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Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland

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This paper examines the effects of population fluctuations of small mammals on the population dynamics (primarily on population fluctuations, clutch sizes and production of young of the Long-eared Owl *Asio otus*, Short-eared Owl *A. flammeus*, Kestrel *Falco tinnunculus* and Hen Harrier *Circus cyaneus* in the large (63 km^2) field plain of Alajoki, western Finland (63° 05′ N, 22° 55′ E) in 1977–82.

Altogether 315 nests or territories of birds of prey were found in the study area. The peak phase of population fluctuations of birds of prey occurred in 1977 (98 breeding pairs), thereafter the populations decreased continuously to about the tenth part in 1981 but a rapid increase occurred next spring (45 pairs). *Asio flammeus* was the most numerous bird of prey in Alajoki (39 % of the breeding pairs) followed by *Falco tinnunculus* (36 %), *A. otus* (20 %), *Circus cyaneus* (3 %), Tengmalm's Owl *Aegolius funereus* (2 %) and Sparrow Hawk *Accipiter nisus* (+).

Field and Common Voles (*Microtus agrestis* and *M. arvalis*) emerged as the most important factors regulating population fluctuations, clutch sizes and the production of young in the birds of prey studied, because *Microtus* spp. are energetically advantageous prey species. *Asio flammeus* had the largest clutch size of birds of prey in Alajoki, followed by *Falco tinnunculus, A. otus* and *Circus cyaneus*, but population fluctuations were greatest in *Circus cyaneus* and *Asio otus* and clearly smaller in *A. flammeus* and *Falco tinnunculus*. These results seem to contradict the theoretical prediction that there is a positive correlation between clutch size and the degree of nomadism.

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1. Introduction

Breeding biology and diet of birds of prey have been studied extensively but the effects of the population fluctuations of available prey species have been less frequently examined (e.g. *Buteo buteo* Sylvén 1982; *B. lagopus* Pasanen & Sulkava 1971; *Circus cyaneus* Hamerström 1979; *Falco tinnunculus* Cavé 1968, Rockenbauch 1968, Ziesemer 1973, Village 1980; *Strix uralensis* Lundberg 1976; *S. aluco* Southern 1970; *Asio flammeus* Clark 1975; *A. otus* Hagen 1965, Ziesemer 1973, Rockenbauch 1978, Nilsson 1981, Village 1981; *Aegolius funereus* Korpimäki 1981a). In particular few studies have attempted to explore the effects of prey density variations on communities of birds of prey (but see Craighead & Craighead 1956, Hagen 1969, Linkola & Myllymäki 1969, Phelan & Robertson 1978, Erlinge et al. 1983). Galushin (1974) has emphasized the importance of such studies in the comparison of different reproductive tactics of birds of prey.

The aim of this paper is to clarify the effects of population fluctuations in small mammals on population dynamics (primarily population fluctuations, clutch size variation and the production of young) of the Long-eared Owl *Asio otus*, Short-eared Owl *Asio flammeus*, Kestrel *Falco tinnunculus* and Hen Harrier *Circus cyaneus* on the large field plain in Southern Ostrobothnia, western Finland. These species comprise the guild of open-terrain birds of prey in the study area (Korpimäki 1978).

2. Study area, material and methods

The field plain of Alajoki in Southern Ostrobothnia lies at the confluence of two rivers, the Lapuanjoki and Kauhavanjoki (63° 05′ N, 22° 55′ E). Only small islands of trees and bushes, large ditches and the two rivers break the flat cultivations. Mainly oats, barley and hay were cultivated in the fields (very few fields were uncultivated; see Korpimäki et al. 1977, 1979).

The study area covers about 63 km^2 (cultivated ground 48 km^2, marshland and forest 11 km^2, open bog 3 km^2 and inhabited area 1 km^2). Floods cover over 400-500 ha of the fields in some springs (e.g. in 1977 and 1982).

The displaying owls were listened for using the point stop method (see Anon. 1977, Lundberg 1978, Holmberg 1979, Korpimäki 1980) from early March to mid-April. The playback technique was also used and this located particularly the territories of *A. otus* and Tengmalm's Owl *Aegolius funereus*. The territories of diurnal hawks and *A. flammeus* were mapped by observing their display.

