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Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey

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Prey choice strategies of the kestrel in a large field plain ($63\,km^2$) in western Finland were studied in relation to available small mammal abundance and other birds of prey in 1977-83. The common vole was the most preferred small mammal species in the diet, followed by the water vole, shrews, bank and field voles, and the brown rat. The birds eaten were those breeding principally in forests, although the main prey group (*Microtus* spp.) only inhabited fields. The sex ratios of the mammals and birds in the diet showed a clear male predominance. This was caused by the greater activity of the males in spring. The kestrel, like *Buteo* spp. and *Circus* spp., belongs to the primarily small mammal prey guild among birds of prey. The food niches of the kestrel, long-eared and Tengmalm's owls overlapped to a great extent in the study area. The food niche appeared to expand as the abundance of the most preferred prey in the field decreased. The data were in agreement with the theory predicting that the relative densities of the non-preferred prey items are unimportant in determining the optimal diet. The predator adopted the energy maximisation strategy in prey choice during breeding in order to maximise reproductive output. Making use of the present and earlier studies concerning the prey choice of avian and mammalian predators, one could put forward a new hypothesis: birds of prey mainly prey on small mammal males and tree-nesting birds, while mammalian predators prey more on small mammal females and ground-nesting birds in spring. This might reduce interspecific competition for food.

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1. Introduction

This paper is part of an extensive study on predation as a regulating factor in small mammal populations which has been carried out since 1977 in a diverse predator community in South Ostrobothnia, western Finland (see Korpimäki et al. 1977, 1979, Korpimäki 1984). The short-eared owl *Asio flammeus* is the most numerous bird of prey in the study area (39.4 % of the breeding pairs in 1977-82, $n = 315$), followed by the kestrel *Falco tinnunculus* (36.2 %), the long-eared owl *Asio otus* (20.0 %), the hen harrier *Circus cyaneus* (2.5 %), Tengmalm's owl *Aegolius funereus* (1.6 %) and the sparrowhawk *Accipiter nisus* (0.3 %, Korpimäki 1984). The most abundant mammalian predators of small rodents are the stoat *Mustela erminea*, the pygmy weasel *M. rixosa* and the red fox *Vulpes vulpes* (Korpimäki unpubl.).

The diet and factors affecting the food of the kestrel in the breeding season were investigated in 1972-83 mainly in the abovementioned study area (Korpimäki 1985a). The first aim of the present paper is to examine the prey choice of the falcon in relation to the availability of the most important prey group (i.e. small mammals, Korpimäki 1985a).

In recent years there has been an increasing interest in the study of the feeding ecology of animals from the evolutionary standpoint (e.g. Pyke et al. 1977 with references). The evolutionary viewpoint on prey selection emphasises that certain ultimate strategies of predation arise as the result of natural selection. These strategies involve the optimisation of energy, time and/or nutritional state (e.g. Schoener 1971, Emlen 1973). The second aim of my study is to elucidate what tactics the kestrel adopts in prey selection during the breeding season, and to test some central predictions of optimal diet selection (summarised by Ellis et al. 1976). In addition, the prey choice of the kestrel is compared with the diets of the other most numerous avian predators in the study area. Finally, the food niche of the kestrel among the Finnish diurnal birds of prey is examined.

2. Study area, material and methods

This study was carried out on the large field plain of Alajoki, western Finland (63°05'N, 22°55'E). The study area is about 63 km^2 in size and it includes mainly (76 %) cultivated ground (for additional details see Korpimäki 1984, 1985a).

The food remains and pellets of the kestrel were gathered during the breeding period at 72 nest sites in Alajoki in 1977-83 (for details on the collecting methods and the determination of prey species see Korpimäki 1985a). The total number of identified prey animals was 2118 (Appendix 1).

The nest of the kestrel sometimes contains a store of food during incubation, hatching and the nestling period. Prey animals from food stores were identified and sexed according to Siivonen (1974, small mammals) and von Haartman et al. (1963-72, birds), the total number of stored prey items in 1977-83 being 40. Prey birds were also divided into three age classes: nestlings, fledglings and adult individuals.

The available small mammal populations in Alajoki were studied using snap traps in May and early June (spring catches) and again in late August and early September (autumn catches) in 1977-83 (a total of 10 844 trap nights, Appendix 2). See Korpimäki (1981, 1984, 1985a) for additional details on the trapping methods.

The available and chosen small mammal food was compared by calculating CSR_i (=catch-supply ratio of species i, see Opdam 1978) values. If CSR_i is higher than one, species i is caught more than would be expected from its availability in the field. $CSR_i < 1$ indicates the reverse situation. In order to measure the importance of the different small mammal species in the kestrel's diet, the preference indices were calculated for some species pairs according to Cock (1978, index 8). This index is suitable when the exploitation of prey animals (i.e. the lowering of the prey catchability by changes in the behaviour and/or microhabitat of evasive prey, Charnov et al. 1976) is a negligible factor and the preference is slight. The index goes from minus one to zero for a negative preference, and from zero to plus one for a positive preference.

The diversities of the available and the chosen food were compared by calculating diversity indexes (H', Shannon & Weaver 1949). The breadth of the food niche was measured with values obtained from Colwell & Futuyama's formula (B'). The food overlap of the different predators was calculated using similarity indices (C, Macnaughton & Wolf 1973). Index $C = 1$ when the diets are exactly the same; if all prey species in the food are different, $C = 0$.

