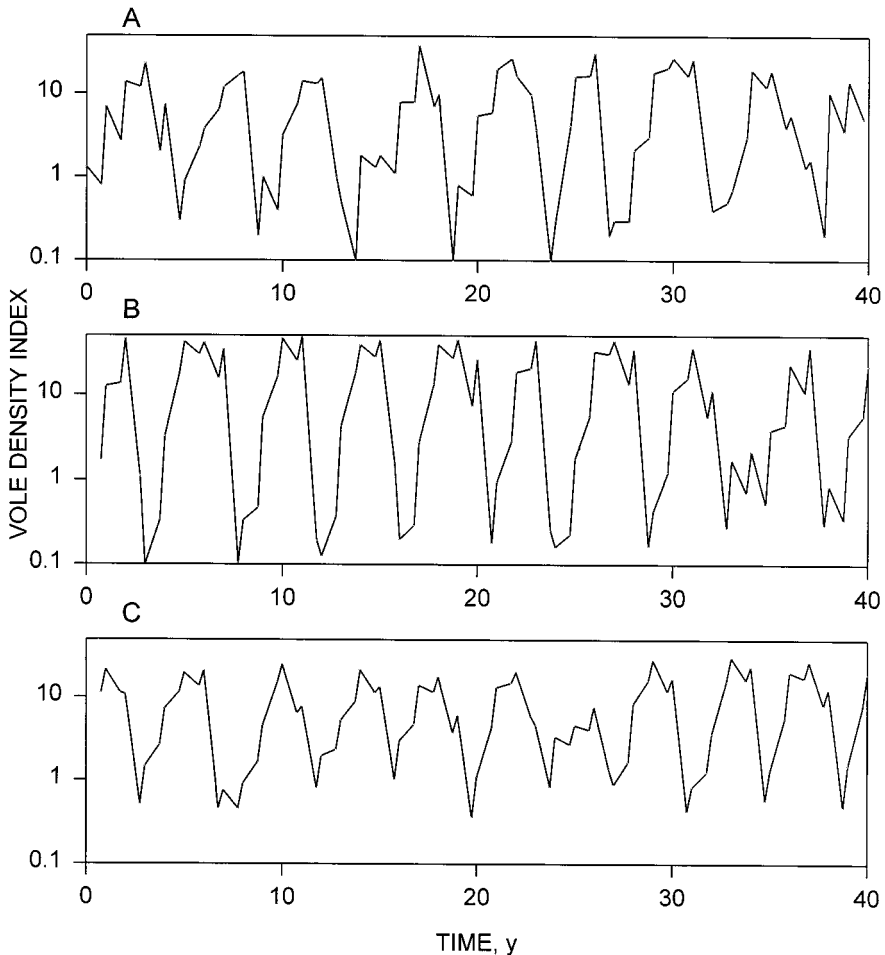
FIG. 9.—Comparisons between time-series data and model predictions. *A,* Population fluctuations of vole numbers in Kilpisjärvi, Finnish Lapland, 1952–1992 (data from Laine and Henttonen 1983; H. Henttonen, personal communication). Two data points (early summer and fall) are plotted for each year. *B,* A trajectory predicted by model (4) in this article. All parameters are at their median values, except $r = 5$. *C,* A trajectory predicted by the model and parameter values of an earlier study (Hanski et al. 1993).

ators. Model dynamics are very sensitive to the value of this parameter (via the ratio D/K). This is a generic feature of predator-prey models of this kind (e.g., the paradox of enrichment; Rosenzweig 1971). For many sites in northern Europe, there are no experimental data from enclosures, and even observational data have not yet been analyzed in any detail. Little is known about variation in K with habitat. It is also possible that K may increase with decreasing latitude (e.g., Henttonen et al. 1987). Thus, one of the pressing tasks for further empiri-

cal work is obtaining reliable estimates of K for sites covering the entire geographical gradient and a variety of habitats.

