Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation

Erkki Korpimäki & Kai Norrdahl

Korpimäki, E. & Norrdahl, K. 1989: Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. — Ann. Zool. Fennici 26:389–400.

The proportion of shrews in the diet of European birds of prey is higher in western Finland than in northern and southern Fennoscandia, and in central, western and southern Europe. In western Finland, 14 (out of 17) species of avian predators consume shrews at least occasionally. The proportion of shrews in the diet is negatively correlated with the body size of avian predators: Tengmalm's owls, short-eared owls, ural owls, long-eared owls and kestrels catching most shrews. Tengmalm's and barn owls are the worst enemies of shrews among European birds of prey. Mammalian predators consume many fewer shrews than avian predators, probably because of their distaste for shrews. The badger, red fox, stone marten and mink consume more shrews than the stoat, common weasel and least weasel.

In western Finland, Tengmalm's owls, short-eared owls, long-eared owls and kestrels shifted to shrews when the density of their preferred prey (*Microtus* voles) declined. However, the density of shrews did not affect these shifts, which is in agreement with the prediction of the optimal foraging theory. The predation impact on common shrews by breeding Tengmalm's owls, short-eared owls, long-eared owls and kestrels tended to be positively density-dependent on *Microtus* and *Clethrionomys* voles, but negatively density-dependent on shrews, suggesting that predation by these birds of prey amplifies the population fluctuations of shrews. These results support our earlier suggestion that birds of prey are the most likely candidates causing synchronous population crashes of coexisting vole and shrew populations.

Erkki Korpimäki, Department of Zoology, University of Oulu, Linnanmaa, SF-90570 Oulu, Finland (present address: kp. 4, SF-62200 Kauhava, Finland).
Kai Norrdahl, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland (present address: Penttiläntie 2, SF-62100 Lapua, Finland).

1. Introduction

In recent years, several ecologists (e.g. Hansson & Henttonen 1985, 1988, Korpimäki 1986a, Hansson 1987, Korpimäki & Norrdahl 1987, 1989a, 1989b, Hanski 1987) have suggested that predation and other extrinsic factors play a key role in the three-to-four-year microtine rodent cycle. Microtines are strongly cyclic in northern Fennoscandia (the northern zone), but more or less non-cyclic in southern Fennoscandia and in central and western Europe (the southern zone). In the transition zone, for example in western and southern Finland, microtines are indistinctly cy-

clic (Hansson & Henttonen 1985, 1988; see fig. 3 in Hansson & Henttonen 1988 for tentative distribution of these zones).

In the northern zone, shrews (Soricidae) tend to have low density synchronously with cyclic microtines (Hansson 1984, Henttonen 1985, Kaikusalo & Hanski 1985, Sonerud 1988), whereas microtines and shrews have non-cyclic and asynchronous dynamics in the southern zone (Hansson 1984). In the transition zone, microtines and shrews usually have simultaneous population declines, although the other phases of their population fluctuations are not regularly synchronous (Korpimäki 1986a). These results

suggest that the population fluctuations of coexisting microtines and shrews are influenced by a common extrinsic factor or factors. As qualitative or quantitative changes in food plants of microtines (e.g. Laine & Henttonen 1983) should not affect the dynamics of insectivorous shrews, Hansson (1984), Henttonen (1985), Kaikusalo & Hanski (1985) and Korpimäki (1986a) suggested that the synchrony could be attributed to predation.

In this paper, we first describe regional differences in the proportion of shrews in the diet of avian and mammalian predators in Europe. Second, we relate the between-year variation in the proportion of shrews in the diet of predators to the population fluctuations of voles in western Finland. Third, seasonal changes in the occurrence of shrews in the diet of predators are examined. Fourth, data are presented on the impact of avian predators on shrew populations in western Finland. And finally, we discuss the role of avian and mammalian predators in the population dynamics of shrews.

2. Material and methods

Data on the diet of European avian and mammalian predators of shrews were compiled from comprehensive journals and handbooks. The diet composition of birds of prey was determined by pellet analysis and that of mammalian predators by studying stomach contents of carcasses or by scat analysis. Whenever possible, data collected over at least four years were used to minimize the effect of year-to-year variation in diet.

Food samples of breeding kestrels *Falco tinnunculus* (a total of 142 samples, Korpimäki 1986b and unpubl.), Tengmalm's owls *Aegolius funereus* (98, Korpimäki 1981, 1988 and unpubl.), short-eared owls *Asio flammeus* (121, Korpimäki unpubl.), long-eared owls *A. otus* (75, Korpimäki 1987 and unpubl.) and ural owls *Strix uralensis* (38, Korpimäki & Sulkava 1987 and unpubl.) were collected in the Kauhava region (63°N, 23°E), western Finland, in 1977–87. Each food sample consisted of pellets and other prey remains collected from the nest-site after the breeding season. Details on the collection and treatment of food samples, and on the idenfication of prey items, are given by Korpimäki (1981, 1986b, 1987, 1988) and Korpimäki & Sulkava (1987).

Scats of the stoat *Mustela erminea* and least weasel *M. nivalis nivalis* were sampled from autumn 1983 to spring 1988, at Alajoki farmland (63°05′N, 22°55′E), in the Kauhava region (Korpimäki & Norrdahl 1987, Korpimäki, Norrdahl & Rinta-Jaskari, unpubl.). The majority of samples were collected during snow-tracking in winters 1983–88. Teeth, bone fragments, and hair and feather remains were used to identify vertebrate prey (a total of 524 prey items of the stoat and 132 prey items of the least weasel). Details on the identification of prey items are described by Korpimäki & Norrdahl (1987).

Abundances of small mammals in the Kauhava region were estimated by snap-trapping in May and early June (spring trappings) and in late August and September (autumn trappings) both in the western part and in the middle of the study area. Four sample quadrats (a cultivated field, an abandoned field, a pine forest and a spruce forest) were trapped each season, year and sub-area. The total number of trap nights was 17430 in the middle sub-area, and 24144 in the western sub-area. Results of three-to-four-night trapping periods were pooled and expressed as the number of animals caught per 100 trap-nights. The index of small mammal abundance which is used in this paper is the average for the two sub-areas (see Korpimäki 1981, 1986a for details).

Data on seasonal changes in the occurrence of shrews in the diet of predators and on the impact of predators on shrews were compiled from the literature (Gerell 1968, Englund 1969, Huhtala et al. 1977, Korpimäki 1986c, Korpimäki & Norrdahl 1989a, and unpubl.).