3. Results

3.1. Choice of mammals

The common vole *Microtus arvalis* was the most preferred prey species of the kestrel; it was found to be chosen about three times more than was to be expected from its availability according to the combined trapping material from 1977-83 (Table 1). Shrews, bank voles *Clethrionomys glareolus* and field voles *Microtus agrestis* were caught significantly less than their relative densities would suggest. On the other hand, both *Microtus* species and all voles together were eaten more than their availability in the study area would lead one to suppose. The kestrel preyed on small mammals significantly more diversely (as measured with H') than would be expected from the trapping results during the whole study period (t-test, $P < 0.01$). The diversities of the available and chosen mammalian food in 1977-83 do not correlate ($r = -0.149$). The food niche appeared to become more extensive when the relative densities of *Microtus* voles decreased in the field, but the correlation was not significant ($r = -0.522$). This may be due to the data from 1980, when voles were very scarce. Thus, the number of invertebrates in the diet was exceptionally high (49.6 %) and this diminished the niche breadth.

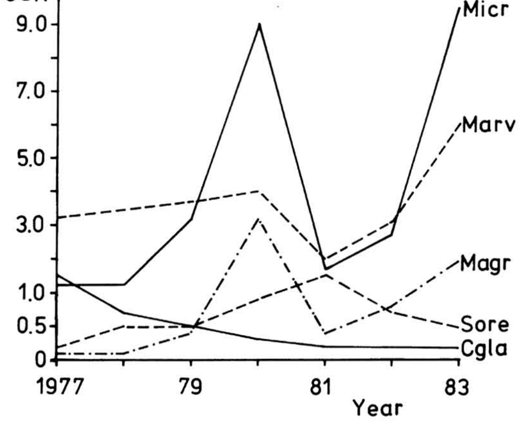

Fig. 1. Annual variation of the choice values (CSR) of the different small mammal species or groups in 1977-83. Micr = *Microtus* voles, Marv = common vole, Magr = field vole, Sore = shrews and Cgla = bank vole.

Table 1. The dependence of choice (C, as percentage proportions in the diet) of mammalian prey on the availability (A, as percentage proportions according to small mammal trappings) of different species in Alajoki in 1977–83. The significance of the difference between available and chosen prey is shown after choice values (*CSR*, χ^2-test, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$). *H'* = diversity index.

	1977			1978			1979			1980		
	A	C	*CSR*	A	C	*CSR*	A	C	*CSR*	A	C	*CSR*
Soricidae	28.8	6.3	0.2***	25.8	12.7	0.5***	34.9	17.2	0.5***	50.0	45.0	0.9
Microtus arvalis	8.0	25.6	3.2***	10.8	26.6	2.5**	4.7	17.9	3.7	2.1	8.3	4.0
M. agrestis	49.6	4.8	0.1***	43.2	2.0	0.1	8.1	3.2	0.4*	2.1	6.7	3.2
Microtus sp., total	64.0	75.8	1.2**	54.1	63.9	1.2	15.1	48.8	3.2***	4.2	38.3	9.1
Clethr. glareolus	7.2	11.1	1.5	20.3	13.9	0.7	50.0	22.5	0.5***	45.8	11.7	0.3**
Microtidae, total	71.2	87.8	1.2***	74.3	78.3	1.1	65.1	71.2	1.1	50.0	51.7	1.0
Prey animals	125	346		74	231		86	187		48	45	
H'	1.27	1.48		1.28	1.57		1.15	1.66		0.87	1.51	

	1981			1982			1983			Total		
	A	C	*CSR*	A	C	*CSR*	A	C	*CSR*	A	C	*CSR*
Soricidae	29.1	42.6	1.5*	33.1	24.6	0.7*	41.5	18.8	0.5**	32.9	18.4	0.6**
Microtus arvalis	4.7	9.6	2.0	4.5	13.8	3.1**	2.4	14.3	6.0	5.7	19.0	3.3**
M. agrestis	12.8	5.2	0.4	13.6	11.4	0.8	2.4	4.5	1.9	22.0	5.8	0.3**
Microtus sp., total	17.4	29.6	1.7*	18.8	51.0	2.7***	4.9	46.4	9.5	29.5	56.8	1.9**
Clethr. glareolus	45.3	7.8	0.2***	47.4	10.6	0.2***	51.2	10.7	0.2***	36.2	13.1	0.4**
Microtidae, total	67.4	40.0	0.6***	66.9	65.5	1.0	56.1	68.8	1.2	66.4	72.2	1.1**
Prey animals	86	75		154	374	41	94		614	1352		
H'	1.39	1.62		1.20	1.81		0.98	1.84		1.38	1.79	

There was, however, great annual variation in the *CSR* values of the different small mammal species (Fig. 1). Common vole predation during the whole study period was greater than its availability implied. The situation was reversed in the field vole (with the exception of the years 1980 and 1983), bank vole (1977), and shrews (1981). Consequently, the choice values of the alternative small mammal species appeared to increase as the availability of the most preferred prey type decreased. There was a significant negative correlation between the relative densities (ind. / 100 trap nights) and *CSR* values for the common vole in 1977–83 (r=<0.771, $P<0.05$), but the correlations for other small mammals were not significant.

In order to measure the relative importance of the alternative small mammals in the predator's diet the preference indices were calculated for some species pairs (Table 2). The mice were not included, since their trappability with snap traps is low (Koskela & Viro 1976). Many authors (e.g. Aulak 1967) have also shown that pitfall traps are

Table 2. Preference index values (Cock 1978, index 8, means from 1977–83) for some small mammal species pairs in the diet of the kestrel in Alajoki. Data on the available small mammal populations were obtained from trapping results.

