NOTES AND COMMENTS

MORE THOUGHTS ON
VERTEBRATE PREDATOR REGULATION OF PREY

Kidd and Lewis (1987) made two critical comments on our paper entitled "Can vertebrate predators regulate their prey?" They claimed that the evidence presented for predation-mediated regulation is inconclusive, and they questioned some of the ways we interpreted our data. Their second criticism concerns the dynamics of the examined *Microtus* population. Kidd and Lewis argued that our data suggest "the possibility of a population fluctuation, albeit of small amplitude" (p. 448). We agree on that. Moreover, recent detailed studies based on the mark-recapture method have confirmed that the vole population fluctuates between years and that the numbers in the autumns of different years vary considerably (fig. 1). The point that we have stressed in our papers (Erlinge et al. 1983, 1984), however, is that the vole population in southern Sweden shows a noncyclic pattern, which is the opposite of the pattern characterizing the microtine populations in northern Sweden (Myllymäki 1977; Hansson 1979; Hörnfeldt et al. 1986). This difference means less between-year fluctuation in the south (no marked population crash following a year with peak densities) and a characteristic seasonal pattern with peak numbers in autumn and low densities in spring and early summer every year. Our study aimed to explain this difference.

Kidd and Lewis's first comment concerns the regulative significance of predation. They argued that population regulation implies density dependence. The predation rate on voles in our study has not been shown to work in a density-dependent way between years, and the delayed density dependence observed over the year would essentially be destabilizing.

Kidd and Lewis are right in many of their comments. We were not able to demonstrate any clear evidence for density-dependent predation in our earlier studies. Instead, we found that predation rate was inversely correlated with changes in vole numbers during most of the year (Erlinge et al. 1983, p. 41, fig. 3). We considered two exceptions important, however. Density-dependent predation occurred in autumn toward the end of the reproductive season and in late spring at the beginning of the breeding season. This timing might have a regulating effect on vole numbers between years. Ricklefs, discussing population regulation, concluded that "for a population to be maintained within narrow limits, stabilizing forces need operate only during a portion of the year that is long enough to
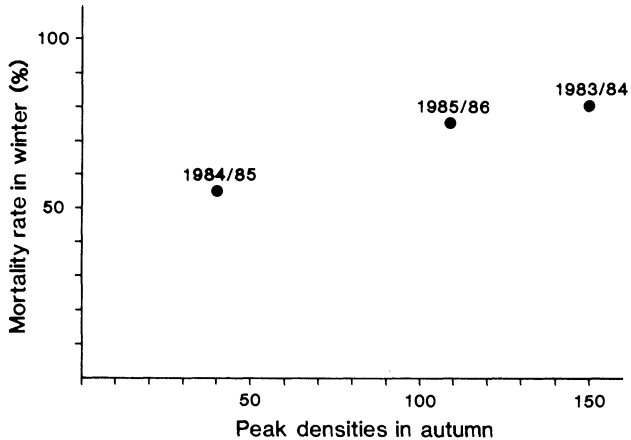
FIG. 1.—Winter mortality rate in relation to peak vole densities ($N/0.5$ ha) during the preceding autumn. Mortality rate (q) is calculated according to the formula $q = d/P$, where d is the mortality from autumn to spring (April) and P the peak density in the autumn. The data are from three years, 1983–1984, 1984–1985, and 1985–1986.

readjust the population to its equilibrium level each year" (1973, p. 474). As Kidd and Lewis have noticed, however, our data on vole numbers in our 1984 paper did not provide any evidence for density-dependent mortality acting between years. Our estimates of small-rodent abundances in autumn, however, were uncertain and contained some errors (see comments in Erlinge et al. 1983). The vole data presented over several years in the 1984 paper were based on broad-scaled sampling that gave mean values for the whole study area. There were great variations between samples in the same series, and we considered these data not useful for analyzing between-year differences.

The dynamics of a population of a local vole, *Microtus agrestis*, were studied using mark-recapture data starting in 1983 in the same study area. Three winter/ spring declines have been recorded so far. Peak densities at the end of the reproductive season have varied considerably, but densities in April (at the beginning of the breeding season) have been similar in the three years. During these years, the mortality rate during the winter and spring shows a density-dependent pattern (fig. 1). These data on between-year variation in mortality rate give a stronger support for our suggestion of density dependence than did our earlier data.

This recent study also includes an experimental test concerning the importance for predation of the spring decline of the vole population (Erlinge 1987). In an area of half a hectare, predation by avian and mammalian predators (apart from weasels) was prevented by fencing. The dynamics of the vole population in the manipulated area were compared with that of controls. Preliminary data support our earlier observation that predation is a primary cause for the spring decline in this vole population.