3. Results

3.1. Occurrence of shrews in the diet of predators in Europe

Avian predators

Data are available from western Finland on the diet of eight raptor, eight owl and one passerine species (the great grey shrike *Lanius excubitor*) that regularly feed on mammals during the breeding season (Table 1). Fourteen of these species kill shrews at least occasionally. In terms of prey numbers, the proportion of shrews is highest in the diet of Tengmalm's owl, followed by the short-eared owl, ural owl, long-eared owl and kestrel. Even the large white-tailed eagle *Haliaeetus albicilla* and eagle owl *Bubo bubo* catch shrews occasionally. The proportion of shrews in the diet is negatively correlated with the body weight of the avian predator (Spearman's correlation, $r_s = -0.54$, $df = 15$, $P < 0.05$), but this relationship is not due to small birds of prey being more specialized on small rodents than large ones ($r_s = -0.15$, $df = 15$, ns for body weight versus proportion of voles in the diet, and $r_s = -0.24$, $df = 15$, ns for body weight versus proportion of mice).

The common shrew *Sorex araneus* was the most frequent shrew species caught by birds of prey in western Finland (Table 2). The pygmy shrew *S. minutus* was the second most frequent species, followed by the water shrew *Neomys fodiens*, the masked shrew *S. caecutiens*, the least shrew *S. minutissimus* and the black shrew *S. isodon*. The proportion of the smallest species (the pygmy and least shrews) seemed to be highest in the diet of the great grey shrike, whereas the largest species (the water shrew) was most often caught by ural and eagle owls. The common shrew was the most abundant species on Alajoki farmland, making up 86% of the 533 shrews collected

Table 1. The percentages of shrews, voles, mice and rats (in terms of prey number) in the diets of breeding birds of prey in western Finland. The mean body weights are from Forsman (1984) (raptors), Korpimäki (1981), Mikkola (1983) (owls) and Haartman et al. 1963–72 (great grey shrike).

Species	Mean weight (g)	Shrews	Voles	Mice and rats	No. of prey items	Source
Great grey shrike	65	5.3	12.5	1.3	1840	Huhtala et al. 1977
Kestrel	207	11.1	39.4	4.4	4637	Korpimäki 1985b, 1986b and unpubl.
Sparrowhawk	209	0.6	12.1	–	2837	Sulkava 1972
Marsh harrier	639	–	35.6	0.5	183	Hildén & Kalinainen 1966
Common buzzard	706	6.7	51.4	0.7	868	Korpimäki & Sulkava unpubl.
Rough-legged buzzard	917	–	84.7	–	98	Korpimäki & Sulkava unpubl.
Goshawk	1149	0.2	9.7	–	2101	Huhtala 1976
Golden eagle	4168	–	1.8	–	2468	Sulkava et al. 1984 and unpubl.
White-tailed eagle	4457	0.2	6.5	–	666	Koivusaari 1980
Pygmy owl	62	3.5	50.0	0.4	2240	Kellomäki 1977
Tengmalm's owl	134	33.1	51.2	3.1	12540	Korpimäki 1981, 1988 and unpubl.
Hawk owl	295	3.2	92.2	1.9	1207	Korpimäki 1972 and unpubl.
Long-eared owl	308	11.3	82.1	4.7	3341	Korpimäki 1987 and unpubl.
Short-eared owl	315	18.3	72.7	5.0	3626	Korpimäki unpubl.
Tawny owl	523	7.4	51.6	6.0	2655	summarized by Korpimäki 1986d
Ural owl	796	12.0	64.1	3.0	1812	Korpimäki & Sulkava 1987
Eagle owl	2625	0.5	51.9	31.0	2373	Huhtala et al. 1976 and unpubl.

Table 2. The species composition (in %) of shrews in the diet of birds of prey in western Finland. N = number of shrews identified. Sources as in Table 1.

Shrew:	water	common	black	masked	pygmy	least	N
Great grey shrike	1.0	64.9	–	2.1	20.6	11.3	97
Kestrel	0.4	97.6	–	–	2.0	–	502
Pygmy owl	–	53.7	–	9.3	35.2	1.9	54
Tengmalm's owl	0.6	95.1	0.4	0.3	3.6	–	667
Hawk owl	2.8	88.9	–	5.6	2.8	–	36
Long-eared owl	0.5	94.9	–	–	4.5	–	376
Short-eared owl	1.0	99.0	–	–	–	–	626
Ural owl	6.0	80.6	–	5.1	6.0	2.3	217
Eagle owl	9.1	90.9	–	–	–	–	11

in pitfalls during 1984–87 (K. Norrdahl, unpubl.). The proportion of the common shrew tended to be even higher in the diet of birds of prey than in pitfall catches, being 98, 95 and 99% of all shrews in the diet of kestrels, long-eared owls and short-eared owls, respectively (Table 2).

In northern Fennoscandia, the kestrel and Tengmalm's owl are the most important predators of shrews (Table 3), though data for the former species are scarce. In central and western Europe, the proportion of shrews is highest in the diet of Tengmalm's owl and the barn owl *Tyto alba*, and in southern Europe the barn owl catches shrews most frequently. There are also marked regional differences in the

composition of shrew species eaten by birds of prey: in southern Europe the most frequent prey is the white-toothed shrew *Crocidura russula*, while in central, western and northern Europe it is the common shrew *Sorex araneus*.

In southern Europe, the proportion of shrews in the diet of birds of prey is similar to that in central and western Europe (Table 3), but in the transition zone birds of prey catch more shrews than in the southern zone. When comparing only those species which have been studied in the southern and transition zones and which consume shrews at least in one of the two zones, the difference in the percentage of shrews in the diet is significant (Wilcoxon test, two-tailed,

Table 3. The percentages of shrews (in terms of prey number, N) in the diets of breeding birds of prey in Europe. Data from western Finland are from Table 1. Sources are given in parentheses.

Species	Northern Fennoscandia			Western Finland	Central and western Europe			Southern Europe		
	%	N		%	%	N		%	N	
Great grey shrike				5.3						
Long-tailed skua	3.7	405	(1)							
Kestrel	22.7	220	(2)	11.1	3.0	5458	(3)	0.2	1624	(4)
Sparrowhawk				0.6	0.0	12116	(5)			
Hen harrier	0.9	570	(2)		0.2	664	(6)			
Montagu's harrier					0.5	734	(6)			
Marsh harrier				0.0	0.0	536	(6)			
Common buzzard	1.0	719	(7)	6.7	0.0	2109	(8)	0.0	211	(9)
Rough-l. buzzard	1.2	2217	(2)	0.0						
Black kite					0.4	282	(10)	0.0	227	(9)
Gyrfalcon	0.1	1410	(11)							
Goshawk				0.2	0.0	4825	(12)			
Lesser s. eagle					1.5	132	(10)			
White-tailed eagle				0.2						
Pygmy owl				3.5	2.5	691	(13)			
Tengmalm's owl	18.3	6907	(14)	33.1	20.6	2891	(15)			
Little owl					0.4	2984	(16)	0.0	605	(9)
Hawk owl	1.7	1124	(17)	3.2						
Barn owl					17.5	73805	(18)	18.5	3672	(19)
Long-eared owl	4.5	736	(2)	11.3	2.2	3752	(20)	3.8	6945	(21)
Short-eared owl	2.9	510	(2)	18.3	2.1	1682	(18)			
Tawny owl				7.4	8.4	20848	(18)			
Ural owl	3.9	1739	(14)	12.0	7.1	282	(22)			
Great grey owl	4.5	5177	(22)							
Snowy owl	0.3	2726	(22)							
Eagle owl	0.1	4476	(23)	0.5	0.1	5809	(10)	0.4	3506	(24)
Mean	4.7			7.1	3.7			3.3		
SD	6.9			8.9	6.1			6.9		
N	14			16	18			7		

