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# Rapid or delayed tracking of multi-annual vole cycles by avian predators?

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## Summary

1. The relationship between the yearly densities of avian predators and their microtine prey in western Finland was studied. Predator densities were determined by checking nest-boxes in forests [Tengmalm's owl (*Aegolius funereus*), hawk owl (*Surnia ulula*) and Ural owl (*Strix uralensis*)] and by searching for nests in farmland [short-eared owl (*Asio flammeus*), long-eared owl (*Asio otus*) and kestrel (*Falco tinnunculus*)]. Tengmalm's, Ural and hawk owls overwinter in Fennoscandia, long-eared owls are partially migratory, and short-eared owls and kestrels are migratory.

2. Prey densities were estimated by snap-trapping in spring (early May) and autumn (mid-September), and by snow-tracking in late February to early March (early spring) and late November to early December (late autumn).

3. The breeding densities of Tengmalm's owls in two study areas were significantly correlated with trap indices of voles in the prevailing spring and in the preceding autumn (6-month lag), but not in the preceding spring (1-year lag). Tengmalm's owl breeding densities in one study area covaried with track indices of voles in the early spring (i.e. the settling period of owls), but not with those in the late autumn.

4. The yearly breeding densities of Ural owls and hawk owls, and the wintering densities of hawk owls were positively related to spring trap indices of voles, but not to indices in the previous autumn and spring.

5. The breeding densities of long-eared owls and short-eared owls were dependent on vole abundances both in the current spring and the preceding autumn, but not in the preceding spring. Kestrel breeding densities fluctuated in accordance with spring vole abundances.

6. The densities of most avian predators tracked rapidly, without obvious time lags, vole abundances at the time the birds of prey settled on their territories. This rapid tracking is mostly based on vole-supply dependent immigration and emigration. Densities of most avian predators did not lag 9 months behind prey densities which, in theory, may drive 3–4-year vole cycles (May 1981).

*Key-words:* owl, raptor, 3–4-year vole cycle, density dependence, time lag.

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## Introduction

It is well-known that multi-annual population fluctuations (usually 3–4-year cycles) of small mammals (voles, mice and shrews) occur at high latitudes in the northern hemisphere (e.g. Kalela 1962; Krebs & Myers 1974; Finerty 1980; Hansson & Henttonen 1985; Henttonen *et al.* 1989). Whether or not predators drive small mammal cycles has been a controversial question for a long time. Some researchers contend that predators kill only surplus individuals doomed to die and do not depress vole densities (e.g.

Errington 1946, 1963; Halle 1988), whereas others argue that predators dampen (Korpimäki 1985b; Korpimäki & Norrdahl 1989a,b, 1991a) or even regulate population fluctuations of small mammals (e.g. Erlinge *et al.* 1983, 1984, 1988; but see Kidd & Lewis 1987).

Andersson & Erlinge (1977) divided vole-eating avian predators into two categories according to their potential impact on population cycles of small mammals: resident generalists and nomadic specialists. However, their division did not consider migratory species that occur at northern latitudes during snow-free periods and overwinter in the south. Accordingly,

I reformulated the above-mentioned division. (i) Non-migratory species use energetically inexpensive sit-and-wait hunting technique (Sonerud 1986), can locate voles below the snow cover and may thus be able to overwinter in snowy regions. Resident generalists (1.1) stay on their territories and shift to alternative prey when voles crash, whereas nomadic specialists (1.2) leave when voles decrease to search for a better vole area in which to overwinter and breed. (2) Migratory species use expensive quartering hunting technique (Sonerud 1986), cannot hunt voles below the snow and may thus overwinter in the south. Migratory generalists (2.1) return to breed on the same territory year after year and use alternative prey if voles are scarce. Migratory specialists (2.2) show long-distance breeding dispersal to find a breeding site with high numbers of voles. Classifying avian predators into these categories is not clearcut, as there is little dispersal data from marked individuals, and intermediate strategies exist. For example, in Fennoscandia, juvenile and female Tengmalm's owls [*Aegolius funereus* L.] disperse when voles crash, but most old males stay on their territories throughout the year (e.g. Korpimäki 1981, 1987b; Löfgren, Hörnfeldt & Carlsson 1986; Korpimäki, Lagerström & Saurola 1987).