Some points in our model need clarification. Kidd and Lewis claimed that there
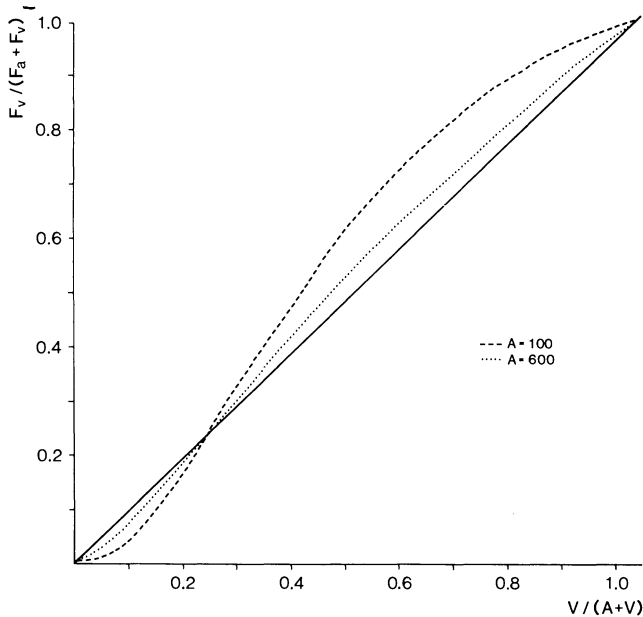
Fig. 2.—Switch functions, giving the proportion of the total prey abundance that is made up of voles, $V/(V + A)$, in relation to the proportion of voles in the predators' diet, $F_v/(F_a + F_v)$. The relationship is given for two values of the alternative-prey density (A), 100 and 600 kg/km^2. The parameters Fr_v and Fr_a are 50 and 150, respectively, in both cases.

is no density-dependent predation in our model and that predation, if operating according to the model, cannot therefore regulate the vole population. Although not explicit, elements of both switching and direct density dependence are in the model. This is a numerical consequence of combining the rule for predator habitat choice (in proportion to the abundance of the two prey types) with a Holling type-II functional response (Erlinge et al. 1984, p. 130, eq. 2):

$$F_v = [V/(V + A)][F_{max}V/(Fr_v + V)] , \tag{1}$$

$$F_a = [A/(V + A)][F_{max}A/(Fr_a + V)] , \tag{2}$$

where F_v and F_a are the predation rates (in biomass per year) on voles and alternative prey, respectively; V and A are the abundances of voles and alternative prey; F_{max} is the maximum predation rate (attained when prey abundance is not limiting); and Fr is the functional-response parameter.

Equations (1) and (2) yield a set of switch functions whose characteristics depend on prey density. Typical switch functions (fig. 2) are obtained using two representative values of the alternative-prey density. The range of values from which these values are taken is encountered in nature and predicted in the simulations (figs. 4, 5). In a typical switch, predation on the more common prey is disproportionately high.

Moreover, the function for predation rate on voles is affected by the abundance of the alternative prey (fig. 3). Under some conditions, density dependence is
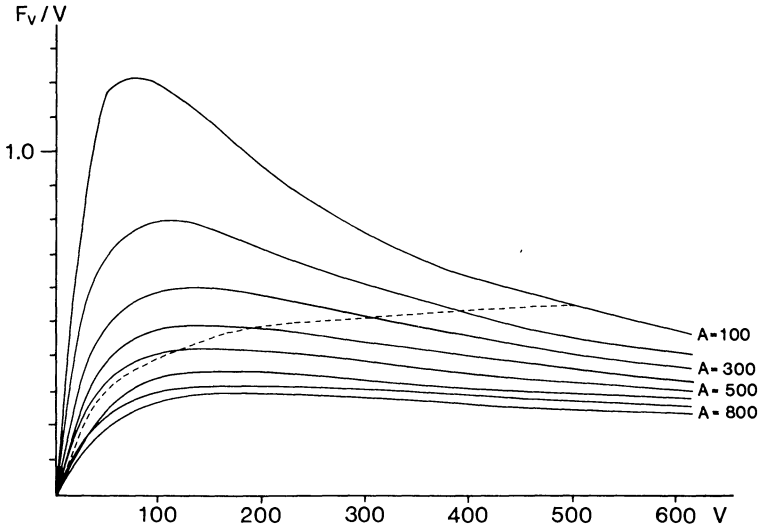
FIG. 3.—The relationship between vole density (V, in kg/km^2) and predation pressure (measured as voles taken per year over voles present). The measures on the y-axis cannot be taken literally (under some conditions proportions over 1.0 are measured), because the simulations use differential equations and instantaneous values. The relationship is given for eight constant values of alternative-prey density, ranging from 100 to 800 kg/km^2. *Dashed line*, The relationship under the condition that total prey density is 600 kg/km^2.

positive: a higher proportion of prey are taken at higher prey densities. This is true for constant and relatively high densities of the alternative prey combined with relatively low vole densities. For a wider range of vole densities, it is also true if one assumes that the total prey density is constant (dashed line). Hence, our model contains elements of both switching and density dependence.