Another difficult parameter is the vole-weasel ratio, Q. This parameter is impossible to estimate without designing a specific experiment, because it specifies the number of voles per each individual predator at equilibrium. In the north, both populations are oscillating and thus are never found at the equilibrium. In the south, where population dynamics are more stable, the observed vole-weasel ratio may be higher than Q as a result of increased avian predation on weasels (Korpimäki and Norrdahl 1989*a*, 1989*b*). In addition, we expect that Q may vary with habitat. For example, forested habitats appear to offer a greater opportunity for voles to escape weasels attacks by climbing shrubs and trees (e.g., Jedrzejewska and Jedrzejewski 1990). Decreased hunting success of weasels would require a higher density of voles at the equilibrium and would tend to increase Q. The whole issue of spatial heterogeneity in Q (and K) remains largely unexplored. Since such a theoretical exploration would require a spatially explicit and, most likely, an individual-based model, it falls outside the scope of this article.

Let us turn now to the effects of seasonality. An earlier analysis (Turchin and Ostfeld 1997) suggested that the strength of density dependence, as measured by the rate of decline in the per capita growth rate with increasing population density, remains constant throughout the year in *M. pennsylvanicus*. In other words, there is parallel seasonal variation in the values of r and K (see fig. 1). The sine function used to model changes in r contrasts with the step function that we used previously (Hanski et al. 1993; Hanski and Korpimäki 1995). The truth most probably lies somewhere in between. Our numerical results suggest that increasing the steepness of the transitions between summer and winter has only minor effects on the quantitative features of dynamics. Nevertheless, the model in this article predicts somewhat different quantitative patterns of vole oscillations, compared with the previous model (Hanski et al. 1993) (fig. 9; note, in particular, the difference in the predicted amplitude). This difference is primarily a result of assuming different parameter values rather than an effect of structural changes.

Finally, in *Generalist Predation Parameters,* we noted that the expected G for Grimsö was much lower than the assumed value (see table 1). This discrepancy suggests that changes in G along at least some south-north gradients in Fennoscandia are not, in fact, linear. Indeed, there are recognized biogeographical boundaries in Sweden and Finland at which largely agricultural landscapes change into largely forested landscapes (Angelstam et al. 1984)). The data on the numbers of raptors in Finland reported earlier (Hanski et al. 1991) suggest that, at such a boundary, the density of generalist predators declines relatively steeply, apparently because of parallel decline in the numbers of alternative prey. The well-studied Grimsö area in central Sweden is of particular interest, because it is located on the border between the landscape dominated by agriculture to the south and the landscape dominated by forest toward the north (Angelstam et al. 1984), which may explain why the estimated density of generalist predators is lower than expected for the latitude (table 1). It is interesting

that both the amplitude and the Lyapunov exponent estimated from vole population data at Grimsö are somewhat higher (although still within the 90% confidence interval) than is predicted by our model, which assumes a linear latitudinal gradient in G (see fig. 7). This observation is consistent with lower-than- expected density of generalist predators at Grimsö (with a caveat that a great deal of uncertainty is associated with an estimate from any single time series; see the confidence limits in fig. 7). To summarize, it is probably not latitude per se but a change in some other correlated environmental variables (such as duration and depth of snow cover) that affect the density of generalist predators. Because it is unlikely that these environmental variables change linearly with latitude, the gradient in G should also not be constant. The effect of abrupt shifts in G would be to make the transitions between stable and oscillatory dynamics even more discontinuous than is predicted by our model.

Obtaining Predictions from the Model

Empirically based models bridge the gap between theory and data. One compelling reason to develop them is their ability to make specific and quantitative predictions that can be tested with experimental or observational data. We envision several empirical approaches to testing our model. One is to design mensurative experiments (e.g., Krebs 1991) for direct estimation of model parameters and tests of model assumptions about population growth and predation. If such studies yield estimates of model parameters that result in a mismatch between observed dynamics and those predicted by the model, then the model should be rejected. The key parameters that should be measured first are $d = D/K$ and $a = C/Q$, because they have the greatest effect on model dynamics, while their estimates are least precise. The second approach is to use the model to predict broad-scale patterns in dynamics as reflected in time-series data. Because many such data sets have been collected in northern Europe, this is the approach we followed here. Another approach, combining the first two, is to make predictions about specific parameters based on information from time-series data. For example, we recently learned that vole populations in northern England are characterized by amplitude $S = 0.5$ and period of approximately 3 yr (S. J. Petty and X. Lambin, personal communication). Using figure 7A, we predict that the 90% prediction interval for G is [70, 120] individuals ha^{-1} yr^{-1}. Field studies to measure generalist predation pressure in this locality are currently under way (X. Lambin, personal communication) and should provide another independent test of our model. Finally, we are planning to use the model in making quantitative predictions on the course of manipulative experiments in which predators are either removed or added to experimental areas. Many other ways to test the model can be envisioned, but the list we give above is sufficient to support our contention that our model can be used to provide specific and quantitative predictions, thus motivating further empirical research.