Numerical responses of predators to changing vole densities may occur either rapidly without obvious time lags (Korpimäki 1985b; Korpimäki & Norrdahl 1989b, 1991b), or with a long delay (Ryszkowski, Goszczynski & Truszkowski 1973; Goszczynski 1977; Erlinge *et al.* 1983, 1984; Korpimäki, Norrdahl & Rinta-Jaskari 1991). In theory, time lags tend to destabilize predator-prey systems (e.g. Murdoch & Oaten 1975). May's (1981) theoretical findings indicated that in seasonal environments 3–4-year vole cycles might be driven by a density-dependent mechanism affecting the growth rate of microtine populations with a 9-month delay. Hörnfeldt (1991) suggested that one mechanism producing this critical lag could be avian predation. His suggestion was based on the finding that breeding densities of Tengmalm's owls correlated significantly with the vole index of the previous autumn but not with that of the prevailing spring (Hörnfeldt *et al.* 1990). On the other hand, Korpimäki (1984, 1985b) and Korpimäki & Norrdahl (1989b, 1991b) showed that breeding densities of Tengmalm's owls, short-eared owls (*Asio flammeus* Pontoppidan), long-eared owls (*Asio otus* L.) and kestrels (*Falco tinnunculus* L.) were significantly positively related to the vole densities in the prevailing spring, but they did not present correlations with the vole densities in the preceding autumn.

In this paper, I present long-term data on the breeding densities of avian predators in relation to vole abundances in western Finland. The species are the Ural owl (*Strix uralensis* Pallas) (category 1.1 in the above classification), the hawk owl (*Surnia ulula* L.) (1.2), Tengmalm's owl (intermediate species between

1.1 and 1.2), the short-eared owl (2.2), the long-eared owl (2.2) and the kestrel (2.2). Because Galushin (1974) suggested that numerical responses of wintering raptors could be more rapid than those of breeding raptors, I also present data on the winter densities of hawk owls. The main questions are: (i) Are there time lags between density changes of voles and avian predators? If so, (ii) what is the length of the lag? (iii) Are there interspecific differences in the speed of numerical responses depending on the migratory or dispersal habits? (iv) Do densities of wintering birds of prey track vole densities with a shorter delay than do those of breeding birds of prey?

## Material and methods

Data on breeding densities of Tengmalm's owls were gathered by checking 99–530 nest-boxes annually during 1973–91 in the Kauhava region (62°55'–63°17'N, 22°55'–23°35'E), western Finland. The study area was gradually extended with the increasing number of nest-sites so that nest-box density remained stable (0.5–1 per km<sup>2</sup>; see Korpimäki 1981, 1987b; Korpimäki & Hakkarainen 1991 for further details). A nesting attempt was defined as laying at least one egg and the index of owl breeding density was the number of nests per 100 boxes. Additional data on the breeding densities of Tengmalm's owls were collected in the Seinäjoki region (62°30'–62°55'N, 22°45'–23°25'E) during 1978–90, where 120 to 280 nest-boxes were checked annually (see Korpimäki 1985a; Korpimäki & Norrdahl 1991c). The minimum distance between these two study areas is 20 km.

Breeding densities of Ural owls were estimated by checking 60–110 nest-boxes that were large enough for this species (see Saurola 1989a) during 1977–90 in the Kauhava and Seinäjoki regions (see Korpimäki & Sulkava 1987 for further details). The density index used for Ural owls was the number of nests per 100 boxes.

Winter territories of hawk owls are close to open areas (personal observation). Hawk owls are easy to observe when they perch on tree tops, etc., as South Ostrobothnia is flat, more than a half of the area is open farmland or marshland and there is a dense network of minor roads. Winter territories were censused during 1976–77 to 1989–90 from November to February by members of the Suomenselkä Ornithological Society in the same areas where Tengmalm's and Ural owls were studied (Korpimäki 1985a, 1990; Korpimäki & Norrdahl 1991c). The total number of territories was used as an estimate of winter density. Although these road counts may include some error (see Fuller 1981), they probably give reliable estimates for among-year comparisons. Nests of hawk owls were searched for in the Kauhava and Seinäjoki regions during 1977–90. A majority of hawk owl nests were found in nest-boxes erected for Tengmalm's and Ural owls, but some pairs also used kestrel boxes and

old stick nests (Korpimäki 1985a, 1990). Accordingly, the total number of nests found in the Kauhava and Seinäjoki regions were taken as an estimate of hawk owl breeding density.

Breeding densities of short-eared owls, long-eared owls and kestrels were taken from Korpimäki & Norrdahl (1991b), who presented the yearly numbers of nests per 47 km<sup>2</sup> of farmland at Alajoki, in the Kauhava region (63°05'N, 22°55'E) during 1977–87. Later, breeding densities of long-eared owls were estimated up to 1988 and those of kestrels up to 1990 by the same methods (E. Korpimäki unpublished).

