EFFECT OF PREY ON PREDATOR: VOLES AND HARRIERS

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ABSTRACT.—Nesting of Harriers (*Circus cyaneus*) in central Wisconsin was strongly linked to vole (*Microtus pennsylvanicus*) abundance during 3 of 4 peak yr within a 16-yr period. Heavy application of DDT on the study area was believed to be the cause of the damped response to one vole high. *Received 5 May 1977, accepted 7 January 1979.*

MOST predator-prey studies have dealt with the effect of the predator on the prey. Galushin (1974) has pointed to the need for more studies to show the effect of prey density on predator populations. This is such a study.

I have studied Harriers (*Circus cyaneus*) for 20 yr on a 16,000-ha area in central Wisconsin. The first summer's (1959) nest survey was incomplete, as I was mainly trying to devise methods for trapping adults. Thereafter, through 1978, virtually every successful nest has been found, directly or by the appearance of fledged young, as explained below. In this time 229 nests were found and 907 Harriers were banded, including 168 breeding adults (essentially all of which were color marked). I deliberately did not make a food habits study, as that would have entailed repeated visits to nests with possible jeopardy to their success.

This paper focuses on four complete 4-yr fluctuations in the vole (*Microtus pennsylvanicus*) cycle, from 1961 through 1976, with supplemental data from partial cycles at each end of the series. For a discussion of vole cycles, see Hamilton (1937).

METHODS

Each summer we trapped breeding Harriers (Hamerstrom 1963) and imped them with colored feathers (Hamerstrom 1942). As a result, it became progressively easier to recognize individual birds, both marked and unmarked, as we did not have to waste time on known breeders whose nests had already been found, and by elimination it grew easier to identify unmarked breeders and territorial non-breeders as well. We recorded the Harriers seen each day. At the end of the season at least two (or more) observers independently prepared maps to show where individual birds, recorded by sex, age, color mark, or other characteristic, had been seen more or less regularly. The maps were then compared and discussed until a concensus was reached. I believe the resulting figures are close enough to permit year to year comparison of the population (see Hamerstrom 1969).

We tried to find all Harrier nests on the study area each year. After 1969 we made it a rule not to walk in to nests until after the eggs had hatched, because Harriers on eggs are sensitive to disturbance. Thus in later years we undoubtedly missed some nests that failed in early stages. Bias caused by this policy was essentially uniform from 1970 through 1978. Of 229 nests, 34 (15%) were discovered after the young had fledged. It is unlikely that we missed any fledged nests as free-flying young were highly visible and showed strong attachment to the nest area for some weeks. Furthermore, their parents often defended the area so vigorously against intruders that we frequently were able to catch one or both adults. It is therefore fair to tally such family groups as successful nests even though the nest proper was not seen.

Vole abundance was measured in two ways. From 1960 through 1963 I used D. Q. Thompson's (pers. comm.) regional index based on percentage of stems cut by voles on sample plots in Wisconsin, northern Illinois, and southeastern Minnesota. Not satisfied that a regional index would reflect local abundance, I ran another, simpler index from 1964 through 1978 based on the number of voles caught per 100 trap-nights during the Harrier breeding season on the study area itself. I used a minimum of 1,200 trap-nights (break-back traps baited with peanut butter) per year. The actual values obtained by these two methods