Nest searches were begun at the end of April and continued to the early part of July. All twig nests, natural cavities and nest-boxes of the forests in the study area were inspected systematically. The nests of ground-nesting *A. flammeus* and *C. cyaneus* were looked for by closely examining those areas where displaying birds had been seen. The nests of *A. flammeus* were searched by proceeding in an observer chain in suitable fields. The fledglings of *A. flammeus* and *A. otus* were looked for by their begging calls at the end of the breeding season. The calls of the young can be heard at a distance of 100-200 m (*A. flammeus*), or even 500 m (*A. otus*).

The small mammal population fluctuations were studied with snap traps in May and early June (spring catches) and in late August and early September (autumn catches) in 1977-82 (totally 9364 trap nights). 50-60 traps were set at distances of 10 m in cultivated fields, abandoned fields, and pine and spruce forests. The area of sample plots ranged from 0.5 to 0.6 ha. The traps were kept in one place for four (sometimes three) days and were checked once a day. Mixed bread was used as bait as it is a relatively good general bait for both voles and shrews (see Korpimäki 1981a).

Table 1. Numbers of nests (A) and further territories (B) of birds of prey in Alajoki in 1977-82.

		1977	1978	1979	1980	1981	1982	Total
Asio otus	A	20	18	12	2	-	6	58
	B	2	1	-	-	1	1	5
Asio flammeus	A	22	20	15	3	-	22	82
	B	12	10	16	2	2	-	42
Aegolius funereus	A	2	-	2	-	-	1	5
	B	-	-	-	-	-	-	0
Falco tinnunculus	A	35	23	19	4	5	10	96
	B	2	-	8	2	2	4	18
Circus cyaneus	A	3	1	1	-	-	-	5
	B	-	2	-	-	-	1	3
Total	A	82	62	49	9	5	39	246
	B	16	13	24	4	5	6	68

3. Results

3.1 Population fluctuations

Altogether 247 nests and further 68 territories of birds of prey were found in the study area in 1977-82 (Table 1). In addition to the species in Table 1 a pair of the Sparrowhawk *Accipiter nisus* bred in Alajoki in 1982. *A. flammeus* was the most numerous species of the study area (39 % of the breeding pairs), followed by *F. tinnunculus* (36 %), *A. otus* (20 %), *C. cyaneus* (3 %) and *A. funereus* (2 %).

Population fluctuations of *A. funereus* have been investigated in the Kauhava region continuously since 1966 (Korpimäki 1981a, 1981b, 1982, 1983) and the highest peak was in the first breeding season of this study (in 1977). In that spring the Field Vole *Microtus agrestis* and Common Vole *M. arvalis* were also especially numerous (Korpimäki 1981a) and the number of breeding pairs of birds of prey was greatest in Alajoki (98). After this peak year the populations decreased continuously to about the tenth part in the year 1981. Thereafter the numbers increased again rapidly.

The relative population fluctuations of *C. cyaneus* were highest (the coefficient of variation $CV = 103\%$) but this is mainly due to the small sample (three being the maximum number of pairs). The population fluctuations of *A. otus* were second highest ($CV = 89\%$) and those of *A. flammeus* ($CV = 67\%$) and *F. tinnunculus* ($CV = 64\%$) somewhat lower than in the previous species. In the lowest year (1980) the breeding population of *F. tinnunculus* was 16 % of the pair numbers of the peak year, but only 5-6 % in *Asio* spp. The edges of the field plain were apparently not suitable biotopes for *A. funereus* as the population was clearly denser east of Alajoki where the fields are smaller (Korpimäki 1981a). My data for this owl are thus not sufficient to describe population fluctuations.

From small mammal trappings the most numerous species in Alajoki are *Microtus agrestis, M. arvalis*, the Bank Vole *Clethrionomys glareolus* and Common Shrew *Sorex araneus* (Table 2). In addition to these some Lesser Shrews *S. minutus*, Water Shrews *Neomys fodiens*, House Mice *Mus musculus*, Water Voles *Arvicola terrestris*, and Norway Rats *Rattus norvegigus*, were caught. For the birds of prey, the prey species of greatest importance were *Microtus* species, *Clethrionomys glareolus* and *Sorex araneus* (Korpimäki et al. 1977, 1979, Korpimäki 1981a). The spring populations of *Microtus* voles peaked in 1977, reached a low phase in 1980 and 1981, and then started to increase again (*CV* = 144%). The peak of *Clethrionomys glareolus* was in 1979 and they were very scarce in spring 1980 (*CV* = 52%). Shrews were most numerous in 1982 (*CV* = 53%).