Sources: 1) Andersson (1976), 2) Hagen (1952), 3) summarized by Korpimäki (1985b), 4) Mouillard (1935) and Glutz v. Blotzheim et al. (1971), 5) Opdam (1979), 6) Schipper (1973), 7) Spidso & Selås (1988), 8) Goszczynski & Pilatowski (1986), 9) Valverde (1967), 10) Uttendörfer (1952), 11) Lindberg (1983), 12) Opdam et al. (1977), 13) Schönn (1980), 14) Jäderholm (1987), 15) summarized by Korpimäki (1981), 16) Haensel & Walther (1966), 17) Ims (1982), Mikkola (1983), Skarén (1983), Niethammer (1984), 18) Erfurt & Stubbe (1987), 19) Herrera (1973), 20) Wijnandts (1984), 21) Araujo et al. (1974), 22) Mikkola (1983), 23) Willgohs (1974), and 24) Jaksić & Marti (1984).

$T = 4$, $n = 10$, $P < 0.02$). In the northern zone, the consumption of shrews by birds of prey again tends to decrease, but the difference between the transition and northern zones is not significant ($T = 9$, $n = 8$, $P < 0.20$).

Mammalian predators

Although there are more sources of error that may bias the results of scat and stomach content analyses than the results of pellet analyses, it is evident that the proportion of shrews in the diet of mammalian predators is substantially lower than in the diet of avian predators throughout Europe (Tables 3 and 4). Note that the percentages of shrews in the diets of avian and mammalian predators are not directly comparable, as only the figures for small mustelids represent the proportion of shrews in terms of prey numbers, whereas the results indicate percentages of occurrence in scats or stomachs for the larger species.

The red fox *Vulpes vulpes* appears to be the most important predator of shrews in the northern zone. In the transition zone, the badger *Meles meles* and the mink *Mustela vison* consume many shrews, as the badger does in the southern zone (Table 4). Accord-

Table 4. The percentages of shrews in the food of mammalian predators in three zones of Europe (zones defined by the dynamics of microtine rodents; Hansson and Henttonen 1985, 1988). The figures are the percentages of shrews in terms of prey number for small mustelids and the percentages of faeces or stomachs in which shrews were found for other carnivores. F = number of faeces, S = number of stomachs, K = number of kills during snow-tracking. Sources are given in parentheses.

Mammalian predator	Northern zone		Transition zone		Southern zone	
	%	F/S	%	F/S	%	F/S
Least weasel			1.5	132F (1)		
Common weasel					0.7	148F (2)
Stoat	0.0	241F (3)	0.6	524F (1)	0.4	2199F (4)
Mink	2.9	1858F (5)	4.9	4392F (5)	0.8	3856F (5)
Polecat					0.4	501S (6)
Pine marten	0.5	401K (7)			0.3	835F (8)
Stone marten					0.1	847F (9)
Otter					0.0	14615F (10)
Red fox	5.0	60S (11)	3.0	133S (11)	3.2	632S (6)
Badger			6.0	290S (12)	20.0	190S (13)
Mean	2.9		2.5		2.9	
SD	2.7		1.9		6.5	
N	5		4		9	

Sources: 1) Korpimäki & Norrdahl (1987), Korpimäki, Norrdahl & Rinta-Jaskari (unpubl.), 2) Erlinge (1975), 3) Erlinge (1987), 4) Erlinge (1981), 5) Gerell (1968), 6) Rzebik-Kowalska (1972), 7) Pulliainen (1981), 8) Goszczynski (1976), 9) Tester (1986), 10) Erlinge (1967), 11) Englund (1969), 12) Skoog (1970), and 13) Andersen (1954).

ing to these data, small mustelids catch shrews only infrequently in all three zones, though occasionally higher proportions of shrews in the diet of small mustelid have been recorded in American (Hamilton 1933, Aldous & Manweiler 1942, Simms 1979) and Russian studies (Ognev 1935, Vershinin 1972), but not in western (Day 1968, Moors 1975, Tapper 1979, King 1980) and central European (Debrot 1981) studies. It is noteworthy that the percentage of shrews in the diet of the stone marten *Martes foina* is relatively high in some southern European studies, for example 7% (the number of scats was 539) and 13% (157) in Spain (Delibes 1978, Amores 1980) and 11% (431) in France (Waechter 1975). The proportion of shrews in the diet of mammalian predators is relatively constant in the three zones (Table 4).

3.2. Between-year variation in the proportion of shrews in the diet of predators

Microtus voles (the field vole *M. agrestis* and the common vole *M. epiroticus*) are the preferred prey of Tengmalm's owls (Korpimäki 1981, 1988), short-eared owls (Korpimäki unpubl.), long-eared owls (Korpimäki 1987), ural owls (Korpimäki & Sulkava 1987) and kestrels (Korpimäki 1985a, 1986b) in the Kauhava region, western Finland. The proportion of *Microtus* voles in the diet of these birds of prey varies in close accordance with their density in the field. Shrews comprise an alternative prey type for these birds of prey. During the period 1977–87, the proportion of shrews was highest in the diet of Tengmalm's owl (mean±SD = 39±18%), followed by the short-eared owl (23±17%), the long-eared owl (19±15%), the kestrel (12±6%) and the ural owl (11±9%).