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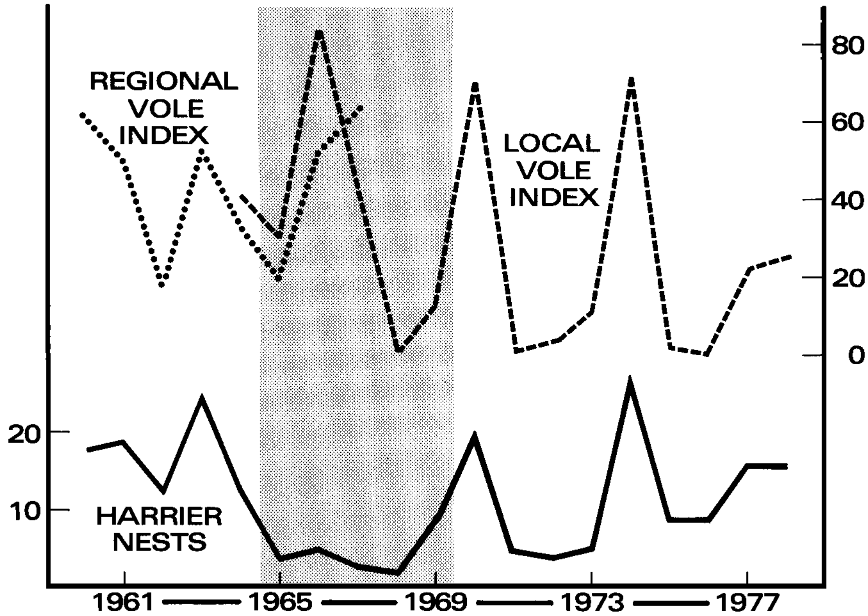

Fig. 1. Relationship between vole abundance and Harrier nesting. The dotted line is the regional index of vole abundance as shown by percentages of stems cut; the dashed line is the local index of vole abundance as shown by the number of voles caught per 100 trap-nights times 1,000; the solid line is the number of Harrier nests, and the stippled area is the "DDT years." Spraying of DDT, mostly from airplanes, dramatically increased on the study area in late summer 1964; its use in Wisconsin was banned in 1970.

are not directly comparable. What can be compared, however, are the shapes of the two curves—the timing of the highs and lows and to some degree the amplitude of the fluctuations. There was a 4-yr period of overlap, during which both curves show a decline in vole numbers from 1964 to 1965, followed by a steep rise to 1966 (Fig. 1); the regional index continues to rise for 1 more yr. D. Follen Sr. (pers. comm.) confirms the 1963 vole high followed by a sharp drop in 1964 at Arpin, 39 km northwest of my study area: in 1963 he rolled 25 hay bales and uncovered 12 *Microtus,* while 375 bales in 1964 yielded only 7. A local high is thus clearly shown. The years 1960–1962 are less firmly established, but the agreement among the three indices—cut stems, bales rolled, and trapping—during the period of overlap seems close enough to warrant acceptance of the regional index as approximately representative of the study area. Local indices are obviously better than regional indices for a study of this sort.

Results and Discussion

The most striking single fact to emerge from this study is that the number of Harrier nests normally increased dramatically when vole numbers were high, and only then (Fig. 1, Table 1). The average number of potential breeders was nearly the same in each of the four cyclic periods (42, 35, 35, 35, respectively). Their yearly numbers, however, fluctuated with vole numbers, although less strongly than the number of nests, from an average of 35 for the lows to 48 for the highs. It appears that a smaller proportion nested during lows than at highs.

Nesting success, as measured by the percentage of nests that hatched at least one young, averaged 74.4% for the 16 yr and varied from 62.1% at vole lows to 83.1% at highs. The number of young per successful nest varied least of all, averaging 3.1 at both highs and lows and 3.2 overall.

TABLE 1. A comparison of some aspects of Harrier productivity, arranged by four periods in the vole cycle. Vole highs (1963, 1966, 1970, 1974) and lows (1962, 1968, 1971, 1976) are shown in Fig. 1. Years of heavy aerial application of DDT are shown in boldface type.

	1961–1964	**1965–1968**	1969–1972	1973–1976	16 yr
Number of potential breeders	(167)	(141)	(139)	(139)	(586)[a]
Average	41.8	35.3	34.8	34.8	36.6
At vole high	53	32	55	53	48.2
At vole low	37	30	35	36	34.5
Number of nests	(70)	(14)	(38)	(50)	(172)
Average	17.5	3.5	9.5	12.5	10.7
At vole high	25	5	20	27	19.2
At vole low	13	2	5	9	7.2
Percent nests successful	(45)	(13)	(28)	(42)	(128)
Average	64.3	92.9	73.7	84.0	74.4
At vole high	80.0	100.0	70.0	92.6	83.1
At vole low	53.8	100.0	80.0	55.6	62.1
Young per successful nest	(144)	(35)	(83)	(143)	(405)
Average	3.2	2.7	3.0	3.4	3.2
At vole high	3.0	2.4	2.8	3.6	3.1
At vole low	3.1	2.5	3.0	3.2	3.1

[a] Numbers in parentheses show sample size.

