Vol. 123, No. 1 The American Naturalist January 1984

CAN VERTEBRATE PREDATORS REGULATE THEIR PREY?

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Submitted November 3, 1982; Accepted May 17, 1983

Whether vertebrate predators can regulate their prey or not has long been a controversial question. At the one extreme it has been claimed that predators have no impact on prey numbers but consume only a doomed surplus (Errington 1946), and at the other that predators strongly interact with their prey causing either stable equilibria or cycles (Tanner 1975; Keith et al. 1977). However, there are no field studies showing a regulatory effect of predation among vertebrates. Here we report on such a study.

FIELD STUDIES

The population dynamics of nine species of vertebrate predators and their main prey were examined during 4 yr (1975–1978) in the Revinge area (40 km^2) of southern Sweden. Prey consumption was calculated for all the predators based on data on their diet, food requirements, and population size (Erlinge et al. 1983; Erlinge 1981; Liberg 1981; Nilsson 1981; von Schantz 1981; Sylvén 1982). Rabbit (*Oryctolagus cuniculus*) and small rodents (*Microtus agrestis* and *Apodemus sylvaticus*) were important prey and constituted about two thirds of the biomass consumed by the predators (table 1). The predator species could be separated into two different groups, one classified as "generalists" (feeding on a variety of prey), and the other classified as "small rodent specialists" (feeding mainly on small rodents; tables 1 and 2).

The field vole (*M agrestis*) population, the predominant rodent species in the area, did not show any significant between-year variations in numbers (Erlinge et al. 1983; for details on methods see Hansson 1979). Vole dynamics were characterized by low densities in spring and early summer, and peak densities in autumn (fig. 1). The predator's consumption approximately equaled the production of field voles (fig. 1), thus preventing cyclic population densities typical of many other microtine populations (Krebs and Myers 1974). Further support for the importance of predators in dampening vole densities was that the marked decrease in vole numbers during the winter (nonreproductive season) equaled the number

Am. Nat. 1984. Vol. 123, pp. 125–133.

TABLE 1

PREY CONSUMPTION (kg) AND THE PROPORTION OF FIELD VOLES AND RABBITS (% weight of food) IN THE PREDATORS' DIET

	GENERALIST PREDATORS						SPECIALIST PREDATORS			
	Meles meles	*Vulpes vulpes*	*Felis catus*	*Mustela putorius*	*Buteo buteo*	*Strix aluco*	*Asio otus*	*Falco tinnunculus*	*Mustela erminea*	
Field voles	181(2.8)	620(4.2)	633(21.1)	68(2.8)	1252(26.1)	229(16.1)	282(68.3)	349(59.0)	238(42.1)	
Rabbits	293(4.5)	11487(78.2)	2060(68.7)	773(32.5)	2085(43.5)	118(8.3)	5(1.2)	...	46(8.2)	Σ 34349
Other prey	6036(92.7)*	2573(17.5)	307(10.2)	1539(64.7)	1453(30.3)	1073(75.6)	126(30.5)**	243(41.0)**	280(49.6)**	

* Mainly earthworms.

** Mainly water voles and wood mice.

TABLE 2

POPULATION SIZES IN SPRING 1975–1978 OF THE DIFFERENT PREDATORS AND THE BREADTH OF THEIR FOOD NICHES (B_F)

	GENERALIST PREDATORS						SPECIALIST PREDATORS		
POPULATION SIZES	*Meles meles*	*Vulpes vulpes*	*Felis catus*	*Mustela putorius*	*Buteo buteo*	*Strix aluco*	*Asio otus*	*Falco tinnunculus*	*Mustela erminea*
1975	30	37	99	24	44	28	26	21	30
1976	42	38	84	27	36	32	4	10	30
1977	33	34	87	24	38	32	6	8	20
1978	?	38	101	?	40	30	10	12	12
$\bar{x}$ ± SD	35.0 ± 6.2	36.8 ± 1.9	92.8 ± 8.5	25.0 ± 1.7	39.5 ± 3.4	30.5 ± 1.9	11.5 ± 10.0	14.8 ± 5.7	23.0 ± 7.5
$\frac{SD}{\bar{x}} \times 100$ ...	17.7	5.2	9.2	6.8	8.6	6.3	86.9	44.5	32.8
$B_F{}^* = \frac{1}{\Sigma\, pi^2}$	1.28	1.43** 2.33***	1.81	3.17	3.09	3.17	1.23	1.36	1.33

NOTE.—Apart from *Asio otus* and *Falco tinnunculus,* who left the area for periods in winters, all the predators stayed in the area throughout the years.