General Implications

Ecologists have debated at length whether explanations for vole oscillations should be sought using a single- or a multifactorial approach (Lidicker 1978,

1988, 1991; Taitt and Krebs 1985; Gaines et al. 1991). Our model represents an approach that does not fit comfortably into this dichotomy. On the one hand, we focus on the interaction between voles and their specialist predators as the primary factor responsible for multiannual oscillations. The primary factor here means that if the specialist predation term is removed from the model, then the model would not exhibit oscillations (by oscillations we mean the kinds of population dynamics that are driven by some endogenous factor acting in a delayed density-dependent manner; oscillations exhibit a certain kind of regularity, in either the periodic or the chaotic sense). Thus, our approach may be classified as a single-factorial one, because we do not invoke other endogenous factors that may act in a delayed manner to cause vole density to oscillate (e.g., interactions with food, parasites and diseases, or a variety of intrinsic factors).

On the other hand, our model includes several other terms that are necessary for a successful prediction of the observed dynamics. For example, the intraspecific regulation term in the vole equation (due to the combined effect of food limitation and social interactions) ensures that weasel-vole oscillations are stable. Without this term, vole numbers would easily outgrow the ability of predators to catch up with them, and no oscillations would ensue. Other factors included in the model are also necessary for a quantitative prediction of vole time-series patterns: seasonal effects account for within-year dynamics in southern populations and allow the model to behave chaotically in the north; generalist predation pressure is necessary to explain the latitudinal gradient; and including stochastic density-independent factors is needed for a quantitative, statistical comparison between model predictions and data. The match between model predictions and the dynamical patterns in the data suggests that the explanation modeled in this article, the generalist/specialist predation hypothesis, is a highly plausible one (at least until somebody can do equally well or better with a model based on one of the alternative hypotheses). It does not mean, however, that factors not included in the model are unimportant. Clearly, shifts in individual behavior, variation in the food supply, parasites and pathogens, and spatial heterogeneity (see fig. 2 in Lidicker 1988) all have an effect on population dynamics, and it is possible that some of the mismatch between model predictions and the data is due to us not modeling one or more of these factors explicitly. Nevertheless, these factors are secondary in the sense that they are not needed to explain the shift from stable dynamics to multiannual oscillations of vole populations in northern Europe.

In our judgment, we have now reached the limit to which the present kind of modeling approach can be usefully pushed. We see two directions for future theoretical research that show great promise. First, alternative hypotheses explaining vole population dynamics should be enfleshed in empirically based models of the kind that we developed for the generalist/specialist predation hypothesis. This would be a good scientific practice, because it has the potential of rejecting the predation hypothesis, if one of the alternative explanations predicts data more accurately. Even more importantly, fluctuations in small rodent populations in different geographical regions may be explained by different hypotheses. This may be especially likely for North American vole populations.

These populations appear to exhibit a very different dynamical pattern from what is observed in Europe—a high amplitude of fluctuations but no evidence of periodicity (Hansson and Henttonen 1985; P. Turchin, unpublished data).

The second direction is constructing structured population models or individual-based simulations. The need for such approaches is especially pressing in developing theoretical understanding of the effects of age structure (e.g., Boonstra 1994) and spatial heterogeneity and dispersal (Stenseth and Lidicker 1992) on vole population dynamics.

Probably the most exciting direction is to combine together theoretical and empirical approaches. In this article, we have identified several population processes and parameters for which good empirical information is lacking, and further efforts to model other hypotheses are likely to identify more gaps in our understanding of vole population ecology. We also perceive great opportunities for testing the predation hypothesis in areas other than Fennoscandia and on species other than voles. Finally, the most satisfying test of the predation model lies in large-scale field experiments. Such experiments are expensive but are now better justified than ever for the generalist/specialist predation hypothesis.

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