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Do nomadic avian predators synchronize population fluctuations of small mammals? a field experiment

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Abstract Three-to-five-year population oscillations of northern small rodents are usually synchronous over hundreds of square kilometers. This regional synchrony could be due to similarity in climatic factors, or due to nomadic predators reducing the patches of high prey density close to the average density of a larger area. We estimated avian predator and small rodent densities in 4–5 predator reduction and 4–5 control areas (c. 3 km² each) during 1989–1992 in western Finland. We studied whether nomadic avian predators concentrate at high prey density areas, and whether this decreases spatial variation in prey density. The yearly mean number of avian predator breeding territories was 0.2–1.0 in reduction areas and 3.0–8.2 in control areas. Hunting birds of prey concentrated in high prey density areas after their breeding season (August), but not necessarily during the breeding season (April to June), when they were constrained to hunt in vicinity of the nest. The experimental reduction of breeding avian predators increased variation in prey density among areas but not within areas. The difference in variation between raptor reduction and control areas was largest in the late breeding season of birds of prey, and decreased rapidly after the breeding season. These results appeared to support the hypothesis that the geographic synchrony of population cycles in small mammals may be driven by nomadic predators concentrating in high prey density areas. Predation and climatic factors apparently are complementary, rather than exclusive, factors in contributing to the synchrony.

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Introduction

Population oscillations of small mammals, cyclic (Akçaya 1992; Hörnfeldt 1994) or chaotic (Hanski et al. 1993), are common at northern latitudes (e.g. Elton 1942; Krebs and Myers 1974; Hansson and Henttonen 1988). One typical character of these density fluctuations is a synchrony at a scale of hundreds of square kilometers (e.g. Elton 1942; Kalela 1962). Two alternative explanations for this synchrony are: (1) it could be due to similarity in climatic factors affecting reproduction and survival of small mammals (Moran 1953; Leslie 1959; Sinclair et al. 1993), or (2) it could be due to nomadic predators concentrating to high prey density patches, and thereby reducing the prey density of these patches close to the average density of a larger area (Galushin 1974; Ydenberg 1987; Korpimäki and Norrdahl 1989; hereafter called the predation hypothesis).

In western Finland, the breeding density of nomadic avian predators, the European kestrel *Falco tinnunculus*, Tengmalm's owl *Aegolius funereus*, the short-eared owl *Asio flammeus* and the long-eared owl *A. otus*, is directly dependent on prey density (Korpimäki and Norrdahl 1989, 1991b), and breeding nomadic avian predators consume a larger proportion of prey populations in high prey density years than in low ones (Korpimäki and Norrdahl 1989, 1991a). When the pooled vole consumption of breeding avian predators during their breeding season exceeded 500 voles per km² of agricultural area, vole populations remained stable or even decreased in the course of the summer despite continuous reproduction of voles (Korpimäki and Norrdahl 1991a). These results, together with the modelling of Ims and Steen (1990), suggest that the predation hypothesis may explain the geographic synchrony of northern small mammal fluctuations.

It is commonly accepted that nomadic avian predators concentrate at high prey density patches but there are still few conclusive data from prey and predator densities collected simultaneously in many areas. In addition, there are no previous data showing that avian predation would decrease the geographic variation in prey densities. Yet these phenomena are vital to the predation hypothesis.

This paper is based on results from a replicated reduction experiment of breeding avian predators during four years. In this paper, we test the predation hypothesis. An earlier paper (Norrdahl and Korpimäki 1995a) studied whether these birds of prey regulate or limit local populations of four prey species. We made three *a priori* predictions based on the predation hypothesis and earlier studies: 1. Nomadic avian predators should concentrate at high prey density areas i.e., array themselves across all rodent populations in the region relative to the local densities of the different populations as ideal free distribution states (Fretwell and Lucas 1970).

2. If avian predation decreases the spatial variation in prey densities, the interareal variation in prey densities should be higher in predator reduction than control areas.