* Based on dietary proportions, in biomass, of small rodents, insectivores, lagomorphs, birds, amphibians, insects, earthworms, and others together, for 1975 and 1976.

** In years (1975 and 1976) with high rabbit densities.

*** In years (1977 and 1978) with low rabbit densities.

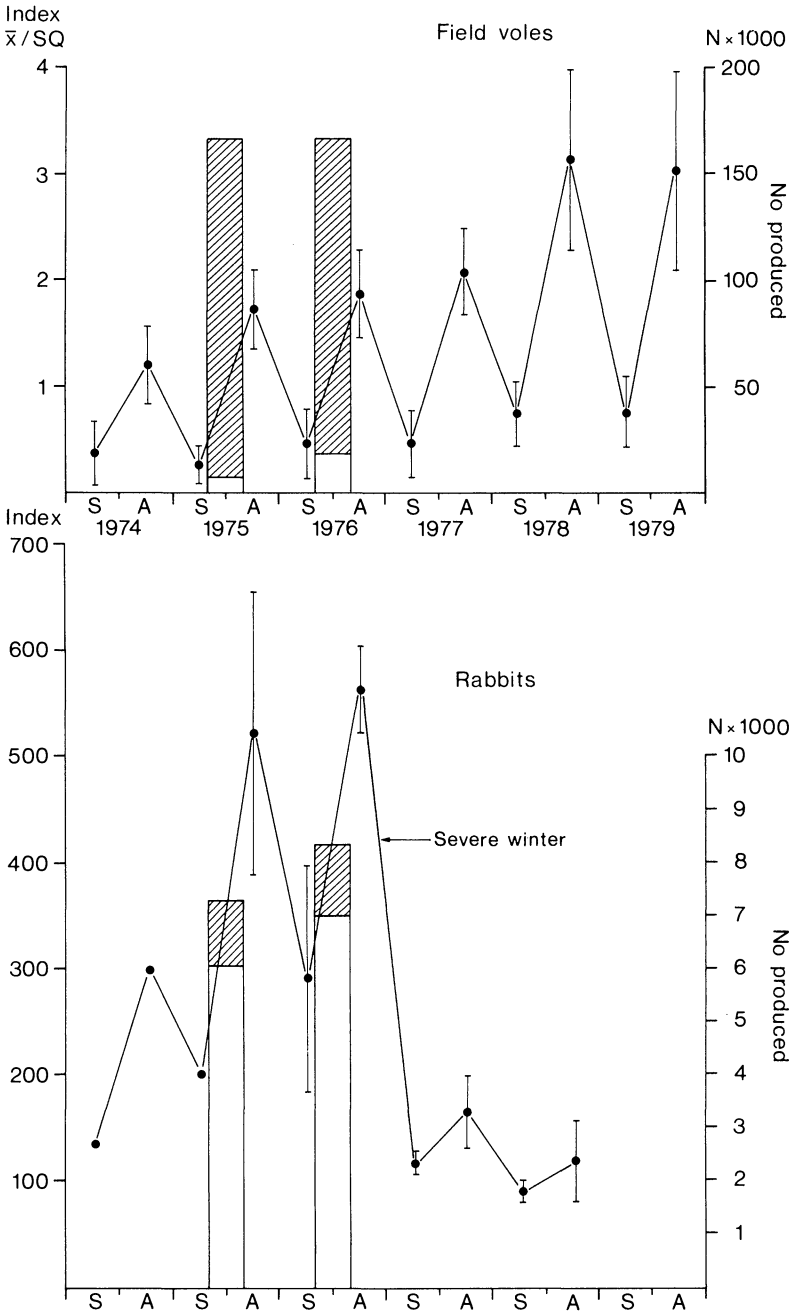

Fig. 1.—Changes in population numbers of the 2 important prey species (field vole and rabbit) in the study area and the impact of predation on the annual production of voles and rabbits. Relative densities of field voles and rabbits were recorded in spring (S) and autumn (A); for voles by snap trap captures in small quadrats (Hansson 1979; Erlinge et al. 1983; 20–

taken by predators during the same period (Erlinge et al. 1983). Also, during the first part of the breeding season, an observed delay in recovery of vole numbers could be ascribed to a high predation rate at that time (Erlinge et al. 1983). The main part (approximately 80%) of predation on field voles was caused by the generalists (Erlinge et al. 1983), although their diet consisted of field voles only to a small degree (table 1). The continuous high predation rate and the dampening of vole cyclicity requires that the predators maintain fairly high numbers as the rate of increase of the predators is less than that of the prey (Tanner 1975). In our area, generalist predators were able to maintain continuous numbers by switching to alternative prey (primarily rabbits) during the annual period of low vole densities (Liberg 1981; von Schantz 1981; Sylvén 1982).

Of the generalists' prey, rabbits dominated and in 1975 and 1976 contributed 51% (biomass) of the food, whereas field voles accounted for only 9%. Rabbit numbers were much less stable than those of the field voles (fig. 1). During the first 3 yr, the rabbit population increased from year to year but then declined during a few winter months with abnormally severe winter conditions in 1976–1977. This winter snow cover lasted for 4 mo whereas in each of the previous winters (1974–1976) it lasted less than 1 mo. The densities remained low in the following years. In 1975 and 1976, predators consumed rabbits corresponding to 20% of the estimated production (fig. 1), and predation apparently had no limiting effect on rabbit density in contrast to the adverse effect on vole density. Rabbit numbers were primarily influenced by weather conditions since adverse winter weather reduced their numbers.