The pair numbers of *A. otus*, *A. flammeus*, *F. tinnunculus* and *C. cyaneus* seemed to follow the densities of *Microtus* voles (Fig. 1). The correlation coefficients between the *Microtus* densities and pair numbers were as follows in 1977-82: *A. otus* $r = +0.814$ ($P<0.05$), *A. flammeus* $r = +0.655$ (ns), *F. tinnunculus* $r = +0.817$ ($P<0.05$) and *C. cyaneus* $r = +0.800$ (ns). The density of *Clethrionomys glareolus* also seemed to affect the population fluctuations of *A. flammeus* ($r = 0.667$) but this correlation coefficient is not significant. *A. flammeus* seemed to utilize relatively dense populations of *Clethrionomys glareolus* particularly in 1979. Shrews are expected to influence the predator fluctuations only when voles are scarce.

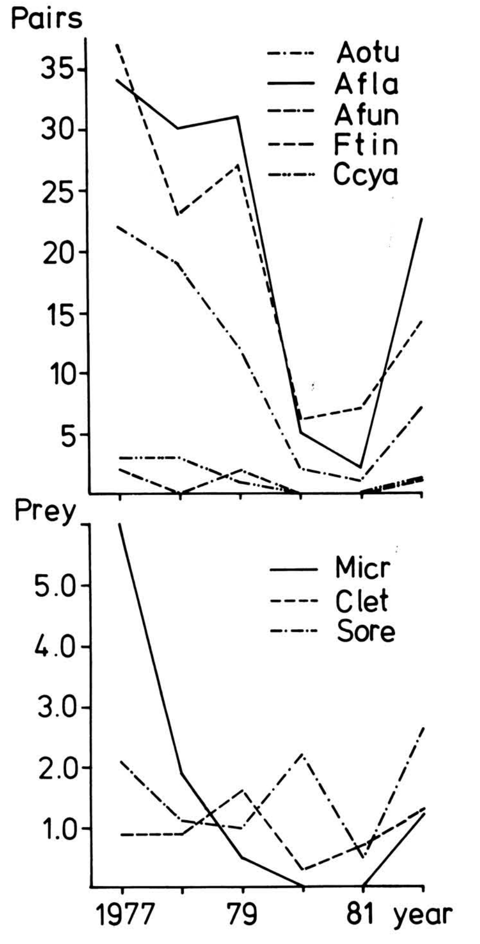

Fig. 1. The dependence of pair numbers of birds of prey (the upper diagram, Aotu = *Asio otus*, Afla = *A. flammeus*, Afun = *Aegolius funereus*, Ftin = *Falco tinnunculus* and Ccya = *Circus cyaneus*) on the population fluctuations of small mammals (the lower diagram, prey/100 trap nights in spring catches, Micr = *Microtus* spp., Clet = *Clethrionomys glareolus* and Sore = *Sorex* spp.) in Alajoki between 1977 and 1982.

Table 2. Results of small mammal trappings (prey/100 trap nights) in Alajoki in spring (S) and in autumn (A) in 1977-82.

	1977		1978		1979		1980		1981		1982		Mean	
	S	A	S	A	S	A	S	A	S	A	S	A	S	A
Microtus total	6.0	5.5	1.8	4.3	0.5	1.0	0.0	0.3	0.0	1.2	1.2	2.0	1.6	2.4
Microtus agrestis	5.6	2.9	1.6	3.3	0.3	0.6	0.0	0.2	0.0	0.9	0.7	1.7	1.4	1.6
M. arvalis	0.4	1.2	0.2	1.0	0.3	0.2	0.0	0.2	0.0	0.3	0.4	0.4	0.2	0.6
Microtus sp.	0.0	1.4	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.3
Clethrionomys glareolus	0.9	0.3	0.9	1.4	1.6	3.4	0.2	3.5	0.7	2.7	1.3	7.0	0.9	3.1
Sorex total	2.1	3.2	1.1	1.9	1.0	2.4	2.2	1.8	0.5	1.6	2.6	3.0	1.6	2.3
Sorex araneus	2.1	3.0	1.1	1.9	1.0	2.3	2.2	1.8	0.5	1.6	2.5	3.0	1.6	2.3
S. minutus	0.0	0.2	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1
Total	9.0	9.1	3.8	7.6	3.1	6.9	2.3	5.7	1.2	6.2	5.2	12.3	4.1	8.0
Trap nights	800	584	560	700	772	900	600	600	760	1248	1000	840	749	812

3.2 Clutch size

The clutch sizes are given in Table 3. They were greatest in *A. flammeus*, followed by *F. tinnunculus*, *A. otus* and *C. cyaneus*. The annual variation and the range of the clutch size was greatest in *A. flammeus* and smallest in *F. tinnunculus* with *A. otus* being intermediate between the previous species.

