Ornis Fennica 74:1–14. 1997

Effect of Sparrowhawk *Accipiter nisus* predation on forest birds in southern Finland

Tapio Solonen

Solonen, T., Luontotutkimus Solonen, Neitsytsaarentie 7 b B, FIN-00960 Helsinki, Finland

Received 21 May 1996, accepted 23 September 1996

Predation patterns of the Sparrowhawk *Accipiter nisus* and the vulnerability of the prey species were studied at territorial and local population levels, on the basis of four data sets of breeding bird censuses and prey remnant samples collected near nests. The magnitude of predation pressure on breeding populations of prey species was estimated. During the breeding season, of the various avian prey individuals (n = 1 674; 62 species), 17.2% were derived from habitats other than forest. The most important prey species by number included *Fringilla coelebs* (17.1%), *Parus major* (10.7%), *Phylloscopus trochilus* (7.8%), *Passer domesticus* (7.2%), *Erithacus rubecula* (6.9%), *Anthus trivialis* (5.4%), and *Turdus philomelos* (5.4%). The prey samples mainly included species and individuals weighing 15–30 g. The mean weight of prey was 26.6 g (n = 1 666). The most important prey species by weight were *F. coelebs* (13.4%), *T. philomelos* (13.4%), *P. domesticus* (8.2%), *P. major* (7.3%), and *T. pilaris* (6.6%). Fifteen species were significantly less vulnerable to Sparrowhawk predation than expected on the basis of their numbers in the environment, in one or more of the data sets studied, while seven species were, in general, more vulnerable than expected. Low vulnerability values were showed especially by *Ph. trochilus*, *Regulus regulus*, *Sylvia borin*, *T. merula*, *Ph. sibilatrix*, and *S. communis*. Especially vulnerable species seemed to be *P. caeruleus*, *P. major*, *F. hypoleuca*, *Carduelis chloris* and *T. philomelos*. Predation on adult birds during the three months of the breeding season was about 5–6%.

1. Introduction

Predation is believed, by some researchers, to be one of the principal forces modifying populations and communities (MacArthur 1972, Connell 1975, Murdoch & Oaten 1975, Glasser 1979, Sih et al. 1985, Diamond & Case 1986, Wiens 1989, Newton 1993). It is said to increase diversity in prey communities by keeping population levels low and thus allowing space for more species through reduced competition. This idea is, however, realistic only if predation is selective, especially on the most abundant species.

Bird populations are affected by predation in two different ways. Firstly, in the breeding season, plundering of eggs, nestlings and fledglings still dependent on their parents may lower the production of young, though compensating repeat clutches are usual in most species (e.g., Perrins & Geer 1980, Hanski & Laurila 1993). Secondly, predation contributes to the mortality of independent, full-grown birds throughout the year (e.g., Newton 1986). In Finland, *Accipiter* hawks (P. Sulkava 1964, S. Sulkava 1964, Lindén & Wikman 1983) and the Pygmy Owl *Glaucidium passerinum* (Kellomäki 1977, Suhonen 1993) are the most important predators upon adult birds and fledged young, whereas nests are vulnerable to a greater range of vertebrate predators (e.g., Solonen 1979, Tiainen 1983, Angelstam 1986).

The Sparrowhawk *A. nisus* is the main predator on small and medium-sized passerines throughout its range (Newton 1986). Almost all bird species of appropriate size, which have occurred in study areas, seem at some time to be taken. Despite the wide range of prey taken, relatively few species have emerged as important for the predator (Tinbergen 1946, P. Sulkava 1964, Opdam 1978, Perrins & Geer 1980, Newton 1986, Frimer 1989, Selås 1993). It has been concluded that Sparrowhawks do not seem to take their various prey species in proportion to the numbers of these prey in the environment. The extent of predation seems to vary greatly from place to place. Vulnerability of any one species depends not only on its own characteristics and numbers, but also on the number of other prey in the same area, and this will vary from one locality to another (Newton 1986). The majority of birds of appropriate size as prey for the Sparrowhawk (weighing usually less than 200 g) in Finland live in forests (Solonen 1994a). Some species may, however, be concentrated in considerable numbers in other habitats.