The populations of generalists in spring were fairly constant throughout the years studied (table 2) because of their territorial behavior, and population sizes remained almost the same even after the rabbit decrease in 1976–1977. During that period, the generalists increased the proportion of field voles in their diet and in some generalists, especially the fox, reproductive output decreased (von Schantz 1981). By contrast, the specialist populations varied considerably (table 2). In early summer, small changes in field vole numbers caused by variations in the onset of vole reproduction (Erlinge et al. 1983) affected the specialists' numbers (Nilsson 1981; Erlinge 1983; G. Högstedt, unpubl.), and after the rabbit decline increased vole predation by generalists resulted in lower numbers of specialist predators (Erlinge 1983).

In conclusion, the rabbit population sustained a high number of generalist predators which exploited small rodents without suffering from the annual lows in the vole population each spring. This feeding pattern of generalist predators in

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40 quadrats each period, mean numbers per small quadrat, *x*/*SQ*, and 95% confidence intervals are given); for rabbits by night counts (5 counts each period) (Liberg 1981; von Schantz 1981, 1984*a*; the censuses in 1974 and 1975 were not in the same sample plots as from autumn 1975 onward but have been recalculated to be comparable). Bars = calculated produced number of voles and rabbits. Method for calculating vole production given in Erlinge et al. 1983; production estimates of rabbits were based on data on sex ratio, litter size, and numbers of litters computed from captures and autopsies (G. Jansson, unpubl.). Hatching = calculated numbers of voles and rabbits consumed by the predators.

combination with territoriality prevented significant between-year fluctuations in rodent numbers.