The proportion of shrews in the diet of Tengmalm's owl varied from 17% to 78% in different years (Fig. 1). The percentage of shrews in the diet tended to correlate negatively with the spring trap index of *Microtus* and bank voles, but was independent of the trap index of the common shrew (Table 5 and Fig. 1). In addition, the proportion of shrews in the diet of short-eared owls, long-eared owls and kestrels seemed to be influenced more by the spring trap index of *Microtus* and bank voles than that of the common shrew. Thus, Tengmalm's owls, short-eared owls, long-eared owls and kestrels shifted to shrews when vole numbers declined, but the abundance of shrews apparently did not affect these shifts in diet. In con-
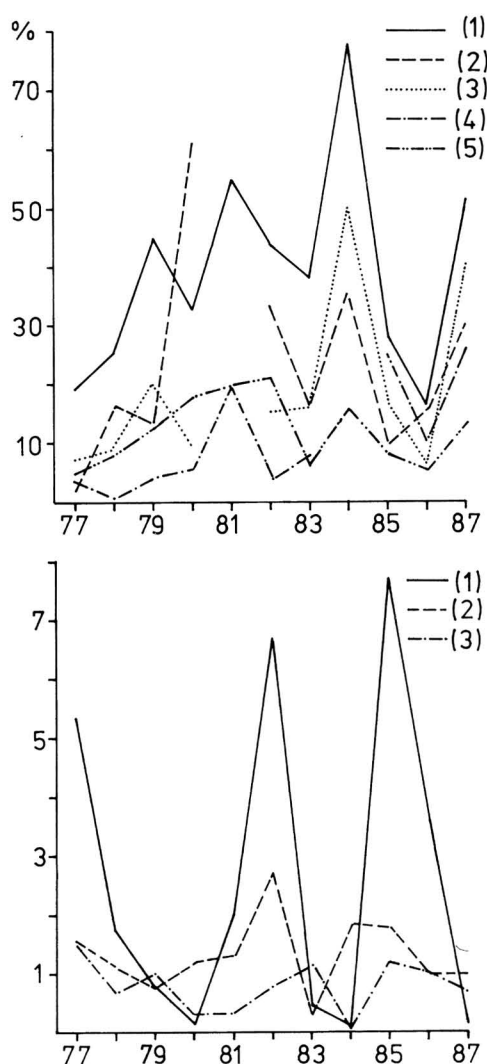
Table 5. Spearman's rank correlation between the spring trap index of *Microtus* voles, bank vole and common shrew (Fig. 1, lower panel), and the percentage of shrews by prey number in the diet of Tengmalm's owls, short-eared owls, long-eared owls, ural owls and kestrels in the Kauhava region, western Finland, in 1977–87 (Fig. 1, upper panel). ns = not significant, * = $P < 0.05$, ** = $P < 0.01$.

	Microtus spp.	bank vole	common shrew
Tengmalm's owl	–0.44 ns	–0.65 *	0.10 ns
Short-eared owl	–0.65 *	–0.86 **	0.22 ns
Long-eared owl	–0.32 ns	–0.37 ns	–0.06 ns
Ural owl	–0.04 ns	–0.07 ns	–0.06 ns
Kestrel	–0.22 ns	–0.67 *	0.36 ns

Table 6. The percentages of shrews in terms of prey number (*N*) in the scats of the stoat and least weasel collected at Alajoki farmland, western Finland, in the winters from 1983/84 to 1987/88.

Winter	Stoat		Least weasel	
	%	N	%	N
1983/84	1.9	106	–	18
1984/85	–	95	–	14
1985/86	–	196	–	52
1986/87	3.3	30	4.0	25
1987/88	–	97	4.3	23
Total	0.6	524	1.5	132

Fig. 1. Upper panel: The proportion of shrews (in terms of prey number) in the food of breeding Tengmalm's owls (1), short-eared owls (2), long-eared owls (3), ural owls (4) and kestrels (5) in the Kauhava region, western Finland, in 1977–87. Lower panel: The spring trap index of *Microtus* voles (1), bank voles (2) and common shrews (3) in the same area in 1977–87.

trast, the occurrence of shrews in the diet of ural owls was independent of the spring trap index of voles (Table 5); water voles *Arvicola terrestris*, young hares and birds are more important alternative prey than shrews for this large owl species (Korpimäki & Sulkava 1987).

The few shrews that were identified in the scats of stoats and least weasels at Alajoki farmland were recorded in poor (1983/84, 1986/87) and intermediate (1987/88) vole winters (Table 6). The data for breeding kestrels, short-eared owls and long-eared owls were also collected at Alajoki, allowing a comparison of the prey choice of mammalian and avian predators in the same area during the same period. In each year, kestrels, short-eared owls and long-eared owls consumed shrews markedly more than stoats and least weasels did (Fig. 1 and Table 6). The fact that food samples of birds of prey were collected in the breeding season while those of small mustelids were collected mainly in winter is unlikely to explain this difference, as the proportion of shrews in the diet of predators is usually higher in winter than in spring (see below).

Table 7. Seasonal changes in the percentage of shrews (in terms of prey number, N) in the diet of Tengmalm's owl during the first half of the year in good (pooled data for 1973, 1977, 1982 and 1985) and poor vole years (1974–76, 1978–81 and 1983–84). Data from the Kauhava region, western Finland (Korpimäki 1986c).

Time period	Good years		Poor years	
	%	N	%	N
1 January–15 March	17.3	150	11.9	294
16–31 March	2.4	125 ⎫	17.1	351
1–15 April	4.6	219 ⎭		
16–30 April	15.9	427	26.0	624
1–15 May	10.5	602	24.0	421
16–31 May	15.8	184	36.8	285
1–30 June	20.0	25	45.8	166
Total	11.8	1732	25.2	2141

Table 8. Seasonal changes in the percentages of shrews, voles and mice (in terms of prey number, N) in the diet of the great grey shrike in central Ostrobothnia (64°N, 24°30′E), western Finland. Pooled data for 1969–75 (Huhtala et al. 1977).

Season	Shrews	Voles	Mice	N
Breeding	5.3	12.5	1.3	1840
Late summer	1.4	2.7	0.7	146
Autumn	6.1	6.6	0.5	198
Winter	14.3	57.7	24.4	168
Early spring	15.0	40.0	10.0	60

3.3. Seasonal changes in the occurrence of shrews in the diet of predators

In good vole years, the proportion of shrews in the diet of Tengmalm's owl was significantly higher before the breeding season (1 January – 15 March) than later on (Table 7). During the breeding season (16 March – 30 June), the percentage of shrews increased gradually and reached the winter level in late May and June. In poor vole years, the increase in the proportion of shrews was nearly linear during the first half of the year. In both cases, the occurrence of shrews in the diet was inversely related to the percentage of *Microtus* voles in the diet (Korpimäki 1986c).

The proportion of shrews in the diet of the great grey shrike was highest in winter and early spring, when voles and mice also played the most important role in their diet (Table 8). In contrast, in the breeding season, late summer and autumn, great grey shrikes

mostly consume insects (Huhtala et al. 1977), which seem to be their preferred prey. In southeastern Sweden, shrews made up 21% of the 1952 prey items identified from pellets collected in winter (Olsson 1986).

The percentage of scats of Swedish minks containing remains of shrews seemed to be higher in winter (7%, number of scats 1627) than in spring (1%, 2306), summer (2%, 2378) and autumn (3%, 3011; Gerell 1968). In contrast, the frequency of voles in the scats was higher in spring (17%), summer (25%) and autumn (26%) than in winter (10%). However, it should be noted that fishes (51%) and invertebrates (30%) are much more frequent than small mammals in the scats of the mink, throughout the year.