3. When the densities of breeding avian predators only are reduced, differences between manipulation and control areas should be most evident in the late breeding season of birds of prey because the possible treatment effects accumulate during the breeding season but, afterwards, an influx of roaming and migrating raptors to high prey density areas should reduce any density differences between areas.

To find out the possible effects of scale on the relationship between avian predation and prey spatial variation, we also studied the intra-areal variation in rodent densities along with interareal variation.

Material and methods

Study area

The study was carried out from 1989 to 1992 in western Finland (c. 63°N, 23 E). In 1989, four manipulation-control pairs of agricultural areas (3 km² each) were chosen for the experiment. The proportion of agricultural fields in the study areas was 70–100% of the total area. In 1990, the number of area pairs was increased to five. Each pair was as similar as possible with respect to habitats inside and surrounding the area. The distance between manipulation and control areas was 4–15 km.

The most important birds of prey in the study areas were the European kestrel (a total of 63 territories in 1989–1992) and Tengmalm's owl (37). These species do not build nests themselves but breed in nest boxes or in cavities (Tengmalm's owl) or on stick nests (kestrel). In manipulation areas, we removed stick nests and filled all natural cavities in late winter, before the breeding season of avian predators. In addition to natural stick nests and tree holes, control areas had several nest boxes for European kestrels and Tengmalm's owls. Thus, we reduced the number of breeding avian predators, but we did not manipulate the number of migrating or roaming birds of prey. Neither did we manipulate the number of avian predators nesting on ground. These consisted of short-eared owls (a total of 26 territories), hen harriers (*Circus cyaneus*, 5), and eagle owls (*Bubo bubo*, 2).

Two voles (*Microtus rossiaemeridionalis* (syn. *epiroticus*) and *M. agrestis*) were the main prey of predators eating small mammals. The bank vole (*Clethrionomys glareolus*), the common shrew (*Sorex araneus*) and the water vole (*Arvicola terrestris*) were the most important other mammalian prey for these predators (Korpimäki 1981; Korpimäki and Norrdahl 1991b; Korpimäki et al. 1991). Rodent population dynamics in the study area are characterized by regular multiannual oscillations with a 3-year periodicity (Norrdahl and Korpimäki 1995b).

Density estimations

Territories of avian predators were located by observing courtship displays, by listening for hooting owls, by following hunting birds and by checking all potential nest-sites (stick nests, natural cavities, and nest boxes). As the areas were small and mostly open terrain (agricultural fields), probably very few territories were missed.

All observed birds of prey were counted during small mammal trap visits (see below) and the total of observed avian predators during a three-day-long trapping period (c. 8 h of observation) was used as an independent index of avian predator hunting activity.

We monitored small mammal populations in the areas by using a "short line method", which was modified from the small quadrat method of Myllymäki et al. (1971) to suit the conditions of agricultural fields. In each manipulation and control area, ditches in agricultural fields were numbered. Twelve forest sites (c. 1 ha) were also numbered in areas including woodland. From these, a random subset was chosen for each trapping occasion (10 or 7 ditches + 3 forest sites in 1990, when vole densities were lowest, 8 or 6 ditches + 2 forest sites/trapping occasion in other years). In each selected ditch, ten mouse snap traps and one rat snap trap were set in a line with a distance of 10 m between traps. The traps were set for 2 nights and were checked once a day. This gave a total of 220 (1990) or 176 (1989, 1991–1992) trap nights per area in each trapping. The areas were trapped in April (early breeding season), late June (late breeding season) and August. In 1989 and 1990, an additional trap sample was taken in late October. Trapping was performed simultaneously in each manipulation-control-pair. We used the pooled number of all trapped rodents as an index of current prey density.

Coefficient of variation (CV) in the number of rodents per trapping line within a study area was used as an index of intra-areal spatial variation. As an index of interareal spatial variation we used the CV in the mean number of rodents per line per area within the treatment groups. Intra-areal variation refers to spatial variation in a small scale (smaller than a raptor breeding territory) whereas interareal variation reflects spatial variation in a larger scale (larger than raptor territories).