In the Kauhava region, spring and autumn densities of voles were estimated annually by snow-tracking and snap-trapping. Snow-tracks were censused in late November to early December 1983–90 soon after the first snowfall (late autumn track censuses), and in late February and early March 1984–91 before snowmelt (early spring track censuses). Lines were skied after a snowfall so that the tracks of only one, or two nights were visible. The total number of track-lines was nine in autumn 1983, 13 in spring 1984, and 34–43 from autumn 1984 onwards [apart from spring 1986 (28) and spring 1991 (18)]. The same lines were tried to check both in spring and the preceding autumn, but varying weather conditions made it impossible to count all the lines each season and year. Track censuses were made during 3–5 days in each season and year [apart from autumn 1990 (2), spring 1990 (2) and spring 1991 (2)]. The minimum distance between track-lines was 50–60 m and the mean ( $\pm$ SD) length of track-lines was 1075  $\pm$  64 m (range from 300 to 2300 m) in autumns 1983–90 and 1057  $\pm$  259 m (200–2300 m) in springs 1984–91 (see Korpimäki, Norrdahl & Rinta-Jaskari 1991; Table 1 for further details). Because the identification of vole species was usually impossible, only two density indices were derived from the data. 'Autumn track index of voles' is the number of small mammals crossing the track lines per km per day in late November and early December, and 'spring track index of voles' is the corresponding number in late February and early March. These indices describe the pooled density of two *Microtus* voles [the field vole (*Microtus agrestis* L.) and the common vole (*Microtus epiroticus* Ondrias)] and the bank vole (*Clethrionomys glareolus* Schreber) (Korpimäki *et al.* 1991).

Snap-trappings were made in early May and in mid-September in four sample plots in the central and western parts of the Kauhava study area. Sample plots were in each of the main habitat types (a cultivated field, an abandoned field, a spruce forest and a pine forest) in both parts of the area. Trap nights totalled 32 448 in the central part during 1973–91 and 25 564 in the western part during 1977–91 (see Korpimäki & Norrdahl 1989b for further details). I pooled the results from four-night trapping periods and standardized them to the number of animals caught per 100 trap nights. The density index derived from the trapping results in the central part of the study area

was used for 1973–76. The index used for 1977–91 was the mean for two parts of the study area.

In the Seinäjoki region, spring and autumn densities of voles were estimated annually from spring 1978 onwards by the same trapping methods as in the Kauhava region. In two parts of the study area (Seinäjoki and Nurmo), two sample plots (farmland and woodland) were snap-trapped in each season, year and area. These trappings totalled 6627 trap nights in Seinäjoki and 5764 trap nights in Nurmo during 1978–90 (see Norrdahl 1985; Korpimäki & Norrdahl 1991c for further details). The density index derived from these trappings was the number of animals caught per 100 trap nights.

I used the following density indices of voles when analysing the synchrony between population fluctuations of microtines and Tengmalm's, Ural and hawk owls. Spring trap index of voles was the pooled number of two *Microtus* voles and the bank vole caught per 100 trap nights in May. Autumn trap index of voles was the corresponding number in preceding September. The density indices of the three voles were pooled, because they are the staple food of the three owls. Field voles average 9% of prey number in the diet of breeding Tengmalm's owls (Korpimäki 1981, 1988a), 28% in that of Ural owls (Korpimäki & Sulka 1987) and 39% in that of hawk owls (Korpimäki 1972; unpublished). The corresponding figures for common voles are 18, 3 and 32%, and for bank voles 24, 11 and 10%.

When analysing the accordance between population fluctuations of voles and short-eared owls, long-eared owls and kestrels, I used the spring and autumn densities (ind. km<sup>-2</sup>) of *Microtus* voles in farmland from Korpimäki & Norrdahl (1991a: Fig. 1, upper panel) for 1977–87. The same densities were estimated by similar methods during 1988–90. The densities of short-eared owls, long-eared owls and kestrels were related to the density indices of *Microtus* voles, as they are the staple prey of these raptors (Korpimäki 1985b, 1987a; Korpimäki & Norrdahl 1991b).

Statistical analyses were made by SYSTAT statistical package (Wilkinson 1988). I computed correlations between predator densities and vole abundances in the prevailing spring (no obvious time lag), in the preceding autumn (6–7-month lag) and in the preceding spring (c. 1-year lag) (Table 1). As estimated by the Pearson correlation, vole abundances in the prevailing spring and the preceding autumn were not intercorrelated, but the opposite appeared to be true by using Spearman rank correlation (Table 2). All statistical tests are two-tailed.