3.4. The impact of avian predation on shrews

Korpimäki & Norrdahl (1989a, and unpubl.) examined the impact of breeding Tengmalm's owls, short-eared owls, long-eared owls and kestrels on the populations of the common shrew in the Kauhava region during 1977–87. The rate of predation on the common shrew was mostly independent of its numbers in the study areas ($r = -0.56$, $P < 0.10$ for Tengmalm's owl, $r = 0.10$, ns for the short-eared owl, $r = -0.40$, ns for the long-eared owl and $r = -0.46$, ns for the kestrel; $df = 9$ in each case). However, the rate of predation by the short-eared owl was significantly higher and that of the long-eared owl nearly significantly higher in good vole years than in poor vole years (Table 9). Similar differences were not found for the rate of predation by Tengmalm's owl and the kestrel on the common shrew.

4. Discussion

4.1. Factors affecting the occurrence of shrews in the diet of predators

Aitchison's (1987) review of North American literature revealed that the predators of shrews include owls and, to a lesser extent, weasels and foxes. Our literature survey from Europe showed that birds of prey feeding on mammals frequently catch shrews also, and that small avian predators consume shrews more frequently than large ones. There were no correlations between the proportions of shrews, voles and mice in the diet of various species of birds of prey, suggesting that the occurrence of shrews in the

Table 9. The mean predation rate (the percentage of prey items taken by birds of prey out of the total number available in the study area) by breeding kestrels, short-eared owls, long-eared owls and Tengmalm's owls on the common shrew in the Kauhava region, western Finland, in 1977–87. Statistical significance of the differences between good and poor years was examined with Mann-Whitney U-test (two-tailed). N = number of years. Data from Korpimäki & Norrdahl (1989a, and unpubl.).

Species	Good years			Poor years			U	P
	Mean	SD	N	Mean	SD	N		
Kestrel	7.5	2.9	6	11.0	14.2	5	13	ns
Short-eared owl	9.0	5.0	6	2.0	2.2	5	1	0.01
Long-eared owl	3.9	2.5	6	1.3	1.8	5	5	0.10
Tengmalm's owl	5.5	0.7	4	4.7	3.7	7	8	ns

diet is related more to the body size of the predator than to its habit of feeding on small mammals. As birds of prey usually are energy maximizers (*sensu* Schoener 1971) in the breeding season (e.g. Korpimäki 1985a), small shrews are likely to be profitable prey items only for small birds of prey. This view is supported by the observations that kestrels, long-eared owls and short-eared owls at Alajoki killed more common shrews and fewer pygmy shrews than could be expected from their availabilities in the field, even if the pygmy shrew moves above ground more frequently than the common shrew (e.g. Ellenbroek 1980) and should, therefore, be more exposed to aerial predators. The smallest shrew species were caught most frequently by the smallest predator, i.e. the great grey shrike, while the largest species, i.e. the water shrew, was caught most frequently by the large ural and eagle owls. These large owls consume many water voles (e.g. Korpimäki & Sulkava 1987, Huhtala et al. 1976), which occupy the same habitat as the water shrew, partly perhaps explaining the above result.

The proportion of shrews in the diet of predators showed Tengmalm's owl to be the worst enemy of shrews in northern and central Europe, while the barn owl is the key predator in central and southern Europe. Tengmalm's owl is also the most frequent bird of prey in Fennoscandian coniferous forests (Merikallio 1958, Ulfstrand & Högstedt 1976), while the barn owl was earlier one of the most common predatory birds in central and southern Europe (e.g. Bunn et al. 1982). In fact, one reason for the abundance of Tengmalm's and barn owls may be their consuming of shrews as an alternative prey when the availability of voles is low. In western Finland, some male Tengmalm's owls are able to provide for their female and

young in poor vole years by preying almost exclusively on shrews (Korpimäki 1981, 1988).

The proportion of shrews in the diet of birds of prey was higher in the transition zone of Fennoscandian microtine cycles than in the southern and northern zones and in southern Europe. We suggest that the regional differences are due to regional variation in the composition of the alternative prey available to birds of prey feeding on small rodents. In central Europe and in southern Fennoscandia, *Apodemus* mice, young rabbits *Oryctolagus cuniculus* and birds serve as the most important alternative prey for birds of prey (e.g. Goszczynski 1977, Erlinge et al. 1983). *Apodemus* species and rabbits do not occur in the transition zone, where the densities of birds are also lower than further south. In the northern zone, birds of prey consuming small rodents as their staple food usually disperse when voles crash (e.g. Galushin 1974, Andersson 1980, Korpimäki et al. 1987), with the result that diet samples for these species are mostly available for good vole years, and the proportion of shrews in their diets is lower than in the transition zone. In arid southern Europe, the availability of voles, mice and shrews is relatively low, and the birds of prey that feed on small mammals in central and northern Europe switch to insects and lizards (e.g. Herrera & Hiraldo 1976, Mikkola 1983, Korpimäki 1985b). In conclusion, the occurrence of shrews in the diet of birds of prey is affected more by the composition of the prey community than by the density of the shrews themselves.

Both in central and northern Europe, mammalian predators catch shrews infrequently. Our data for stoats, least weasels, kestrels, short-eared owls and long-eared owls, coexisting at Alajoki, confirm the view that shrews are an unimportant alternative prey

for small mustelids in comparison with birds of prey (Korpimäki 1986a). We cannot find any other reason for the apparent avoidance of shrews by small mustelids than their well-known bad taste (e.g. King 1980, Erlinge 1981 and references therein). The smell of shrews thus seems to protect them against mammalian predators, but not against avian enemies with poor sense of smell. On the other hand, badgers, red foxes, minks and stone martens eat shrews more than stoats, common weasels and least weasels do.

Mammalian predators have been observed to leave carcasses of shrews untouched after they have been killed (e.g. Polderboer et al. 1941, Rubina 1960, Pulliainen 1981). Thus data based on scat and stomach content analyses may underestimate the numbers of shrews killed by mammalian predators. However, when we snow-tracked stoats (583 km) and least weasels (249 km) at Alajoki in winters from 1983 to 1988, only four untouched carcasses of shrews were found on the trails of the larger species and none on the trails of the smaller one. Although least weasels often move below the snow cover, our data suggest that surplus killing of shrews is rare and its importance to the population dynamics of shrews is likely to be insignificant.

4.2. Between-year and seasonal variation: dependence on the availability of the preferred prey

The optimal foraging theory predicts that only the absolute abundance of the preferred (most profitable) prey influences the optimal prey choice, whereas the abundances of the non-preferred prey types are unimportant (e.g. Pyke 1984). However, some investigators suggest that this prediction is not generally true (e.g. Estabrook & Dunham 1976), and their models predict that the relative densities of non-preferred prey types can also influence prey choice. Our results on between-year variation in the diet composition of breeding kestrels, short-eared owls, long-eared owls, ural owls and Tengmalm's owls, and on seasonal changes in the diet of Tengmalm's owls, indicated that the proportion of shrews in the diet was dependent on the abundance of the preferred prey (*Microtus* voles) but independent of the abundance of shrews. This result is consistent with the prediction of the standard model of optimal foraging.