Species pairs	Preference indexes
M. arvalis / M. agrestis	+0.9
M. arvalis / C. glareolus	+0.8
M. arvalis / A. terrestris	+0.1
M. arvalis / R. norvegicus	+0.9
M. arvalis / S. araneus	+0.7
M. arvalis / S. minutus	+0.6
M. agrestis / C. glareolus	−0.2
M. agrestis / A. terrestris	−0.8
M. agrestis / R. norvegicus	+0.4
M. agrestis / S. araneus	−0.4
M. agrestis / S. minutus	−0.5
C. glareolus / A. terrestris	−0.8
C. glareolus / R. norvegicus	+0.5
C. glareolus / S. araneus	−0.2
C. glareolus / S. minutus	−0.3
A. terrestris / R. norvegicus	+0.9
A. terrestris / S. araneus	+0.7
A. terrestris / S. minutus	+0.6
R. norvegicus / S. araneus	−0.6
R. norvegicus / S. minutus	−0.7
S. araneus / S. minutus	−0.2

Table 3. The division of the available (A) and chosen (C) mammalian food into different weight classes in Alajoki (material from 1977-83 combined). For other explanations see Table 1.

Weight classes (g)	A	C	*CSR*
1-10	32.9	20.8	0.6***
11-20	36.3	20.0	0.6***
21-30	29.5	56.8	1.9***
31-230	1.3	2.3	1.8
Prey animals	614	1352	

appreciably more effective than snap-traps for collecting shrews, particularly smaller ones, but adult voles were able to escape from the shallow jars employed (Skarén 1972). Hence, only the results of snap-trapping have been used to estimate the relative abundances of available small mammals in prey choice studies of predators (e.g. Kellomäki 1977, Erlinge 1981, Korpimäki 1981). The order of importance of the different species seemed to be as follows: water vole *Arvicola terrestris*, lesser shrew *Sorex minutus*, common shrew *S. araneus*, bank vole, field vole and brown rat *Rattus norvegicus*.

The effect of prey weight on food selection was examined by dividing mammals into four weight classes (for mean weights of mammals see Siivonen 1974 and Korpimäki 1981): 1) 1-10 g (lesser shrew, common shrew and harvest mouse *Micromys minutus*), 2) 11-20 g (house mouse *Mus musculus*, bank vole and water shrew *Neomys fodiens*), 3) 21-30 g (common and field vole) and 4) 31-230 g (water vole, brown rat and pygmy weasel). The two heaviest classes were chosen more, and the other groups less, than expected from their availability (Table 3). The most important weight class in the diet was 21-30 g, but in the field small mammals were roughly evenly divided into the three lightest weight classes.

3.2. Choice of birds

The most preferred weight class of the birds was the same as that of mammals (Table 4, see von Haartman et al. 1963-72 for mean weights of birds). Birds belonging to weight groups 51-60 and 101-150 g were taken relatively frequently too. The species of birds preyed on are given elsewhere (Korpimäki 1985a).

Table 4. The division of the chosen bird food (184 birds) into different weight classes in the kestrel's diet. Material from 1977-83 is combined.

Weight class (g)	Chosen %	Weight class (g)	Chosen %
1-10	10.1	61-70	0.8
11-20	9.3	71-80	1.3
21-30	32.9	81-100	2.1
31-40	4.2	101-150	11.0
41-50	0.4	151-250	7.6
51-60	18.1	251-400	2.1

Table 5. The division of the chosen bird food (138 birds) in the kestrel's diet into different ecological groups. Material from 1977-83 is combined.

Ecological groups	Chosen %
Tree-nesters	58.0
Hole-nesters	6.5
Ground-nesting forest birds	6.5
Ground-nesters of open terrain	26.8
House-nesters	2.2

Although the falcon mainly hunted *Microtus* voles living in the fields, the birds eaten consisted primarily of species breeding in the forest (71 % of prey birds, Table 5). Only about a quarter belonged to birds of open terrain, despite the fact that cultivated ground made up 76 % of the study area.

3.3. Choice between sexes and age classes

The sex ratios of the kestrel's prey animals differed significantly from the expected 1:1 ratio among both mammals and birds (Table 6). The voles caught also showed a clear male predominance, although the sex ratios of at least the over-wintered populations of bank voles (Zejda 1967, Viro 1974), field voles (Hansson 1969, Myllymäki 1977) and common voles (Reichstein 1956) have been described as even. In spring and autumn the snap traps, as well as the kestrel, caught male voles to a markedly greater extent than females.

The age class of 163 prey birds in food remains and stored prey items was determined. 69.9 % of birds were adults, 18.4 % were fledglings and 11.7 % nestlings. The number of fledglings and nestlings in the diet was higher in July than it was in May and June (Table 7). The proportion of adults (82.4 %) was signifi-

Table 6. The sex ratios of the kestrel's prey animals compared with those of small mammal trappings in spring and autumn. Significant male or female predominance is indicated after the male percentage (χ^2-test; for other explanations see Table 1).

Prey species or groups	Kestrel prey		Trappings			
			Spring		Autumn	
	Male %	*n*	Male %	*n*	Male %	*n*
Soricidae	50	2	60	86	34***	241
Microtidae	84*	19	69***	171	64***	322
Muridae	100	2	50	2	100	5
Mammalia, tot.	82*	23	67***	314	55*	728
Aves	76*	17				
Total	80**	40				

Table 7. The division (%) of prey birds into two age classes in the different phases (see Korpimäki 1985a) of the breeding season. A significant difference between the phases is indicated in the space between the columns (χ^2-test). For other explanations see Table 1.