The average clutch sizes of *A. otus* correlated positively with *Microtus* densities in 1977–82 (r = 0.895, $P<0.05$). The corresponding correlation coefficients of *A. flammeus* and *F. tinnunculus* were 0.616 and 0.622 (ns). The population fluctuations of *Clethrionomys glareolus* correlated positively only with the clutch sizes of *F. tinnunculus* ($r = 0.776$, ns). The density variations of shrews did not correlate with the clutch sizes of birds of prey.

Table 3. The variation of clutch sizes of *Asio otus*, *A. flammeus*, *Falco tinnunculus* and *Circus cyaneus* in Alajoki in 1977–82.

	Clutch size									Mean	*SD*	*n*
	2	3	4	5	6	7	8	9	10			
Asio otus												
1977				1	3	3				6.3	0.8	7
1978		2	5	1	3	2				4.9	1.4	13
1979	1	1	2	3						4.0	1.2	7
1980	1	-	1							3.0	1.4	2
1982	1	-	-	-	1	1				5.0	2.7	3
Total	3	3	8	5	7	6				4.9	1.6	32
Asio flammeus												
1977			1	1	3	3	2	3	1	7.2	1.7	14
1978			1	1	4	4	5	2		7.0	1.4	17
1979			3	3	2	2	3			5.9	1.6	13
1980	1	-	2							3.3	1.2	3
1982			3	-	3	2	2	3		6.7	1.9	13
Total	1	-	10	5	12	11	12	8	1	6.6	1.8	60
Falco tinnunculus												
1977		1	2	12	15	4				5.6	0.9	34
1978			1	9	9					5.4	0.6	19
1979			1	7	4	1	1			5.6	1.0	14
1980				3						5.0	0.0	3
1981			1	2	1					5.0	0.8	4
1982			1	4	5					5.4	0.7	10
Total		1	6	37	34	5	1			5.5	0.8	84
Circus cyaneus												
Total			1	3						4.8	0.5	4

3.3 Production of young

The production of young was measured by the numbers of fledglings (*F. tinnunculus* and *C. cyaneus*) or by the numbers of young that left the nest (*A. otus* and *A. flammeus*) (Table 4). The range and the annual variation of young produced was greatest in *A. flammeus*, followed by *A. otus* and *F. tinnunculus*.

The correlations between the average number of young produced by *A. otus* and *Microtus* densities in 1977–82 was positive, but not significant ($r = 0.812$). The same was true of the corresponding correlation coefficients for *A. flammeus* and *F. tinnunculus* (0.559 and 0.572). The numbers of *Clethrionomys glareolus* correlated positively with the numbers of fledglings in *F. tinnunculus* (r = 0.766, ns). The previous correlations were impaired by the irregular variation in the proportion of totally destroyed nests (the main nest robbers being man and Pine marten *Martes martes*).

Table 4. The variation of the production of young of *Asio otus*, *A. flammeus*, *Falco tinnunculus* and *Circus cyaneus* in Alajoki in 1977–82.

	Number of young produced								Mean	*SD*	*n*
	0	1	2	3	4	5	6	7			
Asio otus											
1977	4	-	-	3	5	5	1	1	3.5	2.1	19
1978	3	2	2	4	5	3			2.8	1.7	19
1979	6	1	3	1	-	1			1.3	1.6	12
1980	2								0.0	0.0	2
1982	1	1	2	-	2				2.2	1.6	6
Total	16	4	7	8	12	9	1	1	2.6	2.0	58
Asio flammeus											
1977	5	-	2	2	-	2	3	3	3.5	2.8	17
1978	5	1	4	4	1	3	5		3.0	2.3	23
1979	5	1	4	5					1.6	1.3	15
1980	2	-	-	-	1				1.3	2.3	3
1982	2	1	1	4	2	5	2	3	4.1	2.2	20
Total	19	3	11	15	4	10	10	6	3.1	2.3	78
Falco tinnunculus											
1977	6	1	3	5	5	8	8		3.6	2.1	36
1978	6	2	1	7	4	3			2.4	1.8	23
1979	5	-	3	3	4	4			2.7	1.9	19
1980	3								0.0	0.0	3
1981	1	2	1	1	1				1.8	1.5	6
1982	2	-	-	-	1	5	1		3.9	2.3	9
Total	23	5	8	16	15	20	9		2.9	2.1	96
Circus cyaneus											
Total	2	-	2	1					1.4	1.3	5