The proportion of shrews in the diet of avian and mammalian predators tended to be higher in winter than in other seasons. Perhaps the availability of more preferred alternative prey types, such as adult and young birds, lizards and frogs, is higher during snow-free and ice-free seasons than in winter. Predators seem to catch shrews mostly during "lean" periods when other prey types are scarce.

Deep snow cover in winter and high vegetation cover in summer reduce the availability of voles to birds of prey, and they then switch to alternative prey, such as shrews. How is it possible, then, that avian predators are able to catch shrews, which also occupy sub-nivean space in winter and occur below high vegetation cover in summer? We suggest that the following factors make shrews susceptible to avian predation.
1) Shrews are more mobile than voles, as they have to search for food very often (Hanski 1984, 1985).
2) Shrews are much noisier than voles, especially in spring (Heikura 1984, Korpimäki 1986c), which may make them more vulnerable to owls that locate their prey by sound.
3) In good vole years, there may be interspecific competition for sub-nivean space, and shrews may have to move more frequently on the snow surface than voles. In addition, shrews may have to occupy relatively poor habitats in good vole years, which makes them more exposed to predators.

4.3. The role of predation in the population dynamics of shrews

Henttonen (1985) suggested that the most probable predators causing synchronous population crashes of coexisting vole and shrew species are the small mustelids, especially least weasels, whereas Korpimäki (1986a) assumed that birds of prey are the most important predators causing synchronous crashes. Korpimäki & Norrdahl (1987) showed earlier that the proportion of shrews is very low in the diet of stoats and least weasels in the transition zone, and the present, very extensive data confirm this result. Our extensive snow-tracking additionally suggest that surplus killing of shrews by small mustelids is rare. Thus, we can safely conclude that predation by small mustelids is not the cause of the synchronous crashes of voles and shrews in the transition zone. Unfortunately, there are no food data for least weasels in the northern zone. Our literature survey revealed that minks, pine martens, red foxes and badgers feed more on shrews than small mustelids do. Consequently, among the mammalian predators, these medium-sized species are the most likely candidates

contributing to simultaneous crashes of vole and shrew populations, even if the proportion of shrews in their diet is low in comparison with the birds of prey.

The rate of predation of common shrews by Tengmalm's owls, short-eared owls, long-eared owls and kestrels tended to be positively density-dependent on *Microtus* and on bank voles, and negatively density-dependent on common shrews. These results suggest that these birds of prey increase the population fluctuations of shrews by taking a larger proportion of the individuals available at low densities.

It is difficult to assess the importance of predation in the population dynamics of shrews, as there are other extrinsic factors, such as food (e.g. Butterfield et al. 1981, Kaikusalo & Hanski 1985), weather (e.g. Heikura 1984) and interspecific competition (e.g. Ellenbroek 1980, Malmqvist 1985) that may affect their densities. Aitchison (1987) surmised that there is probably more winter mortality associated with food shortage and cold than with predation. The common shrew does not usually reproduce in its year of birth (Crowcroft 1957, K. Norrdahl unpubl.; but see Kaikusalo & Hanski 1985 with references) unlike, for example, field and common voles. Although the mean litter size of the common shrew in our study area is somewhat larger than that of *Microtus* and bank voles (K. Norrdahl unpubl.), its rate of reproduction is lower. Thus, birds of prey that remove overwintered females in spring, even after the birth of the first litter, may cause a marked decrease of shrew densities in late summer and autumn, provided that reproduction of young females is density-independent (but see Kaikusalo & Hanski 1985). We therefore suggest that predation, especially avian predation, may be more important in limiting the densities of shrews than has been traditionally believed. We stress that more attention should be paid to predation in studies on the population dynamics of shrews.

References

Aitchison, C. W. 1987: Review of winter trophic relations of soricine shrews. — Mammal Rev. 17:1–24.

Aldous, S. T. & Manweiler, J. 1942: The winter food habits of the short-tailed weasel in Northern Minnesota. — J. Mammalogy 23:250–255.

Amores, F. 1980: Feeding habits of the stone martens, Martes foina (Erxleben, 1777), in south western Spain. — Säugetierk. Mitt. 28:316–322.

Andersen, J. 1954: The food of the Danish badger (Meles meles) danicus Degerbol) with special reference to the summer months. — Danish Rev. Game Biol. 3:1–75.

Andersson, M. 1976: Population ecology of the long-tailed skua (Stercorarius longicaudus Vieill.). — J. Anim. Ecol. 45: 537–559.

—"— 1980: Nomadism and site tenacity as alternative reproductive tactics in birds. — J. Anim. Ecol. 49:175–184.

Araujo, J. J., Rey, M., Landin, A. & Moreno A. 1974: Contribution al estudio del buho chico (Asio otus) en Espana. — Ardeola 19:397–428.

Bunn, D. S., Warburton, A. B. & Wilson, R. D. S. 1982: The barn owl. — T. & A. D. Poyser, Calton.

Butterfield, J., Coulson, J. C. & Wanless, S. 1981: Studies on the distribution, food, breeding biology and relative abundance of the pygmy and common shrews (Sorex minutus and S. araneus) in upland areas of northern England. — J. Zool., Lond. 195:169–180.

Crowcroft, P. 1957: The life of the shrew. — Max Reinhardt, London.

Day, M. G. 1968: Food habits of British stoats (Mustela erminea) and weasels (Mustela nivalis). — J. Zool., London 150:485–497.

Debrot, S. 1981: Trophic relations between the stoat (Mustela erminea) and its prey, mainly the water vole (Arvicola terrestris Sherman). — In: Chapman, J. A. & Pursley D. (eds.), Worldwide Furbearer Conference Proceedings: 1259–1289. Donneley & Sons, Falls Church, Virginia.

Delibes, M. 1978: Feeding habits of the stone marten, Martes foina (Erxleben, 1777), in northern Burgos, Spain. — Zeitschr. Säugetierk. 43:282–288.

Ellenbroek, E. J. M. 1980: Interspecific competition in the shrews Sorex araneus and Sorex minutus (Soricidae, Insectivora): a population study of the Irish pygmy shrew. — J. Zool., Lond. 192:119–136.

Englund, J. 1969: The diet of foxcubs (Vulpes vulpes) in Sweden. — Viltrevy 6:1–39.

Erfurt, J. & Stubbe, M. 1987: Gewöllanalysen zur Untersuchung der Ernährungsbiologie von Eulen. — Populationsökologie Greifvögel und Eulenarten 1:429–451.