## Results

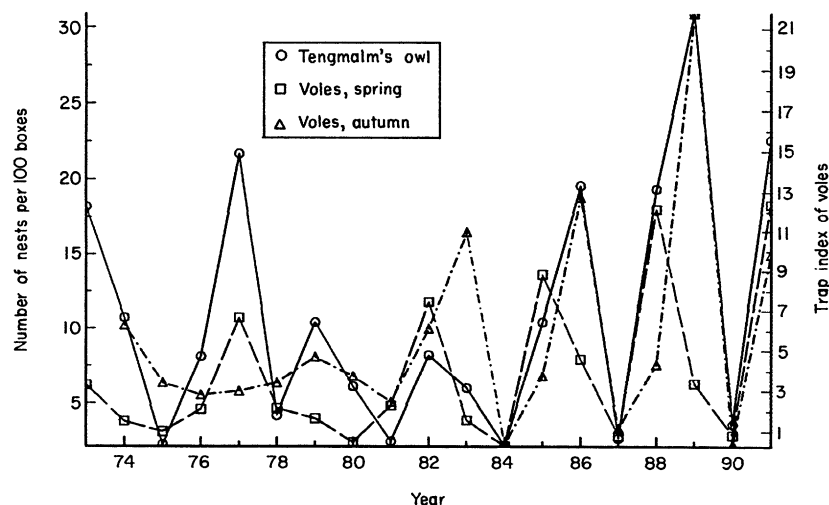
In the Kauhava region, breeding densities of Tengmalm's owls were significantly correlated with trap indices of voles in the prevailing spring and the preceding autumn, but not in the preceding spring (Fig.

**Table 1.** (a) Spearman ( $r_s$ ) and Pearson ( $r$ ) correlations between the breeding densities of Tengmalm's owls, Ural owls and hawk owls ( $n$ ), and density indices of voles (pooled number of *Microtus* and bank voles per 100 trap nights) in the prevailing spring, the preceding autumn and the preceding spring. For hawk owls, the correlation between the number of wintering territories ( $T$ ) and density indices of voles is also presented. (b) Correlations between the breeding densities of kestrels, short-eared owls and long-eared owls, and density indices (individuals per km<sup>2</sup>) of *Microtus* voles

Bird of prey species and region (study period)	Density index of voles						Data sources
	Prevailing spring		Preceding autumn		Preceding spring		
	$r_s$	$r$	$r_s$	$r$	$r_s$	$r$	
(a)							
Tengmalm's owl							
Kauhava region (1973–91)	0.73**	0.58**	0.72**	0.73***	0.12 NS	0.38 NS	1
	$n$	19		18		18	
Seinäjoki region (1978–90)	0.74**	0.71**	0.43 NS	0.69*	0.40 NS	0.31 NS	2
	$n$	13		12		12	
Ural owl							
South Ostrobothnia (1977–90)	0.34 NS	0.60*	0.38 NS	0.46 NS	0.22 NS	0.41 NS	3
	$n$	14		14		14	
Hawk owl							
South Ostrobothnia, (1977–90)	$N$ 0.73**		0.40 NS		–0.03 NS		2
	$n$	14		14		14	
	$T$ 0.82**	0.70**	0.69*	0.37 NS	0.06 NS	0.06 NS	2
	$n$	14		14		14	
(b)							
Long-eared owl							
Alajoki (47 km <sup>2</sup> ) (1977–88)	0.76**	0.60*	0.62*	0.64*	0.42 NS	0.52 NS	4
	$n$	12		11		11	
Short-eared owl							
Alajoki (47 km <sup>2</sup> ) (1977–87)	0.88**	0.88***	0.79**	0.78**	0.16 NS	0.39 NS	4
	$n$	11		10		10	
Kestrel							
Alajoki (47 km <sup>2</sup> ) (1977–90)	0.80**	0.86***	0.44 NS	0.30 NS	0.44 NS	0.25 NS	4
	$n$	14		13		13	

Significance levels (two-tailed): \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ .

Data sources: (1) Korpimäki (1985b: Fig. 1) and unpublished data; (2) present study; (3) Korpimäki & Sulkava (1987) and unpublished data; and (4) Korpimäki & Norrdahl (1991b: Table 2) and unpublished data.



**Fig. 1.** The variation in the yearly breeding densities of Tengmalm's owls (the number of nests per 100 nest-boxes) and in the trap indices of voles in the prevailing spring and the preceding autumn during 1973–91 in the Kauhava region.