Age class	1 May - 15 June	16-30 June	1-31 July
Adult birds	75.0	83.3*	59.5
Fledglings and nestlings	25.0	16.7*	40.5
No. of birds	12	48	42

cantly higher in small birds (mean weight ≤ 30 g) than in medium-sized and large birds (64.3 %, mean weight > 30 g) (the χ^2-test, $P < 0.05$). All the water voles found in stores of the kestrel were young individuals ($n = 6$).

3.4. Prey choice of different birds of prey in Alajoki

The prey choice of most common birds of prey in Alajoki was investigated in 1977, when populations of *Microtus* voles were in a peak phase (Table 8). Predation by short-eared and long-eared owls was almost entirely concentrated on *Microtus* spp. (90 and 84 %). In addition, only some shrews, bank voles, water voles, mice and birds were taken. The food of the kestrel and Tengmalm's owl was most catholic; the proportions of *Microtus* spp. in the diets of these were 58 and 51 %. The kestrel relatively often caught mice and invertebrates, while Tengmalm's owl took bank voles and birds.

Table 8. A comparison of the prey chosen by birds of prey in Alajoki in 1977. The data are derived from the present study for the kestrel = Ftin and from Korpimäki et al. (1977) for the long-eared = Aotu, short-eared = Afla and Tengmalm's = Afun owls. Mean weights of predators from Korpimäki (unpubl.) for the kestrel, from Korpimäki (1981) for Tengmalm's owl and from von Haartman et al. (1963-72) for other species.

Prey species or group	Ftin	Aotu	Afla	Afun
Soricidae	6.1	2.3	2.4	6.6
Microtus arvalis	17.1	64.8	72.2	30.2
M. agrestis	3.9	6.1	8.7	4.7
Microtus sp.	37.3	12.9	8.7	16.0
Microtus sp., total	58.3	83.8	89.6	50.9
Clethr. glareolus	10.2	11.0	7.9	18.9
Arvicola terrestris	0.9	0.8	–	–
Microtidae, total	69.4	95.5	97.6	69.8
Muridae	4.6	1.1	–	1.9
Mammalia, total	80.1	99.0	100.0	78.3
Aves	4.4	1.1	–	21.7
Reptilia	0.5	–	–	–
Invertebrates	15.0	–	–	–
No. of prey animals	432	264	126	106
Niche breadth	1.95	1.21	0.95	1.95
Prey species	22	12	5	14
Mean prey weight (g)	21.4	24.2	22.8	20.8
Mean weight of predator	200	276	315	136

Table 9. The food overlaps among the birds of prey in Alajoki in 1977. For species abbreviations see Table 8.

Species	Aotu	Afla	Afun
Ftin	0.49	0.40	0.57
Aotu		0.90	0.68
Afla			0.54

The food niche was broadest in the kestrel and Tengmalm's owl and narrowest in the short-eared owl. The number of prey species was greatest in the kestrel and smallest in the short-eared owl. Although the body weights of the raptors studied varied from 136 to 315 g, there were no significant differences in the mean prey weights of the predators (*t*-test). The food overlap was widest between the long-eared and short-eared owls (as measured with the similarity index, Table 9). On the other hand, the diets of the kestrel and short-eared owl showed the smallest overlap.

Table 10. The diets of the Finnish diurnal birds of prey in the breeding season. The data are derived from the following sources: kestrel = Ftin (Korpimäki 1985a), merlin = Fcol (P. Sulkava 1971), hobby = Fsub (Curry-Lindahl 1945), peregrine = Fper (Huhtala & S. Sulkava 1977a), gyr falcon = Frus (Mikkola & S. Sulkava 1972), sparrowhawk = Anis (P. Sulkava 1964), goshawk = Agen (S. Sulkava 1964), buzzard = Bbut (Suomus 1953), rough-legged buzzard = Blag (Pasanen & S. Sulkava 1971), honey buzzard = Papi (Itämies & Mikkola 1972), hen harrier = Ccya (Hagen 1952), marsh harrier = Caer (Hildén & Kalinainen 1966), osprey = Phal (Häkkinen 1978), golden eagle = Achr (S. Sulkava 1967) and white-tailed eagle = Halb (Koivusaari et al. 1980).

Prey group	Ftin	Fcol	Fsub	Fper	Frus	Anis	Agen	Bbut	Blag	Papi	Ccya	Caer	Phal	Achr	Halb
Small mammals	64.8	–	–	–	14.0	10.4	2.0	53.5	55.7	–	56.8	35.3	–	0.5	–
Other mammals	0.1	–	–	–	4.1	–	10.2	0.6	–	–	1.6	–	–	25.7	3.1
Mammalia, total	64.9	–	–	–	18.1	10.4	12.2	54.1	55.7	–	58.4	35.3	–	26.2	3.1
Passeriformes	8.1	98.4	7.8	14.5	1.5	74.9	30.2	8.5	7.0	2.9	26.0	24.6	–	0.1	–
Other birds	1.0	1.6	–	85.5	79.6	2.0	54.4	4.8	36.3	–	14.0	35.8	–	73.7	24.9
Aves, total	9.1	100.0	7.8	100.0	81.1	76.9	84.6	13.3	43.3	2.9	40.0	60.4	–	73.8	24.9
Reptilia	0.5	–	–	–	–	–	–	5.4	–	–	0.4	–	–	–	–
Amphibia	0.3	–	–	–	–	–	–	20.2	1.0	4.8	–	1.1	–	–	–
Pisces	–	–	–	–	0.7	–	–	–	–	–	–	1.1	100.0	–	72.0
Invertebrates	25.3	–	92.2	–	–	–	–	–	–	92.3	1.2	–	–	–	–
Unidentified	–	–	–	–	–	12.7	3.2	6.9	–	–	–	2.1	–	–	–
Prey animals	2613	61	103	211	270	2044	342	358	203	480	570	187	914	977	?
Niche breadth	0.93	0.08	0.27	0.41	0.69	0.79	1.11	1.39	0.93	0.32	1.09	1.26	0.00	0.61	0.69