Erlinge, S. 1967: Food habits of the fish-otter, Lutra lutra L., in south Swedish habitats. — Viltrevy 4:371–443.

—"— 1975: Feeding habits of the weasel Mustela nivalis in relation to prey abundance. — Oikos 26:378–384.

—"— 1981: Food preference, optimal diet and reproductive output in stoats Mustela erminea in Sweden. — Oikos 36:303–315.

—"— 1987: Why do European stoats Mustela erminea not follow Bergmann's rule? — Holarctic Ecol. 10:33–39.

Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T., v. Schantz, T. & Sylvén, M. 1983: Predation as a regulating factor in small rodent populations in southern Sweden. — Oikos 40:36–52.

Estabrook, C. F. & Dunham, A. E. 1976: Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. — Amer. Nat. 110:401–413.

Forsman, D. 1984: Rovfågelsguiden. — Lintutieto Oy, Helsinki.

Galushin, V. M. 1974: Synchronous fluctuations in populations of some raptors and their prey. — Ibis 116:127–132.

Gerell, R. 1968: Food habits of the mink, Mustela vison Schreb., in Sweden. — Viltrevy 5:117–211.

Glutz v. Blotzheim, U. N., Bauer, K. M. & Bezzel, E. 1971: Handbuch der Vögel Mitteleuropas. Band 4. — Akademische Verlagsgesellschaft, Wiesbaden.

Goszczynski, J. 1976: Composition of the food of martens. — Acta Theriol. 21:527–534.

—"— 1977: Connections between predatory birds and mammals and their prey. — Acta Theriol. 22:399–430.

Goszczynski, J. & Pilatowski, T. 1986: Diet of the common buzzards (Buteo buteo L.) and goshawks (Accipiter gentilis L.) in the nestling period. — Ekol. Polska 34:655–667.

Haartman, L. v., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin. — Otava, Helsinki.

Haensel, J. & Walther, H. J. 1966: Beitrag zur Ernährung der Eulen im Nordharz-Vorland unter besonderer Berücksichtigung der Insektennahrung. — Beitr. Vogelk. 11:345–358.

Hagen, Y. 1952: Rovfuglene og viltpleien. — Gyldendal Norsk forlag, Oslo.

Hamilton, W. J. 1933: The weasels of New York. — Amer. Midl. Nat. 14:289–344.

Hanski, I. 1984: Food consumption, assimilation and metabolic rate in six species of shrew (Sorex and Neomys). — Ann. Zool. Fennici 21:157–165.

—"— 1985: What does a shrew do in an energy crisis? — In: Sibly, R. M. & Smith, R. H. (eds.), Behavioural ecology: 247–252. Blackwell, Oxford.

—"— 1987: Populations of small mammals cycle — unless they don't. — Trends Ecol. Evol. 2:55–56.

Hansson, L. 1984: Predation as the factor causing extended low densities in microtine cycles. — Oikos 43:255–256.

—"— 1987: An interpretation of rodent dynamics as due to trophic interactions. — Oikos 50:308–319.

Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. — Oecologia (Berlin) 67:394–402.

—"— 1988: Rodent dynamics as community process. — Trends Ecol. Evol. 3:195–200.

Henttonen, H. 1985: Predation causing extended low densities in microtine cycles: further evidence from shrew dynamics. — Oikos 44:156–157.

Heikura, K. 1984: The population dynamics and the influence of winter on the common shrew (Sorex araneus L.). — Carnegie Mus. Nat. Hist. Spec. Publ. 10:343–361.

Herrera, C. M. 1973: Regimen alimenticio de Tyto alba en España sudoccidental. — Ardeola 14:359–394.

Herrera, C. M. & Hiraldo, F. 1976: Food-niche and trophic relationships among European owls. — Ornis Scand. 7: 29–41.

Hildén, O. & Kalinainen, P. 1966: Über Vorkommen und Biologie der Rohrweihe, Circus aeruginosus (L.) in Finnland. — Ornis Fennica 43:85–124.

Huhtala, K. 1976: Kanahaukan ravinnosta. — Suomen Luonto 35:304–306.

Huhtala, K., Finnlund, M. & Korpimäki, E. 1976: Huuhkajan pesimäaikaisesta ravinnosta Vaasan läänissä. — Suomenselän Linnut 11:4–13.

Huhtala, K., Itämies, J. & Mikkola, H. 1977: Beitrag zur Brutbiologie und Ernährung des Raubwürgers (Lanius excubitor) im Österbotten, Finnland. — Beitr. Vogelk. 23: 129–146.

Ims, R. A. J. 1982: Forekomst, habitat og byttevalg hos haukugle i et smågnagerår i Ost-Finnmark 1978. — Fauna 35:133–139.

Jaksić, F. M. & Marti, C. D. 1984: Comparative food habits of Bubo owls in Mediterranean-type ecosystems. — Condor 86:288–296.

Jäderholm, K. 1987: Diet of the Tengmalm's Owl Aegolius funereus and the Ural Owl Strix uralensis in Central Finland. — Ornis Fennica 64:149–153.

Kaikusalo, A. & Hanski, I. 1985: Population dynamics of Sorex araneus and S. caecutiens in Finnish Lapland. — Acta Zool. Fennica 173:283–285.

Kellomäki, E. 1977: Food of the Pygmy Owl Glaucidium passerinum in the breeding season. — Ornis Fennica 54: 1–29.

King, C. M. 1980: The weasel, Mustela nivalis, and its prey in an English wood. — J. Anim. Ecol. 49:127–159.

Koivusaari, J. 1980: Merikotkan Haliaeetus albicilla L. ravintobiologiasta. — Ph. Lic. thesis, Dept. Biol., Univ. Kuopio.

Korpimäki, E. 1972: Hiiri- ja helmipöllön pesinnästä ja ravinnosta samalla biotoopilla. — Suomenselän Linnut 7: 36–40.

—"— 1981: On the ecology and biology of Tengmalm's owl (Aegolius funereus) in Southern Ostrobothnia and Suomenselkä, western Finland. — Acta Univ. Ouluensis A 118. Biol. 13:1–84.

—"— 1985a: Prey choice strategies of the kestrel Falco tinnunculus in relation to available small mammals and other Finnish birds of prey. — Ann. Zool. Fennici 22: 91–104.

—"— 1985b: Diet of the kestrel Falco tinnunculus in the breeding season. — Ornis Fennica 62:130–137.

—"— 1986a: Predation causing synchronous decline phases in microtine and shrew populations in western Finland. — Oikos 46:124–127.

—"— 1986b: Diet variation, hunting habitat and reproductive output of the kestrel Falco tinnunculus in the light of the optimal diet theory. — Ornis Fennica 63:84–90.

—"— 1986c: Seasonal changes in the food of the Tengmalm's owl Aegolius funereus in western Finland. — Ann. Zool. Fennici 23:339–344.