4. Discussion

The proportion of *Microtus* voles in the diets of raptors was studied in 1977, when it was 96 % for *A. otus*, 98 % for *A. flammeus* and 88 % for *F. tinnunculus* (Korpimäki et al. 1977). Consequently *M. agrestis* and *M. arvalis* were the most important prey for the birds of prey studied in Alajoki. The importance of small rodents is central also in the diet of *C.*

cyaneus (in Norway 57 %, Hagen 1952). *A. funereus* is a more catholic predator and they eat *Clethrionomys glareolus* (29 % of the diet at the end of the breeding season), shrews (27 %), *Microtus* voles (26 %) and birds (14 %, Korpimäki 1981a).

Microtus agrestis and *M. arvalis* are clearly the most abundant small mammals in the fields of the study area. *Clethrionomys* voles occurred most in the forests and shrews both in fields and forests. *M. arvalis* in particular also thrive in cultivated fields, particularly near ditches. *Microtus* spp. are energetically advantageous and easy prey for open-country birds of prey because they are heavy (almost twice as heavy as *Clethrionomys glareolus* and 3-4 times heavier than shrews; for the average weights, see Korpimäki 1981a) and catching *Microtus* voles take only as much time and energy as catching *Clethrionomys glareolus* or shrews. As predators try to minimize the amount of energy spent in searching for food (Schoener 1971), *Microtus* voles are the most important prey species. They also affect the population fluctuations, clutch sizes and number of young produced of the bird species studied. The density of *Microtus* spp. also regulates the population fluctuations, clutch sizes and number of young produced of *A. funereus*, although their importance in the diet is less pronounced (Korpimäki 1981a).

The coefficient of variation of *Microtus* numbers was substantially greater than that of predator populations, while the population fluctuations of *Clethrionomys* voles and shrews were smaller than in birds of prey. The hawks and owls had at least some inclination to stay in the same breeding areas despite the decreasing *Microtus* populations, and at that time the raptors must catch alternative prey species (e.g. *Clethrionomys* and *Arvicola* voles, shrews, mice, birds and cold-blooded animals, Korpimäki unpubl.). Migration to other breeding areas occurred only when the populations of the main prey species were in the low phase. Some territories of *A. otus* and *A. flammeus* as well as of *F. tinnunculus* and *C. cyaneus* were occupied for several consecutive years, indicating nest-site tenacity, even though the birds could not be identified individually. Nest-site tenacity decreases the synchrony in the density variations of *Microtus* voles and birds of prey. This dependence is also reduced by spring floods. The floods covered over 400-500 ha of suitable breeding areas for *A. flammeus* in the peak years (1977 and 1982).

The amplitude of population fluctuations of voles and the regional synchrony of vole peaks decrease from north to south whereas the vole cycles become longer towards the north (Kalela 1962). The annual population fluctuations of *A. otus* (e.g. Wendland 1957, 1958, Ziesemer 1973, Glue 1977, Rockenbauch 1978, Joschko 1978, Hegger 1979 and Village 1981) and *F. tinnunculus* (Cáve 1968, Rockenbauch 1968, Ziesemer 1973, Piechocki 1975, Riddle 1979 and Village 1980) were clearly lower in Central Europe and the British Isles than in Alajoki. Instead, the coefficients of variation in some populations of *A. otus* in Southern and Central Sweden were either as large as or larger than in my northern study area (80-130 %, summarized by Nilsson 1981). The nest-site affinity of *A. flammeus* was low in my study area; this species has earlier been described as highly nomadic (e.g. Gerber 1960, Hölzinger et al. 1973, Andersson 1980, 1981, Saurola 1983). Alajoki is quite an optimal breeding habitat at least for *Asio* spp.

According to Andersson (1980) the cyclic food production and large clutch size favour nomadism among birds. The largest clutch size among the birds of prey breeding in Alajoki was in *A. flammeus*, followed by *F. tinnunculus*, *A. otus* and *C. cyaneus*. My data seem to contradict Andersson's (1980) prediction in the sense that *A. flammeus* and *F. tinnunculus* were less nomadic (as measured by population stability in the breeding season) than *A. otus* and *C. cyaneus*, although longer time series will be needed in order to analyse the fluctuation patterns statistically.

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