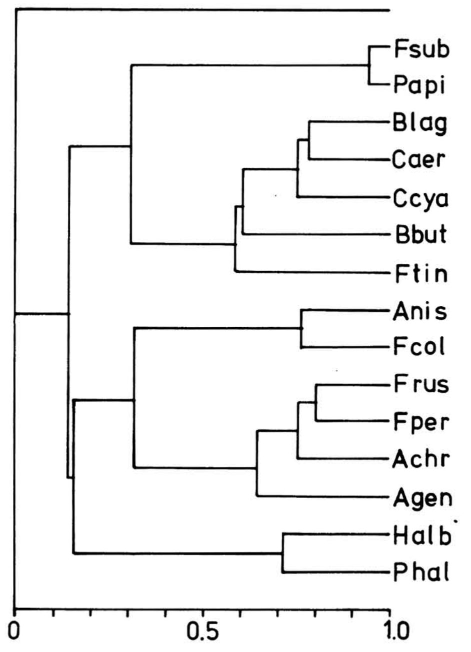

Fig. 2. Food overlap in the Finnish community of diurnal birds of prey during breeding. The diets of the predators were compared in pairs and food overlaps were calculated according to the formula presented by Macnaughton & Wolf (1973). The dendrogram was constructed according to Cody (1974). For species abbreviations see Table 10.

3.5. Food niche of the kestrel among Finnish diurnal birds of prey

There is a total of 15 regularly breeding species (with a pair number of more than ten over the whole country, Hyytiä et al. 1983) of diurnal birds of prey in Finland. The diets of all these species have been studied during the breeding season in northern Europe (then hen harrier in Norway, Hagen 1952 and the hobby *Falco subbuteo* in Sweden, Curry-Lindahl 1945; the other species in Finland, Table 10 and Fig. 2).

The food niches of the Finnish diurnal birds of prey were divided into five groups: those eating mainly small mammals (five species), small passerine birds (two species), non-passerine birds (four species), fishes (two species), and invertebrates (two species). The first guild consisted of the rough-legged buzzard *Buteo lagopus*, the buzzard *B. buteo*, the kestrel, the hen harrier and the marsh harrier *Circus aeruginosus*. Overlapping of the food niches was narrowest within this group, mainly due to the different alternative prey groups (i.e. birds for *Circus* spp. and the rough-legged buzzard, lizards and frogs for the buzzard, and invertebrates for the kestrel). The proportion of small mammals was highest in the diet of the kestrel, followed by the hen harrier, the rough-legged buzzard, the buzzard and the marsh harrier. The material from the food of the rough-legged buzzard was collected in Forest Lapland, where the number of birds may be exceptionally high. In "subarctic" areas of Finland the proportion of small mammals is greater (e.g. 98.8% at Kilpisjärvi, Lagerström et al. 1982). Hence, one can assume that the species is the greatest small rodent specialist among Finnish diurnal birds of prey.

The merlin *Falco columbarius* and the sparrowhawk belonged to the mainly small passerine bird catching group and their food niches overlapped to quite a large degree. The niche breadth of the sparrowhawk was, however, markedly larger than that of the former species. This was due to its predation on small mammals. The guild of the mainly medium-sized and large non-passerine bird eating raptors consisted of the gyr falcon *Falco rusticolus*, the peregrine *F. peregrinus*, the golden eagle *Aquila chrysaetos* and the goshawk *Accipiter gentilis*. The food niches of *Falco* species overlapped in the highest degree within this group, but the bird species eaten in the main are different, the main groups for the gyr falcon being *Lagopus* spp. (71.5% of the diet, Mikkola & S. Sulkava 1972) and for the peregrine waders *Charadrii*, ducks *Anatidae* and gulls *Larus* spp. (79–93% of the diet, Huhtala & S. Sulkava 1977a). The goshawk was a markedly more catholic predator than the former species. The food niche of the golden eagle differed from the other birds of this guild in the sense that prey animals were mostly heavier (S. Sulkava 1959, 1967).

The white-tailed eagle *Haliaetus albicilla* and the osprey *Pandion haliaetus* belonged to the cluster of mainly fish-eating raptors. The former species also took mammals and birds, but the latter preyed almost entirely on fishes, although it may occasionally take some water voles and frogs (Saurola 1984). The hobby and the honey buzzard *Pernis apivorus* were the only invertebrate (principally insect) eating predators and overlapped to the greatest extent in the classes used for the present material. The insect species chosen are quite different, since the former mainly preyed on dragonflies (Odonata, Curry-Lindahl 1945) and the latter wasps (Vespidae, Itämies & Mikkola 1972). A clear distinction also exists in the alternative prey: small birds for the hobby and frogs for the honey buzzard. Small birds may also form the main prey group in the diet of the hobby, at least in Central Europe (Fiuczynski 1979, Fiuczynski & Nethersole-Thompson 1980). The food overlap between the kestrel and the mainly invertebrate eating guild was greater than between the kestrel and the mainly bird catching group.