—"— 1986d: Niche relationships and life-history tactics of three sympatric Strix owl species in Finland. — Ornis Scand. 17:126–132.

—"— 1987: Dietary shifts, niche relationships and reproductive output of coexisting kestrels and long-eared owls. — Oecologia (Berlin) 74:277–285.

—"— 1988: Diet of breeding Tengmalm's owls Aegolius funereus: long-term changes and year-to-year variation under cyclic food conditions. — Ornis Fennica 65:21–30.

Korpimäki, E. & Norrdahl, K. 1987: Low proportion of shrews in the diet of small mustelids in western Finland. — Zeitschr. Säugetierk. 52:257–260.

—"— 1989a: Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. — Oikos 54: 154–164.

—"— 1989b: Avian predation on mustelids in Europe 2: impact on small mustelid and microtine dynamics — a hypothesis. — Oikos 55:273–276.

Korpimäki, E., Lagerström, M. & Saurola, P. 1987: Field evidence for nomadism in Tengmalm's owl Aegolius funereus. — Ornis Scand. 18:1–4.

Laine, K. & Henttonen, H. 1983: The role of plant production in microtine cycles in northern Fennoscandia. — Oikos 40:407–418.

Lindberg, P. 1983: Relations between the diet of Fennoscandian peregrines Falco peregrinus and organochlorines and mercury in their eggs and feathers, with comparison to the gyrfalcon Falco rusticolus. — Ph. D. thesis, Dept. Zool., Univ. Gothenburg.

Malmqvist, M. G. 1985: Character displacement and biogeography of the pygmy shrew in Northern Europe. — Ecology 66:372–377.

Merikallio, E. 1958: Finnish birds. Their distribution and numbers. — Fauna Fennica 5:1–181.

Mikkola, H. 1983: Owls of Europe. — T. & A. D. Poyser, Calton.

Moors, P. J. 1975: The food of weasels (Mustela nivalis) on farmland in north-east Scotland. — J. Zool., London 177:455–461.

Mouillard, B. 1935: Notes sur la biologie du Faucon crècelle. — Alauda 7:522–534.

Niethammer, J. 1984: Rötelmäuse (Clethrionomys) in Gevöllen der Sperbereule. — Säugetierk. Mitt. 31:171–177.

Ognev, S. I. 1935: Mammals of U.S.S.R. and adjacent countries. — Israel Program for Scientific Translations, Jerusalem.

Olsson, V. 1986: Varfågelns Lanius excubitor vintervanor V. Bytesval. — Vår Fågelvärld 43:405–414.

Opdam, P. 1979: Feeding ecology of a sparrowhawk population (Accipiter nisus). — Ardea 66:137–155.

Opdam, P., Thissen, J., Verschuren, P. & Müskens, G. 1977: Feeding ecology of a population of goshawk Accipiter gentilis. — J. Ornithol. 118:35–51.

Polderboer, E. B., Kuhn, L. W. & Hendrickson, G. O. 1941: Winter and spring habits of weasels in central Iowa. — J. Wildl. Managem. 5:115–119.

Pulliainen, E. 1981: Food and feeding habits of the pine marten in Finnish Forest Lapland in winter. — In: Chapman, J. A. & Pursley, D. (eds.), Worldwide furbearer conference proceedings: 580–598. Donneley & Sons, Falls Church, Virginia.

Pyke, G. H. 1984: Optimal foraging theory: a critical review. — Ann. Rev. Ecol. Syst. 15:523–575.

Rzebik-Kowalska, B. 1972: Badania nad pokarmem ssakov drapieznych w Polsce. — Acta Zool. Crac. 17:416–506.

Rubina, M. A. 1960: Some features of weasels (Mustela nivalis L.) ecology based on observations in the Moscow region. — Byull. Mosk. o-va Ispyt. Prir. Otd. Biol. 65:27–33 (Translated from the Russian by British Lending Library, Boston Spa, Yorks, trans. no. RTS 2292).

Schipper, W. J. A. 1973: A comparison of prey selection in sympatric harriers (Circus) in western Europe. — Le Gerfaut 63:17–120.

Schoener, T. W. 1971: Theory of feeding strategies. — Ann. Rev. Ecol. Syst. 2:369–404.

Schönn, S. 1980: Der Sperlingkauz. — Die Neue Brehm-Bücherei, Wittenberg-Lutherstadt.

Simms, D. A. 1979: North American weasels: resource utilization and distribution. — Can. J. Zool. 56:386–390.

Skarén, U. 1983: Hiiripöllö (Surnia ulula) pesivänä Tiilikalla. — Savon Luonto 15:18–24.

Skoog, P. 1970: The food of the Swedish badger, Meles meles L. — Viltrevy 7:1–120.

Sonerud, G. A. 1988: What causes extended lows in microtine cycles? Analysis of fluctuations in sympatric shrew and microtine populations in Fennoscandia. — Oecologia (Berlin) 76:37–42.

Spidso, T. K. & Selås, V. 1988: Prey selection and breeding success in the common buzzard Buteo buteo in relation to small rodent cycles in southern Norway. — Fauna Norv., Ser. C, Cinclus 11:61–66.

Sulkava, P. 1972: Varpushaukan, Accipiter nisus L., pesimisbiologiasta ja pesimisaikaisesta ravinnosta. — Ph. Lic. thesis, Dept. Zool., Univ. Helsinki.

Sulkava, S., Huhtala, K. & Rajala, P. 1984: Diet and breeding success of the golden eagle in Finland 1958–82. — Ann. Zool. Fennici 21:283–286.

Tapper, S. 1979: The effect of fluctuating vole numbers (Microtus agrestis) on a population of weasels (Mustela nivalis) on farmland. — J. Anim. Ecol. 48:603–617.

Tester, U. 1986: Comparative study on the diet of the stone marten, Martes foina (Erxleben, 1777)) in urban and rural habitats. — Säugetierk. Mitt. 33:37–52.

Ulfstrand, S. & Högstedt, G. 1976: Hur många fåglar häckar i Sverige? — Anser 15:1–32.

Uttendörfer, O. 1952: Neue Ergebnisse über die Ernährung der Greifvögel und Eulen. — Neudamm.

Valverde, J. A. 1967: Estructura de una communidad de vertebrados terrestres. — Monografias de la estacion biologica de donana, Madrid.

Vershinin, A. A. 1972: The biology and trapping of the ermine in Kamchatka. — Byull. Mosk. o-va Ispyt. Prir. Otd. Biol. 77:16–26.

Waechter, A. 1975: Ecologie de la fouine en Alsace. — Terre et Vie 29:399–457.

Wijnandts, H. 1984: Ecological energetics of the long-eared owl (Asio otus). — Ardea 72:1–92.

Willgohs, J. F. 1974: The eagle owl Bubo bubo (L.) in Norway. Part I. Food ecology. — Sterna 13:129–177.