This paper is an attempt to estimate the effect of Sparrowhawk predation on southern Finnish birds by a combination of approaches, at the territorial and the local population levels. The results concerning single Sparrowhawk pairs are expected to be more accurate but less general than those concerning local hawk populations. The main question is whether predation by Sparrowhawks can be considered to have any marked consequences for the structure of forest bird communities. In more detail, I consider the following questions:

1 Is it probable that the predation upon full-grown birds causes changes in the composition of forest bird communities?
2 How drastic is the quantitative effect of predation on adult birds of each species during the breeding season?

2. Material and methods

Study areas where the bird communities were monitored were situated in southern Finland (Solonen 1996), mainly in Uusimaa (about 60°N, 25°E), but older data from Suomenselkä (62°N, 22°E) (P. Sulkava 1964, 1972) were also included (Table 1). Diet composition of the Sparrowhawk was estimated on the basis of prey remains (pluckings) found near nests (see Newton 1986). The samples used were collected from eight territories in Suomenselkä in 1960–1961 (P. Sulkava 1964, 1972) and from 22 territories in Uusimaa in 1989–1990 (this study), giving a total of 1 674 individual bird remains (Appendix). In addition, the total sample from Uusimaa included 11 (1.2%) voles. Mean body weights of prey species were taken from a recent compilation (Solonen 1994a). Food niche breadth (B; Ludwig & Reynolds 1988), indicating the width of the food spectrum available, was calculated for each data set from the formula:

$$B_i = \frac{1}{\sum_j^r (p_{ij}^2)} \qquad (1)$$

where p means the proportion of prey species (resource classes, r) used by Sparrowhawks in each

Table 1. Area size in the regions where bird populations were monitored (see Solonen 1996), census methods (see Koskimies & Väisänen 1991), the number of individuals of avian prey in the samples studied, and the respective study years. The data of Ilmajoki are based on Sulkava (1972).

Study areas	Kauniainen	Uusimaa Helsinki	Sipoo–Vantaa	Suomenselkä Ilmajoki
Size of the study area (km^2)	0.86	0.84	96.0	0.93
Census method	Mapping	Mapping	Line transect	Main belt
Census years	1989–1990	1990	1987–1991	1960–1961
Avian prey individuals (n)	268	174	460	772
Sampling years	1989–1990	1989–1990	1989–1990	1960–1961

area (data set), subscripts i and j represent the ith area and the jth resource species. The basic difference between the two prey data sets used, besides the fact that they represent different periods of time, was that they were from different forest environments. The data of Suomenselkä came from a barren remote area, while those of Uusimaa came from a relatively rich environment near dense human habitation.

The effect of predation of single breeding Sparrowhawk pairs, as well as local breeding populations on their prey populations were considered. In assessing the size of prey populations during the breeding season, mapping and line transect censuses were used (Table 1; for details of the census methods, see Koskimies & Väisänen 1991). The census areas were intended as representative samples of forests of the total foraging areas of the hawks considered. The densities of prey caught by Sparrowhawks during the breeding season were calculated from the proportion of prey in remnant samples, as well as the estimates of the size of the foraging area and total prey need of the predator. The average density of breeding Sparrowhawk populations of Uusimaa was estimated at about 0.2 pairs/km^2 forest (Solonen 1993, 1996), while a lower value of 0.1 pairs/km^2 was used for Suomenselkä (cf. P. Sulkava 1972). These values correspond, then, to potential non-overlapping foraging areas of 5 and 10 km^2, respectively. As an approximate average estimate of prey requirements of an individual male and female Sparrowhawk, I used two and three prey individuals (averaging 30 g) per day, respectively, and during the feeding period a brood was considered to need as much prey as their parents together (see Newton 1978, 1986).