**Table 2.** Spearman ( $r_s$ ) and Pearson ( $r$ ) correlations between the density indices of voles in the prevailing spring and the preceding autumn. Region, study period and significance levels as in Table 1

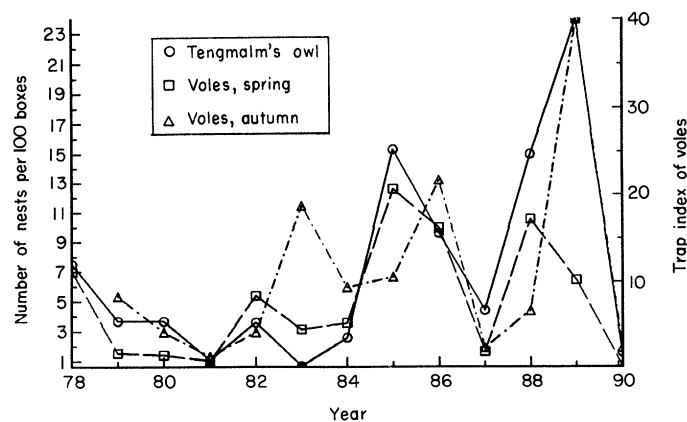
Region (study period)	$r_s$	$r$
Kauhava region (1973–91)	0.48*	0.20 NS
Seinäjäki region (1978–90)	0.64*	0.37 NS
South Ostrobothnia (1977–90)	0.66*	0.24 NS
Alajoki (47 km <sup>2</sup> ) (1977–90)	0.53 NS	0.02 NS

1, Table 1). The Pearson correlation coefficient for the autumn trap indices of voles was not significantly higher than that for the spring trap indices of voles [test of homogeneity among two correlation coefficients (Sokal & Rohlf 1981);  $t = 0.80$ ,  $n_1 = 18$ ,  $n_2 = 19$ , NS], and the Spearman rank correlation coefficients ( $r_s$ ) were equal. Yearly median laying dates ranged between 14 March and 27 April during 1973–89; most females started laying in late March or early April (Korpimäki 1987c; Korpimäki & Hakkarainen 1991). Accordingly, spring trap indices of voles reflected the food abundance in the nestling period of owls (i.e. at least 1.5–2 months later than female owls settle on their territories) and autumn trap indices of voles *c.* 6 months before the mating and egg-laying periods (i.e. at the time when juvenile and female owls search for wintering areas).

Yearly breeding densities of Tengmalm's owls in the Seinäjoki region significantly covaried with the vole abundances in the current spring (Fig. 2, Table 1). The Pearson correlation coefficient for the spring trap indices of voles was not significantly larger than for the autumn trap indices ( $t = 0.10$ ,  $n_1 = 13$ ,  $n_2 = 12$ , NS). One can argue that vole abundance in autumn partially determines breeding density by

affecting the number of owls that disperse from or to the study area (e.g. Hörnfeldt *et al.* 1990). I tested this by computing linear regressions between breeding densities of Tengmalm's owls ( $y$ ) and trap indices of voles in the current spring ( $x$ ), and by computing residuals as the observed value of the dependent variable minus the fitted value. There was no significant correlation between the residuals and trap indices of voles in the previous autumn ( $r_s = 0.44$ , NS for the Kauhava region and  $r_s = -0.18$ , NS for the Seinäjoki region). In every case where spring vole densities were actually higher than those of the preceding autumn, owl breeding densities showed major increases over the previous spring (Figs 1–2). This happened despite relatively low autumn vole densities. This seems like good evidence that the owls track increases that occur even during winter. On the other hand, the owls tended to 'overshoot' (i.e. breed at high densities after voles have peaked) in 1986 and 1989 (Fig. 1) and in 1989 (Fig. 2), but not during other vole peaks.

Early spring snow-track censuses of voles were made during the main settling period of female Tengmalm's owls (i.e. in late February and early March). I suggest that it is the vole abundance during the settling period of owls which determines their breeding density in the following spring. This suggestion is supported by the fact that breeding densities were significantly correlated with the early spring track indices of voles (Fig. 3;  $r_s = 0.90$ ,  $n = 8$ ,  $P < 0.01$ ), but not with the late autumn track indices of voles ( $r_s = 0.64$ ,  $n = 8$ , NS). [Because vole track indices are not normally distributed (Fig. 3), the use of rank correlation is appropriate.] Track and trap indices of voles are intercorrelated in autumn ( $r_s = 0.76$ ,  $n = 8$ ,  $P < 0.05$ ), but not in spring ( $r_s = 0.62$ ,  $n = 8$ , NS). Weak correlation in spring is probably due to that vole densities often crash rapidly from early March to early May (K. Norrdahl & E. Korpimäki, unpublished), because snow melts leaving voles without protective cover before vegetation grows up in late May onwards.