For more information on the study areas, predator and prey species, and methods, see Norrdahl and Korpimäki (1995a).

Results

The difference in the mean number of vole-eating birds of prey between control and reduction areas varied from 2.8 to 7.4 pairs (Fig. 1; Norrdahl and Korpimäki 1995a). The difference was largest for breeding kestrels and Tengmalm's owls. In late breeding season (June), the number of vole-eating avian predators observed during three-day small mammal trapping periods was significantly lower in reduction than control areas during 1989–1990, but not during 1991–1992 (Fig. 1).

In April (early breeding season), the current rodent density could explain the observed variation in the number of hunting short-eared owls but not in the number of

hunting hen harriers or kestrels (Table 1). Our index for the current rodent density reflects prey abundance on a small spatial and temporal scale (current density within a 3-km² area). However, the number of raptors hunting in the study areas may partly depend on prey availability on a larger spatial and temporal scale, i.e. on the rodent abundance the birds of prey encounter in the region surrounding our study areas while they are moving towards our study sites in spring. Because of the regularity of rodent oscillations around our study areas (see above) and the geographic synchrony in these oscillations, we could

use the phase of the rodent cycle as an estimate of prey availability on a larger scale. In statistical analysis, the phase of the cycle significantly affected the observed variation in the number of hunting short-eared owls and nearly significantly that of hen harriers but not that of kestrels. In June (late breeding season), the current local rodent density explained the number of observed individuals in kestrels alone. In hen harriers, the number of observed individuals was explained by the local territory number. After the breeding season (in August), the current rodent density could explain the observed hunting activity of diurnal raptors (Table 1).

The general dynamics of rodent densities was very similar in manipulation and control areas (Fig. 2). Avian predator reduction apparently did not affect the variation in rodent numbers in a scale smaller than a raptor breeding territory, but tended to increase variation among areas (Fig. 3). In 1989–1990, when the difference in the number of hunting avian predators between reduction and control areas was significant (Fig. 1), the interareal variation in rodent density was also significantly higher in reduction than in control areas (repeated measures ANOVA, $F = 3.9$, $df = 1$, 2-tailed $P = 0.03$; Fig. 3). In 1991–1992, when there was no significant difference in

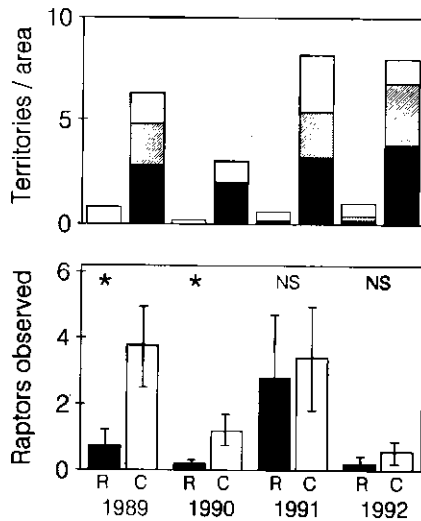


Fig. 1 The mean territory number of kestrels (black bar), Tengmalm's owls (hatched bar) and other avian predators (white bar) in 3 km² avian predator reduction (R) and control (C) areas (upper panel), and the mean (\pm SE) number of vole-eating avian predators observed in the same areas during 3-day small mammal trapping periods in June (lower panel) during 1989–1992. The number of area pairs was 5 (4 in 1989). The difference in the pooled number of territories between reduction and control areas was highly significant in all years (Mann-Whitney U -test, 2-tailed). The significance of difference in the number of hunting raptors between reduction and control areas was tested with ANOVA (* 2-tailed $P < 0.05$, NS 2-tailed $P > 0.1$)