4. Discussion

4.1. Choice of mammals and birds

The kestrel always takes its prey from the ground and it locates small mammals by sight (e.g. Uttendörfer 1952). The high vegetation provides a shelter against hunting hawks (Wolff 1962). Hence, the kestrel mainly hunts in cultivated fields with low grass (Korpimäki 1978), where in the study area the common vole is the most abundant small rodent. The field vole favours high vegetation and abandoned fields while the bank vole most often occupies only the edges of cultivated areas (Korpimäki 1985a). Consequently, the catchability of common voles was highest among the voles of the study area. This species also exhibits considerable changes in availability in the course of the day, associated with its need for above-ground feeding about every two hours (Daan & Slopsema 1978). Such behaviour increases the vulnerability of common voles to hunting kestrels.

The kestrel caught small mammals more diversely than snap traps did, and it obviously utilised all available small mammal resources. One central hypothesis of optimal foraging theory predicted that the food niche of the predator should expand as the abundance of the most preferred prey decreases (Schoener 1971, Ellis et al. 1976, Pyke et al. 1977). The present results were partly in agreement with this hypothesis, but when common voles were very scarce the food niche also shrank.

The models of optimal foraging theory presented by Pulliam (1974), Charnov (1976) and Pyke et al. (1977) predict that the relative abundances of the non-preferred prey types are unimportant for the optimal diet: only the absolute abundance of the preferred prey is important. On the other hand, models by Emlen (1966), Rapport (1971), Estabrook & Dunham (1976), and Stenseth & Hansson (1979) predict that the relative abundances of non-preferred prey types can also have an effect on the optimal diet when these prey items became relatively very abundant. The observed negative correlation between *CSR* values and the relative densities of common voles, and the absence of correlations in other small mammal species, were in agreement with the prediction of the former model but contrary to the latter one.

Optimal foraging theory assumed that a predator should maximise the positive difference between foraging gains and costs (Pianka 1974). One important feeding decision concerned which prey types or species to hunt (MacArthur 1972). For the kestrels in the study area the choice is mainly between the medium-sized mammals (water vole and brown rat), voles and shrews. The energy costs for catching and handling those prey animals are probably rather similar and the search time is largely related to the density and behaviour of the different species. As the catchability of common vole is very high one would expect a preference for them. The energy content of a water vole, however, is higher than that of other small rodents and its "above-ground" activity (Gaisler & Zejda 1973) increases in summer. These factors may cause the highest choice value of water voles among the alternative prey types. The energy content of the light shrews is very small, but they should be quite easy to catch, since shrews move and eat almost continuously (e.g. Stroganov 1957). The ground surface activity of the lesser shrew is more intensive than that of the common shrew (Holisova 1969) and this behaviour may result in its being preferred among shrews. The energy contents of bank and field voles are almost similar to that of the common vole, but these species are quite difficult to catch due to the nature of the habitat. The same reason may cause the non-preferability of the brown rat, which lives mainly in inhabited areas.

The preference order of the different mammalian species showed that the prey types providing the greatest net energy yield were preferred. This indicated that the predator adopted the energy maximisation strategy in diet selection (Ellis et al. 1976) during breeding. This tactic hypothesises that fitness is maximised when the net energy intake for a given feeding time is maximised (Schoener 1971), and this increases the reproductive output of the kestrel. Thus, selection should be founded primarily upon the energy content of various food types and the energy expenditure involved in their capture (Emlen 1973).

In time minimisation strategy the maximum fitness is associated with minimising the amount of time spent in satisfying daily energy demands (Schoener 1971). This might be expressed in species in which minimisation of foraging period leaves time for other activities such as predator avoidance, territory defense or mate selection (e.g. some lizards, Schoener 1971). This strategy does not seem to be valid in the kestrel during the nestling period since predator avoidance is not an important activity owing to the bird's rapid flight and safe nesting places (Korpimäki 1984). Falcons also tend to be mainly non-territorial, defending only a small area around their nest sites (Cave 1968, Village 1983a).

The third strategy, optimising nutritional balance, suggests that animals should select those food types which most readily satisfy both energy and nutrient demands (Emlen 1973, Curio 1983). The present results are contrary to this hypothesis since the nutritional value of different prey animals to carnivores are quite similar (Ellis et al. 1976). In general, predators mainly adopt the strategy of energy maximisation and herbivores that of optimising nutritional balance, whereas omnivores are principally time minimisers (Ellis et al. 1976).

It has been suggested that for prey of varying sizes any preference order should generally correspond to the order of size (Schoener 1971, Werner 1974, Pyke et al. 1977). Field data from the present study are in agreement with this suggestion, i.e. regarding the weight classes of the mammalian and avian prey. On the other hand, these results are contrary to the previous suggestion in consideration of different small mammal species. However, factors other than size are also important in prey choice and the preference can vary for many reasons (e.g. density, behaviour, habitat and distaste of prey types), as was discussed above.