The period 1965–1968 was aberrant. I believe the cause of the strongly damped response to the vole high of 1966 to be heavy application of DDT on the study area. As DDT was applied late in the season after most Harriers had hatched, 1964 is not included in the "DDT years" (Table 1), although heavy aerial application began that summer. Use of DDT in Wisconsin was banned in 1970, so 1969 is the last of the DDT years.

That Harrier nesting began to increase in 1969, a year before the ban on DDT, is not the contradiction that it seems. The use of DDT in Wisconsin had decreased by about 90% before the ban was ordered, as reported for the nearby Lake Michigan region of Wisconsin by Chesters and Simsiman (1973) and statewide by Libby and Koval (1970). There are no specific data for my study area, but G. Chesters (pers. comm.) has pointed out that the reasons for the general reduction in the use of DDT apply: it was found that insects were building up immunity to DDT and, furthermore, residues in some crops made them unsaleable.

The rapid resynchronization of Harrier nesting with vole abundance in the late 1960's was unexpected, and was apparently due to immigration. Successful breeders tend to come back to the study area (Hamerstrom 1969), but of 97 breeding birds marked before 1969, only one returned to breed in 1969, and thereafter none was seen there again. During the worst nesting years (1965–1968) the number of potential breeders was reduced but did not drop enough to suggest such a loss (Table 1). There had been a 70% decrease in the number of migrants through the area from 1960 through 1965 (Hamerstrom 1969), suggesting a widespread population decline. Despite these evidences of both local and general decline, the high quality of the habitat appears to have attracted enough birds from the floating population to effect a rapid replenishment. Other signs of population recovery were the return of sky dancing behavior and the replacement of talon-to-talon aerial food transfers by normal transfers, both of which changes occurred in the early 1970's (see Hamerstrom 1969 for a description of the abnormal behaviors of the 1960's).

Whether DDT or something else caused the poor response in the period 1965–

1968 is not germane to the main point of this paper. A general pattern is clear. In all 7 yr when the vole index was low (less than 15), Harrier productivity was also low (fewer than 10 nests). In 4 of the 5 yr when the vole index was high (45 or higher), Harrier nests were at their maximum (18 or more). Intermediate indices show intermediate numbers of nests. The only exceptions were all in the period 1965–1968, when the highest vole index of all, in 1966, had no corresponding peak in nests. The increase from 4 to 5 nests in 1966 might indeed have been in response to the vole high, but so few nests are hardly conclusive, and the increase was far short of the normal. That Harrier nesting so closely followed the unusual pattern in the still incomplete local vole cycle in 1977 and 1978 (Fig. 1) reinforces my conclusion that the two population phenomena are interlocked.

Thus, quite apart from any influence that DDT may have had and whatever the reason for the discrepancies in one period, the point of this paper is that Harrier nesting normally was inextricably linked with vole abundance.

Why this relationship should be so strong is not clear. Galushin (1974) has pointed out that raptors that depend on a small number of prey species do indeed fluctuate in synchrony with their prey, in contrast to those predators whose populations lag behind changes in the prey base. But Harriers are not limited to voles for food and have a widely varied diet (Errington and Breckenridge 1936, Clark and Ward 1974). The mechanism may be related to size as well as availability of prey, and in particular, the frequency of presentation of prey between birds may be important. When voles are abundant, males present females with small tidbits often. When voles are scarce, Harriers in central Wisconsin turn to larger quarry (e.g. birds), and the female is less often stimulated. The sexual urge and food presentation seem interrelated in *Circus cyaneus* (Balfour 1963). Sheer biomass of prey presented by the male seems not to be a likely factor, as females hunt successfully themselves before nesting begins. Whatever the connection, it is impossible to understand Harrier biology or to monitor this species effectively without taking the vole cycle into consideration.

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