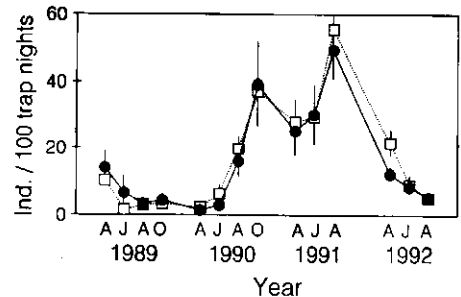


Fig. 2 The mean (\pm SE) number of rodents trapped per 100 trap nights in avian predator reduction (black dots) and control (open squares) areas during 1989–1992. Trapping months were April (A), June (J), August (A) and October (O; only in 1989–1990). The number of reduction-control area pairs was 5 (4 in 1989)

Table 1 Nested ANOVA table concerning the effect of rodent cycle phase^a, territory number and current rodent density on the number of birds of prey observed during 3-day trapping sessions of small mammals in 3-km² study areas. For the kestrel, only unmanipulated areas were included in the analysis. For the hen harrier and the short-eared owl (not manipulated), all study areas were included

Source:	Cycle phase (df=2)			Territories (df=1)			Rodent density (df=4)		
	MS	F	P	MS	F	P	MS	F	P
	Kestrel								
April	0.4	0.2	0.8	6.3	2.6	0.14	1.1	0.5	0.8
June	0.6	0.8	0.5	0.0	0.0	0.99	6.2	8.0	0.003
August	5.8	2.5	0.12	2.1	0.9	0.4	9.6	4.2	0.03
Hen harrier									
April	1.9	3.1	0.06	2.0	3.2	0.08	1.0	1.6	0.2
June	0.1	0.8	0.5	1.2	8.8	0.006	0.1	0.4	0.8
August	10.5	4.6	0.02	5.8	2.5	0.12	9.1	4.0	0.01
Short-eared owl ^b									
April	1.0	8.5	0.0012	0.2	1.4	0.2	1.3	11.4	0.0001
June	1.1	0.3	0.8	11.9	3.1	0.09	4.6	1.2	0.3

^a 1990=increase, 1991=peak, 1989 and 1992=decrease

^b Short-eared owls shift to nocturnal habits in August. Therefore, there were not enough observations for analysis in August

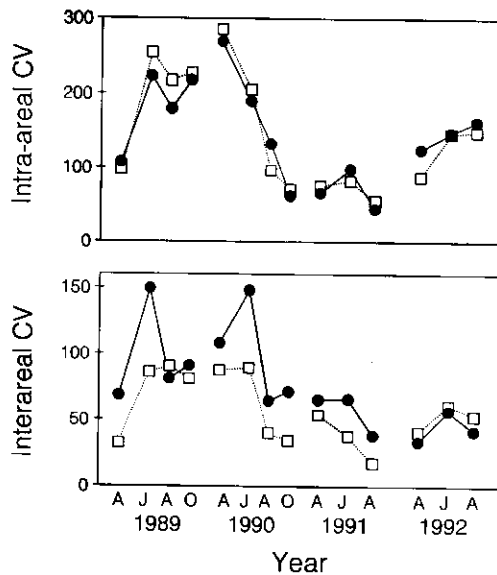


Fig. 3 Coefficient of variation (CV) of rodent density within 3-km² avian predator reduction (black dots) and control (open squares) areas (upper panel) and among these areas (lower panel) in 1989–1992. Trapping months were April (A), June (J), August (A) and October (O; only in 1989–1990). The number of reduction-control area pairs was 5 (4 in 1989)

the number of hunting avian predators (Fig. 1), there was no significant difference in the interareal variation in rodent density ($F = 0.6$, $P = 0.5$; Fig. 3). As we only reduced the number of breeding avian predators, the difference in the interareal variation should have been largest at the end of the breeding season. This was also the case as predator reduction did not affect interareal variation of rodent density in April and August ($F = 1.5$, $df = 1$, $P = 0.3$, and $F = 0.9$, $P = 0.4$, respectively), but tended to do so in June ($F = 6.4$, $P = 0.09$; Fig. 3).