The predation pattern on field voles in our study area differs in two important respects from that in northern Sweden where vole populations greatly fluctuate in a cyclic pattern (Hörnfeldt 1978). First, as shown above, in southern Sweden generalist predators sustained by rich alternative food supplies (primarily rabbits) account for the main vole predation, whereas in northern Sweden there is little alternative food for vole predators (Englund 1965). Second, in our area the response of the predators to changing vole numbers primarily was a switching to other prey with only a short time delay; in northern Sweden, the response of the predators is primarily numerical (Hörnfeldt 1978) and, therefore, time delay is greater than in southern Sweden.

SIMULATIONS

Methods

We used a simulation model to study the effect of predation on the population dynamics of small rodents in two systems, i.e., with and without alternative prey. The model is based on the idea that the two prey types live in separate habitats where their dynamics are affected by intrinsic processes and predation. When both prey species are present we assume that the predator distributes its feeding time in these two habitats in proportion to the relative abundance of the two prey species.

Parameter values used in the simulations are representative for the prey species, the field vole and the rabbit, and for the generalist predators in the Revinge area. The values used are given in parentheses below.

The vole population was modeled by a difference-delay equation that was based on the logistic equation:

$$dV/dt = V \cdot r_v \cdot (1 - V_{t-T}/K_v) - F \cdot P. \tag{1}$$

where V is prey biomass per unit area; r_v is intrinsic growth rate of prey (4.0); T is time lag in years (0.4); and K_v is the carrying capacity of the environment (fluctuating on a seasonal basis between 200 and 600); F is predator feeding rate; and P is predator density (individuals per unit area). The delay mimics either a delayed feedback between vegetation and the herbivorous prey species (May 1973) or cyclic genetic changes in the prey population (Krebs et al. 1973). The lag was chosen so as to produce cyclicity in the prey species, in the absence of predators (fig. 2*A*). Two-yr cycles, as produced by the model, have been observed in natural vole populations (Gliwicz 1980; Gaines and Rose 1976). Feeding rate of the predator depends on prey density and reaches its maximum value asymptotically (Holling's [1965] functional response of type II):

$$F = F_{\max} V/(Fr + V) \tag{2}$$

where FR (Fr_v and Fr_a when referring to predation on voles and alternative prey, respectively) is a measure of how fast feeding rate increases with increasing prey

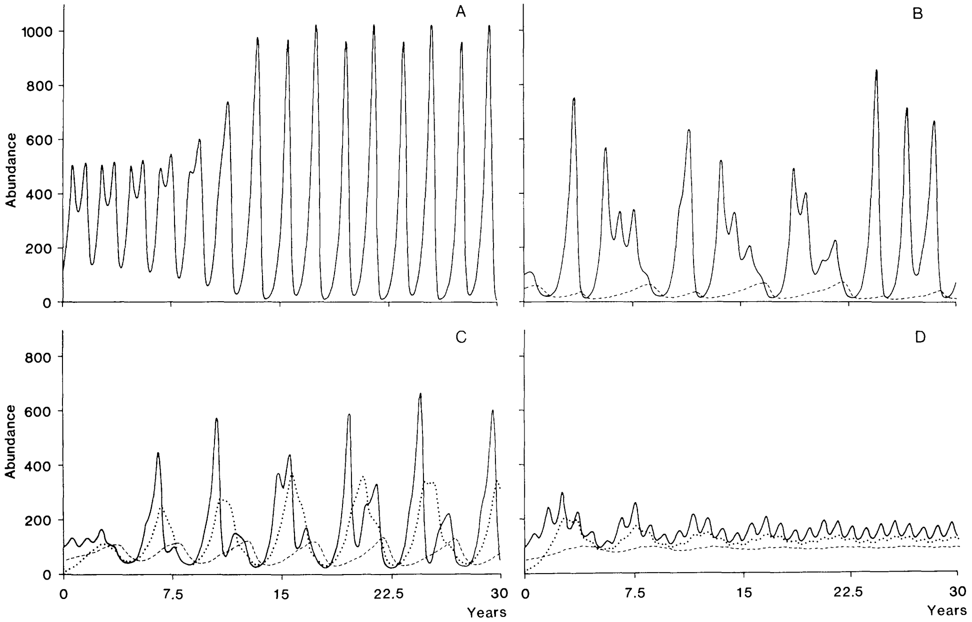

FIG. 2.—Simulations of the model systems. *A*, Vole population (solid line) alone. *B*, Vole population and a territorial predator population (broken line). *C*, Vole population, a nonterritorial predator population and an alternative prey population (dotted line). *D*, The vole population, a territorial predator population and an alternative prey population. Abundance is measured in weight units (voles), weight units × 10 (alternative prey), and in individuals × 100 (predator).