**Fig. 2.** The same as in Fig. 1, but for the Seinäjoki region during 1978–90.

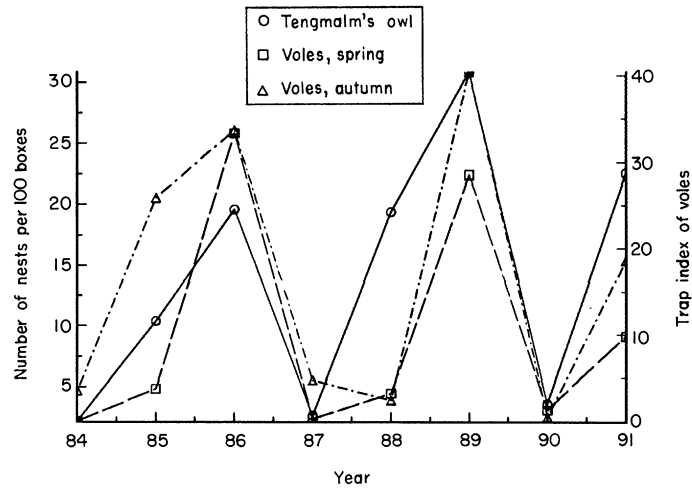


Fig. 3. The same as in Fig. 1, but for the breeding densities of Tengmalm's owls, and the early spring and late autumn track indices of voles in the Kauhava region during 1984–91.

Ural owls occupy their territories throughout the year (Saurola 1987, 1989a), but the proportion of breeding pairs varies from 10–20% to 80–90% among years (Pietiäinen 1989). In South Ostrobothnia, breeding densities of Ural owls covaried with the trap indices of voles in the prevailing spring (Table 1, Fig. 4), but not with those in the preceding autumn and spring. However, using rank correlation removes the statistical significance of this relationship (Table 1). Non-significant correlations were also obtained by Korpimäki & Sulkava (1987) for spring trap indices of voles during 1975–85 in the Kauhava region. One reason for the weak relationship may be the apparent increase of Ural owls in South Ostrobothnia in 1980s (Fig. 4). However, Saurola (1989a,b) also found no correlation between breeding densities and vole abundances in a South Finnish Ural owl population that showed no long-term changes.

Hawk owls are highly nomadic in Fennoscandia

(Mikkola 1972; Huhtala, Korpimäki & Pulliainen 1987), although juveniles and adult females move more than adult males (Byrkjedal & Langhelle 1986). They usually settle in South Ostrobothnia in late October or November and leave in early March, if they do not stay to breed (Korpimäki 1972, 1985a; Korpimäki & Norrdahl 1991c). Hawk owls are infrequent breeders, being found nesting in only 5 of 14 years (Fig. 5), but in these springs voles were abundant (Table 1). Breeding density did not correlate with the vole trap index in the preceding autumn and spring. [Because the density index of hawk owls is not normally distributed (Fig. 5), the use of rank correlation is appropriate.]

The number of wintering territories of hawk owls was larger during springs and autumns of vole abundance than during those of vole scarcity (Fig. 5 and Table 1). Also, the regression residuals of wintering densities on trap indices of voles in the next spring

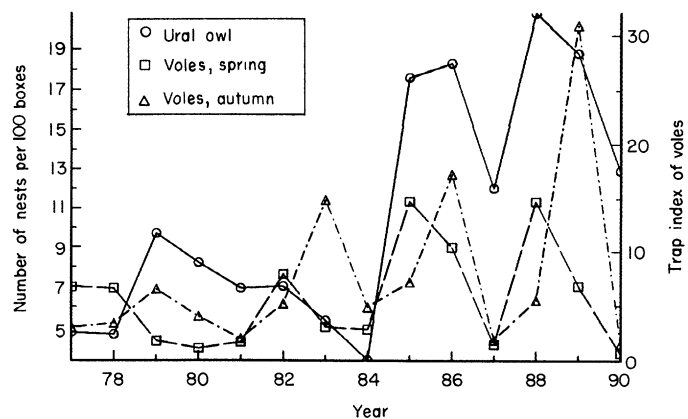


Fig. 4. The same as in Fig. 1, but for the Ural owl and trap index of voles in South Ostrobothnia (pooled data from the Kauhava and Seinäjoki regions) during 1977–90.