Discussion

Did avian predators concentrate in high prey density areas?

Current prey density explained well the distribution of avian predators after the breeding season of birds of prey (in August). During the breeding season, the relationship between current rodent density and the number of avian predators observed was less uniform. Territory number could explain the number of hen harriers observed within breeding season better than local prey density. The same was true for short-eared owls in late breeding season (in June). In addition to territory number and current local prey density, also the variation in prey density on a larger temporal and spatial scale seemed to affect the number of avian predators observed: the phase of the vole cycle (increase, peak or decrease phase) could partly explain the observed variation in the number of hunting short-eared owls and hen harriers in April. Thus, it seems that

the number of birds of prey moving within or through our study region was partly determined by the prey density level on a year-to-year scale, and that the avian predators moving within our study region distributed themselves according to current local prey density, at least after the breeding season.

During the breeding season, however, the situation was partly different. Hen harriers and kestrels arrive at the study area mainly in late March and April, and immediately occupy territories if prey availability is high enough (Korpimäki and Norrdahl 1991b; Palokangas et al. 1992). After territory occupation, birds of prey perform visible courtship displays. Therefore, a relationship between the number of observed diurnal raptors and territory number in April could be expected. However, this relationship was partly masked by migrants observed in the study areas at the same time. Later in the breeding season, breeding avian predators are confined to the nest vicinity: they hunt within a radius of few kilometers from the nest (e.g. Norrdahl and Korpimäki 1995a). The densities of most breeding birds of prey track prey abundances at the time the avian predators settle on their territories (Korpimäki 1985, 1994; Korpimäki and Norrdahl 1991b) but rapid changes in rodent densities may happen within the breeding season, especially in years with decreasing vole density (e.g. Norrdahl and Korpimäki 1993). This probably explains why the current rodent density could not explain the distribution of hen harriers and short-eared owls in the late breeding season. That the current rodent density could explain the distribution of kestrels at the same time may be explained by the superior ability of kestrels to find prey patches: kestrels use vole scent marks visible in ultraviolet light as rapid cues in hunting (Viitala et al. 1995).

To conclude, non-breeding nomadic and migrating avian predators apparently did array themselves across all rodent populations in the region relative to the local densities of the different populations. This was the first assumption of Ydenberg (1987), Korpimäki and Norrdahl (1989), and Ims and Steen (1990) who described the synchronizing effects of avian predation on the spatial variation in prey densities. Our results are in accordance with the proposition of Galushin (1974), who suggested that numerical responses of non-breeding avian predators to changes in prey densities happen faster than those of breeding avian predators.

Spatial and temporal variation in rodent densities

As the densities of small rodents were similar in manipulation and control areas, spatial variation of prey densities in predator reduction and control areas can be compared without considering the effect of rodent density. We focused on interannual differences to find out whether the difference in the variation between the raptor reduction and control areas was largest at a time when the predation hypothesis states, i.e. when the difference in the number of hunting birds of prey between reduction and control areas was highest. This was the case: in

1989–1990, when we observed significantly more hunting avian predators in the late breeding season in control than in the reduction areas, also the interareal variation in rodent densities was significantly higher in reduction than in the control areas, whereas, in 1991–1992, there was no such difference.

If breeding avian predators were responsible for the observed differences in the interareal variation of prey densities, the difference between predator reduction and control areas should have been largest in the late breeding season (our third prediction). This was the case: we observed a nearly significant difference in the late breeding season but not at the beginning of or after the breeding season. Therefore, predation by breeding avian predators apparently decreased the spatial variation in prey densities, in accordance with the predation hypothesis.