density. We chose the value 50 for Fr_v. This is appropriate as it produces a cyclic two-species system; such a system is the starting point of the analysis.

The alternative prey is modeled with the same equation as for the vole population (1). The following parameter values are used: $r_a = 2.0$, $K_a = 200\text{–}600$, $T = 0.8$, $Fr_a = 150$. Fr_a must be larger than Fr_v because the predators are considered to be more efficient in capturing voles than the alternative prey. The ratio Fr_a to Fr_v influences the dampening effect of the alternative prey and as an example the effect of a ratio 3:1 is shown. A smaller ratio will give less dampening.

The predator population is modeled by the following equation (modified from Tanner 1975):

$$dP/dt = \text{maximum of } -6 \cdot P \text{ and } P \cdot r_p \cdot (2 - F_{\max}/F). \qquad (3)$$

Population decrease takes the value of $-6 \cdot P$ when no food is available; this means that the population cannot die out instantaneously; r_p is the intrinsic growth rate of the predator (0.8); $F_{\max}$ is the predator's maximum food intake (9 kg/yr). As an alternative, we assume that the predator is intrinsically regulated, e.g., by territorial behavior (Watson and Moss 1970; von Schantz 1984*b*). In this case growth rate depends both on feeding rate and current population density. Such a predator population is modeled by the following equation:

$$dP/dt = \text{maximum of } -6 \cdot P \text{ and } P \cdot r_p \cdot [2 - F_{\max} \cdot (P + K_p)/(F \cdot K_p)] \tag{4}$$

where K_p is the limiting density of predators in the sense that the predator population would reach this density when feeding at a maximum rate (400).

Results

Simulation with one predator and one prey species produces a cyclic system (fig. 2*B*), thus agreeing with the pattern observed in northern Sweden. Similar results were obtained whether the predator was territorial (as in the simulation) or nonterritorial. The model was then simulated with two prey species and with a nonterritorial predator (fig. 2*C*). A cyclic system remained. However, with a territorial predator and two prey species, there was a drastic decrease in between-year fluctuations and only seasonal variations remained (fig. 2*D*). Thus, alternative prey has the capacity to dampen the fluctuations in a cyclic prey population provided that the predator is regulated intrinsically. These conditions were present in our study area: Alternative prey (rabbits) were available and the predominant predators showed a high degree of numerical stability due to territorial behavior (in foxes, von Schantz 1981, 1984*a*; in buzzards, Sylvén 1982).

SUMMARY AND CONCLUSION

Small rodent populations in our area in southern Sweden do not cycle as they do in the north, but stay fairly stable between years. The noncyclic pattern can be ascribed to a continuous high predation rate from some generalist predators, viz., common buzzard, red fox, and domestic cat. They subsisted mainly on other prey, rabbits, which were not regulated by predation but fluctuated stochastically (adverse winter weather and myxomatosis). These generalist predators showed numerical stability but changed their diet in response to changing prey densities. The generality of our observations was tested in a simulation model. The results of the simulations were in agreement with field data. We conclude that vertebrate predators can regulate a prey population and promote between-year stability provided that alternative prey are available in excess and that the predator populations are intrinsically regulated.

ACKNOWLEDGMENTS

We thank Lennart Hansson for providing data on vole numbers, Steffi Douwes for drawing the figures, John Byers for correcting the English, Ylva Zachrison for typing the manuscript and an anonymous referee for valuable comments. Grants were obtained from the Swedish Natural Science Research Council and the National Swedish Environment protection board (to Erlinge).

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