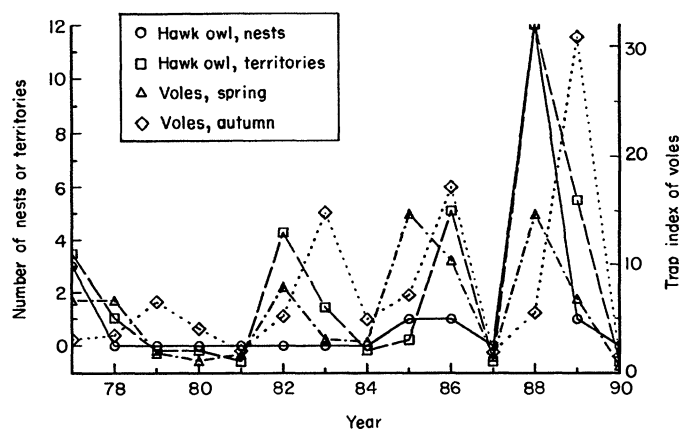


Fig. 5. The variation in the number of nests and wintering territories of hawk owls and in the current spring and previous autumn trap indices of voles in South Ostrobothnia during 1977-90.

were not correlated with vole indices in the preceding autumn ( $r_s = 0.34$ ). The number of wintering hawk owls was positively related to the number of nests in the same year ( $r_s = 0.70$ ,  $n = 14$ ,  $P < 0.05$ ).

Long-eared owls are partially migratory in Fennoscandia staying north during winters of vole abundance, but migrating in years of vole scarcity (Sulkava 1965; Nilsson 1981; Saurola 1983; Korpimäki & Norrdahl 1991b). The breeding densities of long-eared owls were correlated with vole densities both in the prevailing spring and the previous autumn, but not in the previous spring (Table 1). There was no difference in the Pearson correlation coefficients for the spring and autumn vole densities ( $t = 0.11$ , NS). The regression residuals of owl breeding densities on vole densities in the prevailing spring were correlated with vole densities in the preceding autumn ( $r_s = 0.64$ ,  $P < 0.05$ ). Rank correlations revealed nearly similar relationships; however, correlations for the vole abundances in the current spring were stronger than for the abundances in the previous autumn.

Short-eared owls are usually migratory in Fennoscandia (Mikkola & Sulkava 1969; Korpimäki 1984; Village 1987), but some individuals may overwinter in western Finland in years of vole abundance (E. Korpimäki, unpublished). They returned to Alajoki from late March to late April (E. Korpimäki unpublished). Yearly breeding densities of short-eared owls were significantly positively related to the vole densities both in the current spring and the previous autumn, but not in the previous spring (Table 1). The Pearson correlation coefficient with current spring vole density was not significantly larger than that for the previous autumn density ( $t = 0.74$ , NS). The regression residuals of short-eared owl breeding densities on current spring vole densities did not covary with the previous autumn vole densities ( $r_s = 0.36$ , NS).

Kestrels are migratory in Fennoscandia (Kor-

pimäki 1987a, 1988b; Village 1990), but a few individuals overwinter in the north during winters of vole abundance (Mikkola 1968; E. Korpimäki, unpublished). Kestrels arrived at Alajoki from late March to early May (Palokangas *et al.* 1992). The highest correlation between breeding density of kestrels and vole numbers occurred during current spring (Table 1). The Pearson correlation coefficient for the prevailing spring vole density was significantly larger than that for the previous autumn density ( $t = 2.27$ ,  $P < 0.025$ ). The regression residuals of kestrel breeding densities on the current spring vole densities were not correlated with the preceding autumn vole densities ( $r_s = 0.27$ , NS). The results did not change by using rank correlation.

## Discussion

I found that the breeding densities of most avian predators were more closely related to the prey densities in the current spring than to the prey densities in the previous autumn (6-7-month lag). In addition, there was no indication of 1-year lag between prey and predator density fluctuations. Changes in the breeding density of a migratory species that starts to lay in late April to late May (the kestrel) covaried with the fluctuations in the spring vole abundances. The breeding densities of Ural owls and hawk owls that overwinter in Fennoscandian snowy areas were also related to vole numbers in the prevailing spring, and vole numbers in the previous autumn did not have obvious effects on their breeding densities. In migrating short-eared owls, in partially migrating long-eared owls and in Tengmalm's owls overwintering in Fennoscandian snowy areas, breeding densities were associated with the vole abundances both in the current spring and the previous autumn. In Tengmalm's owls, however, this was probably due to the too late estimation of vole densities, because snap-trappings



were made at least 1.5–2 months later than owl females settled on territories. This interpretation is supported by the fact that Tengmalm's owl breeding densities were significantly positively related to the vole numbers during the settling period (as estimated by the snow-track censuses), but no obvious relationship was found to the vole numbers 3 months earlier.