The difference in the interareal prey density variation between the avian predator reduction and control areas disappeared soon after the breeding season of raptors when they are no longer confined to their breeding territories. This indicates that avian predators may rapidly bring the high prey density areas close to the average density of a larger geographic area, thereby maintaining the synchrony of prey population fluctuations over wide areas. Although breeding birds of prey do not seem to regulate prey populations in the long-term (Norrdahl and Korpimäki 1995a), our results imply that even a short-term impact on prey populations may be enough in the context of spatial synchrony.

Avian predation evidently decreased the spatial variation in prey densities despite the fact that the calculated small rodent predation rates by the main avian predators in our study area (usually less than 10% of the summer production; Korpimäki and Norrdahl 1991a) were lower than those needed (> 15–20%) according to a model of Ims and Steen (1990). This indicates that either our previous calculations of small rodent predation rates are underestimates, or that the model was not very accurate in predicting the effects of nomadic predators. An alternative explanation is that changes in prey behaviour occur under high avian predation pressure (Ydenberg 1987), and that the direct (i.e. killing) and indirect (i.e. behavioural changes in prey) effects of avian predators combined have a stronger impact on the spatial variation in prey densities than the direct effects of predation alone. Available data (e.g. Gerkema and Verhulst 1990; Longland and Price 1991; Hakkarainen et al. 1992; Jedrzejewski et al. 1993; Korpimäki et al. 1995) indicate that avian predation risk may have a substantial impact on the behaviour of small rodents. Yet more experimental evidence on the behavioural changes in prey under avian predation risk is needed before the proposition of Ydenberg (1987) can be evaluated.

The question of scale

Population oscillations of northern small mammals are synchronous over hundreds of square kilometers (e.g. El-

ton 1942; Kalela 1962), but our manipulation experiment operated at finer scales: within areas (a scale of a few hundred meters) and between areas (a scale of 4–15 kilometers). Yet the key to understanding large-scale patterns lies in the elucidation of mechanisms underlying these patterns; mechanisms, which typically operate at a finer scale than those on which the patterns are observed (Levin 1992). Thus, it is likely that the key to understanding the large-scale geographic synchrony of population fluctuations can be found at finer scales.

The reduction of birds of prey increased the interareal variation in prey density, but had no apparent effect on spatial variation in prey densities within the 3-km² areas. Thus, the synchronizing impact of avian predation on prey population oscillations seems to operate only at a large scale (a scale larger than the size of an avian predator breeding territory). This might be the answer to the question why there is a wide geographic synchrony in population oscillations of small mammals despite the large spatial density variation at a smaller scale.

Predation and climate: complementary factors?

Differences in meteorological factors were unlikely to affect our results, as the climate was very similar in the study plots (all plots were within an area of < 800 km², and mainly level agricultural fields on 26–52 m above sea level). Thus, avian predation could have a synchronizing impact on prey population oscillations independent of climatic factors. Yet our experiment did not test the effects of meteorological factors on spatial variation in rodent densities and, thus, cannot reveal the relative importance of meteorological factors and avian predation in causing the geographic synchrony of population fluctuations in small mammals.

In Canada, Sinclair et al. (1993) found a relationship of snowshoe hare (*Lepus americanus*) population oscillations to sunspot activity and annual snow accumulation. Accordingly, they suggested that the 10-year snowshoe hare cycle was indirectly modulated by solar activity through an amplified climate cycle that affects the whole boreal forest ecosystem. However, climate cycles appear not to be a general explanation of the geographic synchrony of population fluctuations in small mammals, as sunspot cycles with an 11-year period (Moran 1953; Keith 1963) appear not to be a plausible explanation of the geographic synchrony in vole cycles with a 3 to 5 year period. Instead, climatic factors may occasionally contribute to the geographic synchrony of vole cycles, for example, by forcing animals to move to exposed places with higher predation risk, or by reducing reproductive output to such levels that reproduction in prey is not able to compensate for losses due to predation. Thus, predation and climatic factors apparently are complementary, rather than exclusive, factors in contributing to the synchrony.

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