The most abundant bird species in the diet were tree-nesting forest birds (i.e. redwing *Turdus musicus*, fieldfare *T. pilaris*, *Phylloscopus* spp. and chaffinch *Fringilla coelebs*, Korpimäki 1985a). Although, for example, *Turdus* spp. also forage in the fields, the kestrel might catch birds in the forests, too, when *Microtus* voles living in the fields are scarce. Hence, the hawk apparently hunted opportunistically in selected patches in order to optimise the utilisation of the available food resources (see also Royama 1970). Prey preference may also be based upon the development of a specific searching image, which arises when the predator learns to utilise a particular prey and/or habitat (e.g. Tinbergen 1960, Croze 1970). This response has earlier been recorded as an important factor in the prey selection of the American kestrel *Falco sparverius* (Mueller 1971, 1974). On the other hand, open terrain birds of the study area (the most common species being the sky lark *Alauda arvensis*, whinchat *Saxicola rubetra*, reed bunting *Emberiza schoeniclus* and lapwing *Vanellus vanellus*, Korpimäki & Hast 1979, Korpimäki unpubl.) are quite difficult to catch owing to their protective colouring and behaviour. As Kellomäki (1977) and Korpimäki (1981) also discovered a bias toward tree-nesting forest birds in the diets of the pygmy owl *Glaucidium passerinum* and Tengmalm's owl, one may hypothesise that in general avian predators mainly prefer tree-nesting birds for food, while ground-nesting birds most easily fall prey to mammalian predators. This may reduce competition between the different predator groups.

4.2. Choice between sexes and age classes

The catchability of small mammals also differs according to age, sex, and season (Smith et al. 1975). The main reason for male predominance among mammalian and avian prey of the kestrel and among those trapped in spring was the greater activity of males. For example, common shrew males are more active during the breeding season than females (Pucek 1959), the total activity of bank vole males in summer is greater than that of females (Pearson 1962), and the home range of mature common vole males is about four times larger than that of the females (Reichstein 1960). The activity of male birds in the breeding season is likewise greater than that of the females due to the defense of the territory and song behaviour. The same reasons have already been put forward by Southern & Lowe (1968) for male predominance among bank voles and yellow-necked field mice *Apodemus flavicollis* in the diet of the tawny owl *Strix aluco*, by Lagerström & Häkkinen (1978) for that of bank voles and *Microtus* spp. in the food of the tawny owl, and by Korpimäki (1981) for that of several small mammal species in the diet of Tengmalm's owl.

Mammalian predators perhaps prey more on small mammal females, since the limited activity of the latter evidently protects them against avian predators but not so effectively against mammalian predators. For example, the weasel in Alaska ate mainly female lemmings *Lemmus trimucronatus* from their winter nests (MacLean et al. 1974). The ecological significance of this food niche separation may be found in the reduced competition for small mammal prey between the different predator groups.

Korpimäki (1981) showed that the male predominance of small mammals in the diet of Tengmalm's owl decreased during breeding. The same tendency is described in the foraging of the pomarine skua *Stercorarius pomarinus*, which preys on brown lemmings in Alaska (Maher 1970). The sex ratio in the diet can become balanced due to selective avian predation, which reduces male small mammals in the field. This idea is also supported by the fact that males of *Microtus townsendii* in populations which are protected from avian predation have higher survival rates, higher immigration rates, and maintain higher densities than in unprotected populations (Taitt & Krebs 1983). Other reasons can, however, exist for the more balanced sex ratio in the diet, e.g. changes in the activity of the sexes and in the vegetation cover.

The number of young birds in the field increased as the breeding of the kestrel proceeded. This caused an increase of nestlings and fledglings in the food. The same response was documented earlier respecting bird predation by the goshawk (S. Sulkava 1964), sparrowhawk (P. Sulkava 1972), pygmy owl (Sonerud et al. 1972, Mikkola & Jussila 1974 and Kellomäki 1977) and Tengmalm's owl (Korpimäki 1981). As young individuals of large birds and water voles appeared in the field towards the end of the kestrel's breeding period, the number of available prey species again increased just when the energy requirements of the nestlings were at their highest. This coincidence may increase the reproductive output of the predator.

4.3. Prey choice and interspecific competition of the raptor community in Alajoki

Emlen (1973) predicted that food specialisation should be more common among small animals than large ones. The present results are contrary to this prediction, since the largest birds of prey (short-eared (315 g) and long-eared (276 g) owls) in Alajoki were food specialists, while the two smallest species (kestrel (200 g) and Tengmalm's owl (136 g)) were generalists. In earlier investigations too the short-eared owl was shown to be a vole specialist (e.g. Mikkola & S. Sulkava 1969), but the long-eared owl could be a more catholic predator (see Tinbergen 1933, P. Sulkava 1965, Nilsson 1981). The results of the present study are in agreement with the earlier conclusion that the kestrel (Cavé 1968, Korpimäki 1985a) and Tengmalm's owl (Korpimäki 1981) are food generalists.

A feeding specialist should take fewer prey categories than a generalist (e.g Pyke et al. 1977). This suggestion was also valid in this study, since the numbers of prey species in the diets of the kestrel and Tengmalm's owl were higher, while they were lower in the food of *Asio* spp.

The sharp difference in the size of birds of prey in the study area indicated that they ought to differ by feeding on different-sized prey (e.g. Storer 1966, Schoener 1968), the short-eared owl taking the largest prey and Tengmalm's owl the smallest one. However, the present results were the opposite of this prediction, since there were no significant differences in average prey weights between species. When the observed mean prey weights were compared with the expected ones by using the regression slope presented by Schoener (1968) for predatory birds, one could conclude that all species in Alajoki used obviously smaller prey than predicted. This might indicate that the regression line (i.e. intercept) is too high for raptorial species, as Hespenheide (1971) also concluded concerning owls, or that the regression slope should be less steep for birds of prey. On the other hand, this study only concerned the peak year for *Microtus* voles. This "superabundant" food (see Lack 1946) might result in the relatively high specialisation of all raptors towards voles. Consequently, the mean prey weights of all predatory birds were almost the same. When voles are scarce and alternative prey are mainly used, the weights and also the food niches may differ more sharply.