The crucial question is whether this property of the model contributes to the damping effect on vole population fluctuations that we observed in the simulations (Erlinge et al. 1984, fig. 2). We compare the model with a modified version in which switching and positive density dependence are removed. Here, total predation rate is first determined by the function

$$F = F_{max}(A + V)/(Fr + A + V) . \tag{3}$$

This predation is then divided between both prey types in proportion to their densities:

$$F_v = FV/(V + A) ; \tag{4}$$

$$F_a = FA/(V + A) . \tag{5}$$

Simulating this model gives less damping than does the original model (fig. 4), suggesting that the presence of regulating mechanisms, such as switching, indeed contributes to the damping effect.

Finally, we wish to examine whether our model behaves like that of Kidd and Lewis (1987) with respect to the contribution of high predation pressure per se to
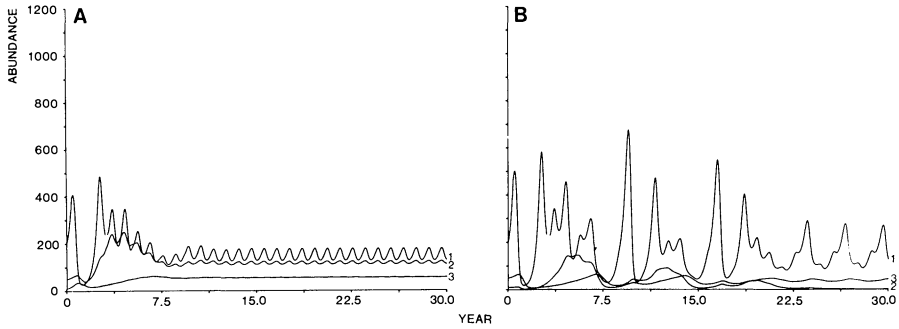
FIG. 4.—The outcome of simulating the model with switching (A) and without (B). A, B, F_{max} = 1440 and K_p (the territorial limit to predator density in individuals per km^2) = 2.5. A, Fr_v = 50 and Fr_a = 150; B, Fr = 100. 1, Vole density, in kg/km^2; 2, alternative-prey density, in kg/km^2; 3, prey density in the number of individuals times 160 per km^2. The factor 160 is a scaling factor.

the damping of vole fluctuations. The following equation in our original model governs the predator dynamics:

$$dP/dt = \text{maximum of} - 6P \text{ and } Pr_p(2 - F_{max}/F) , \qquad (6)$$

where r_p is the predator's rate of increase,

$$F = F_{max} V/(Fr + V) . \qquad (7)$$

Changing F_{max} does influence total predation (eq. 7) but not (directly) predator dynamics, since F and F_{max} change proportionately (eq. 7) and these changes cancel (eq. 6). Simulating our original model (fig. 5) shows that changing the overall level of predation does affect vole dynamics. Thus, our model agrees with that of Kidd and Lewis (1987) in that predation level per se does contribute to the damping of vole fluctuation.

How can high predation rate and high predator density be maintained? According to our field data (Erlinge et al. 1983, 1984; Erlinge 1987), the presence of alternative prey makes this possible. In addition, our more recent field data show a density-dependent mortality rate between years. Previous evidence suggests that this is caused almost completely by predation. The modeling exercise presented here suggests that switching (disproportionately high predation on the more common prey) does enhance the damping effect on vole population fluctuation. Under these conditions, one can truly speak of regulation.
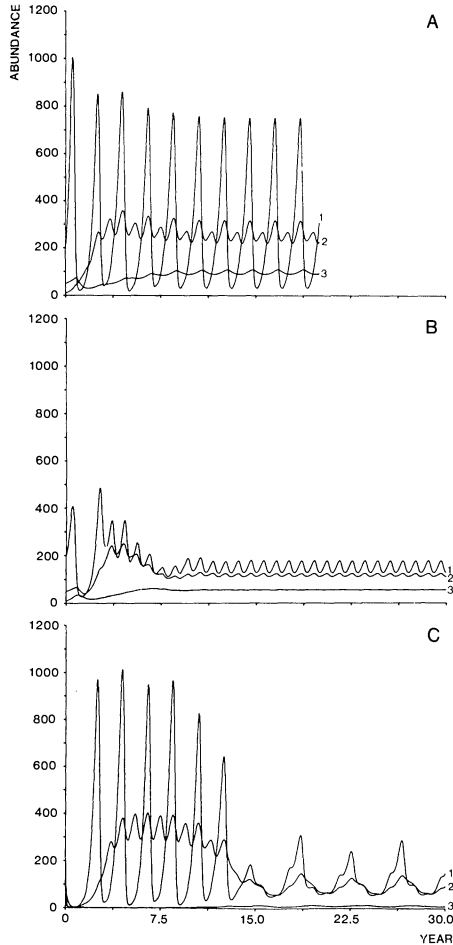
Fig. 5.—The outcome of simulating the model with different predator feeding rates: A, $F_{max} = 360$; B, $F_{max} = 1440$; C, $F_{max} = 7300$. Other parameters as in figure 4; abundances as in figure 4.

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