I conclude that the breeding densities of most avian predators tracked rapidly, without time lags or with short delays, vole abundances at the time the birds of prey settled on the territories (see also Korpimäki 1985b). The regression residual analyses showed that there were no obvious indications of 9-month lags between population fluctuations of voles and breeding birds of prey (apart from the long-eared owl). At most, the length of lags was 1–2 months, which may be too short to affect the growth rate of microtine populations with the 9-month lag and to drive 3–4-year vole cycles as suggested by May (1981). Hörnfeldt (1991) surmised that time lags also exist between population fluctuations of voles, hawk owls and other avian predators. This suggestion was partly based on my short-term data from birds of prey in the present study area (Korpimäki 1984, 1985b), but my long-term data show that this may be true for long-eared owls only.

Wintering densities of hawk owls did not track prey densities with a shorter delay than did breeding densities, which disagrees with the suggestion of Galushin (1974). I suggest that this is because nomadic species distribute themselves in relation to vole abundances two times per year: first, they search for good vole areas to settle in during autumn or early winter, and secondly, they stay to breed on the same site or search for a new breeding site in late winter or early spring. Accordingly, decisions to move both before winter and before breeding are dependent on the prevailing local food supply. In addition, nomadic raptors may move throughout the year, as it is likely that there are some individuals that fail to find good vole areas quickly. Supporting evidence for this suggestion comes from the presence of vagrant birds of prey at bird observatories along the Baltic coast in spring (Korpimäki & Hongell 1986; Sykkö & Vikström 1987). Also, during the increase phase of the vole cycle, most female Tengmalm's owls and about half of the males seemed to arrive at breeding grounds after the early owl pairs had laid eggs (Carlsson 1991). There are no data from winter movements, but autumn irruptions of owls seem to continue until late November (Saurola 1979; Sykkö & Vikström 1987, 1988).

My results from Tengmalm's owls contrast with Hörnfeldt *et al.*'s (1990) results from the same species in northern Sweden. The differences may be due to shorter duration (7 years) of their study, due to deeper and longer-lasting snow cover in Sweden than in my study area (Korpimäki 1986), and due to less spatial synchrony of local vole populations in my study area

which lies in the transition zone between northern strongly cyclic vole populations and non-cyclic ones in southern Fennoscandia (see Hansson & Henttonen 1985; Korpimäki 1986). Also, Hörnfeldt *et al.* (1990) made their spring trappings of voles in late May, but fig. 6 of their paper reveals that Tengmalm's owls initiated egg-laying in late March to early April in good vole years. This means that they estimated spring vole densities at least 2–3 months after the settling period of the owls. Ideally, prey densities should be measured during the settling period of birds of prey to study the existence of time lags between changes in predator and prey densities. However, trapping small mammals below snow is difficult. Therefore, I estimated early spring densities of voles by snow-tracking, which probably gives better approximation of vole densities during the settling period of early arriving owls than does trapping in the previous autumn. This is because rapid vole crashes mostly happen during the melting period of snow (see above).

How can the densities of avian predators track vole densities without obvious time lags, although the reproductive rate of the prey is substantially higher than that of the predator? Nomadic avian predators probably have evolved to take advantage of local vole peaks by dispersing widely to search for favourable vole areas. Accordingly, the recruitment rate of predators to the local population is dependent not only on natality, but much more on immigration that is closely related to vole increases. In theory, high recruitment rate of predators should stabilize predator–prey systems (Kuno 1987).

There is apparently an evolutionary race between voles and their predators: both try to reproduce at the time when survival prospects of their offspring are high. I state that it is adaptive for vole-eating avian predators to find increasing vole populations, as in that phase of the vole cycle they are able to produce more surviving offspring (i.e. to gain larger fitness) than in the peak phase (Korpimäki & Lagerström 1988; Korpimäki & Hakkarainen 1991; Korpimäki 1992). This is due to the fact that their offspring can live for 1 year under increasing food conditions, whereas offspring born in the peak phase experience decreasing food conditions during their first year of life. Accordingly, selection for those traits that improve the ability to track density changes of voles should be strong among vole-eating predators. Presumably, it is adaptive to find a vole population that is at the start of increase in autumn, as avian predators can then overwinter subsisting on these voles [winter reproduction of voles is not unusual in the increase phase (e.g. Hansson 1984; present study, Figs 1–2)]. In the next spring birds of prey can reproduce under good food conditions and offspring survival will be high. The ability to search over long distances, to predict where to search, and to assess the direction of vole density changes are thus traits that may be strongly selected for.

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