The food niches of birds of prey in Alajoki overlapped in relatively high degrees. This should indicate that there is quite keen competition for food in the breeding season, when the abundance of voles is lower than at other times of the year. The possible forms of this competition are the following: exploitation and interference competition (e.g. Hanski & Järvinen 1977), as well as resource depression (Charnov et al. 1976). The small mammal populations in Alajoki are exposed to relatively high predation by several mammalian and avian predators (see "Introduction"). Therefore, it seems probable that in most breeding seasons kestrels suffer from a shortage of food due to keen diffuse competition (MacArthur 1972). The strong exploitation competition and "food depression" caused by numerous predators could then result in the falcons needing to prey on many different prey groups in addition to voles. This supports the idea presented by Pulliam (1974) that interspecific competition will tend to cause greater generalisation in the diet. On the other hand, the effect of interference competition on the prey choice of the kestrel might be quite limited, since there are only a few records of "combats" taking place between different birds of prey in the study area (Korpimäki 1985b).

4.4. Food niche of the kestrel among Finnish diurnal birds of prey

The kestrel belongs to the mainly small mammal eating guild among diurnal birds of prey. Its food niche overlapped to the greatest extent the diet of the hen harrier and that of both *Buteo* species. There is, however, quite obvious niche separation between the previous species in terms of habitat or range. The hen harrier lives principally in marshlands and other wet habitats, although it, too, may breed near fields (e.g. Korpimäki 1983). The buzzard most frequently occupies dry habitats on small or medium-sized open areas (e.g. Sylvén 1978). The kestrel mainly breeds in dry habitats with large open areas (e.g. in field plains, Kuusela 1983). The rough-legged buzzard is a northern species and its range overlaps only to a rather small extent that of the kestrel. As a consequence, one may conclude that niche separation within this guild is relatively extreme. On the other hand, resource competition between small mammal eating owls (e.g. long-eared and Tengmalm's owls) and the kestrel appeared to be appreciably keener than within the above mentioned guild, as was noted in the previous section.

Most Finnish diurnal birds of prey principally consume mammals and birds (73 % of the regularly breeding species). In addition to these, only two fish- and two invertebrate-taking species are found among our raptors. There are no species of Finnish predatory birds specialised mainly in frogs, lizards or carrion. The cold-blooded frogs and lizards are available in the field only during the warm part of the year. Hence, these animal groups, like carrion, may be too scarce for birds of prey in Finland due to impoverished, cold environmental conditions. Thus, no species can specialise in these, although the buzzard and honey buzzard use frogs as their alternative prey and both the golden eagle (Huhtala & S. Sulkava 1977b, Tjernberg 1981) and white-tailed eagle (Fischer 1982) consume carrion especially in winter. There are no diurnal birds of prey in Finland catching primarily mammals living in forest habitats (Tiainen & Pietiäinen 1980), although the goshawk, buzzard, sparrowhawk and golden eagle often prey on these. There is probably strong resource competition from owls and smaller mammalian predators, since it appears that diurnal birds of prey are not as effective predators of night-active small mammals as these competitors.

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Appendix 1. The diet of the kestrel (as percentage proportions by numbers) in Alajoki in 1977-83 according to analysis of pellets and prey remains.

	1977	1978	1979	1980	1981	1982	1983	Total
Soricidae	6.1	7.6	12.2	15.0	21.2	20.6	5.1	11.8
Microtus sp.	58.3	39.4	32.8	13.4	6.0	45.4	14.3	35.7
Clethr. glareolus	10.2	8.6	18.3	4.7	3.8	9.2	4.1	9.0
Arvicola terrestris	0.9	0.3	–	0.8	1.6	3.4	4.4	1.8
Microtidae, total	69.4	48.3	51.1	18.9	11.4	58.0	22.8	46.5
Muridae	4.6	4.2	8.0	1.6	8.2	7.1	4.1	5.5
Mustela rixosa	–	0.3	–	–	–	–	–	0.1
Mammalia, total	80.1	60.3	71.4	35.4	40.8	85.8	32.0	63.8
Aves	4.4	3.4	9.2	14.2	13.6	5.5	20.7	8.7
Amphibia	–	–	0.8	–	1.1	0.2	0.7	0.3
Reptilia	0.5	0.5	–	0.8	–	0.2	1.7	0.5
Invertebrates	15.0	35.8	18.7	49.6	44.6	8.3	44.9	26.6
No. of prey animals	432	383	262	127	184	436	294	2118
Nests	22	11	11	5	7	9	7	72

Appendix 2. The results of small mammal trappings (ind. / 100 trap nights in spring and autumn catches) in Alajoki in 1977–83.

	1977	1978	1979	1980	1981	1982	1983	Total
Soricidae	2.60	1.51	1.79	2.00	1.25	2.77	1.12	1.86
Microtus sp.	5.78	3.17	0.78	0.17	0.75	1.58	0.13	1.77
Clethr. glareolus	0.65	1.19	2.57	1.83	1.94	3.97	1.38	1.93
Arvicola terrestris	–	–	–	–	0.20	0.05	–	0.04
Microtidae, total	6.43	4.37	3.35	2.00	2.89	5.60	1.51	3.74
Muridae	–	–	–	–	0.25	–	0.14	0.06
Total	9.03	5.87	5.14	4.00	4.28	8.37	2.70	5.63
Trap nights	1384	1260	1672	1200	2008	1840	1520	10884

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Erratum: On p. 93, left column, 15th line, for $r = <0.771$ read $r = -0.771$.