The general similarity of total abundance distributions of available prey and eaten prey was tested with correlation coefficients (log-transformed data). The vulnerability (V; also known as catch per supply ratio of Opdam 1978) of breeding forest bird species to Sparrowhawk predation was estimated by comparing the proportion of each species in the hawk's diet by number with their proportion in the total prey community (Tinbergen 1946). Indices higher than 1 indicate that prey were taken more than expected on the basis of abundance, and indices lower than 1 indicate that prey were taken less often than expected on the basis of their abundance. The significance of differences between proportions was tested with the G-test adjusted by Williams' correction (Sokal & Rohlf 1981). The magnitude of the predation pressure (PP) on each prey species was estimated using the data on the abundance of the Sparrowhawk and its prey species, as well as food requirements (above) and observed or suggested predation patterns of the predator during three months of the breeding season (May, June, and July; 90 d).

3. Results

3.1. General predation patterns of Finnish Sparrowhawks during the breeding season

In total, 62 species of birds were found in the prey samples (Appendix). In analyses, data for *Phylloscopus collybita* and *Ph. trochilus* were combined. The percentage distributions of prey in the two regions studied followed a similar pattern ($r = 0.53$, $df = 59$, $P < 0.001$, arcsin-transformed data), though there were some pronounced differences between individual species (Appendix). Food niche breadth (B) was 12.2 for Uusimaa (rich habitats) and 9.4 for Suomenselkä (poor habitats). Of all avian prey individuals, 17.2% were derived from habitats other than forest. This proportion was 20.8% and 11.9% for Uusimaa and Suomenselkä, respectively.

The most important prey species by number ($\geq 5\%$) included *Fringilla coelebs* (17.1%), *Parus major* (10.7%), *Ph. trochilus* (7.8%, including some specimens of *Ph. collybita*), *Passer domesticus* (7.2%), *Erithacus rubecula* (6.9%), *Anthus trivialis* (5.4%), and *Turdus philomelos* (5.4%) (Appendix). Four to five species made up 50% of the diet. The prey data for Uusimaa were characteristically dominated by species that commonly inhabit urban and rural habitats, in addition to *F. coelebs* (12.2%), especially by secondary hole-nesters nesting in artificial nest-boxes and buildings: *P. major* (17.8%), *P. domesticus* (12.2%), *Ficedula hypoleuca* (8.2%), *Motacilla alba* (6.1%). The data for Suomenselkä characteristically included open-nesting forest birds: *F. coelebs* (22.7%), *Ph. trochilus/collybita* (13.1%), *A. trivialis* (9.8%), *E. rubecula* (9.3%), *Emberiza citrinella* (8.4%), *T. philomelos* (8.2%).

The prey samples mainly included species and individuals weighing 15–30 g (Table 2). Less than 10% of the prey individuals were heavier than 60 g (the weight of *T. iliacus*, see Appendix). In the total data set, the mean weight of prey (not including the heaviest species not preyed upon as adults, see Appendix) was 26.6 g (n = 1 666). The mean weights of prey for Uusimaa and Suomenselkä were similar (z-test), 26.5 g (n = 900) and 27.4 g (n = 766), respectively. The most important prey species by weight (total biomass more than 5% in Appendix) were *F. coelebs* (13.4%), *T. philomelos* (13.4%), *P. domesticus* (8.2%), *P. major* (7.3%), and *T. pilaris* (6.6%).

In the prey individuals sexed (Table 3), both sexes were equally represented (G-test). The proportion of juveniles in prey samples increased during the breeding season (Table 3). In May, the prey consisted mainly of adult birds ($G = 57.7$, $df = 1$, $P < 0.001$), in June, both age groups were equally represented, and in July, juveniles predominated ($G = 22.6$, $P < 0.001$).

3.2. Patterns of predation in relation to available prey

In different data sets, about 70–90% of the prey caught by the Sparrowhawk were forest species (Table 4, cf. Section 3.1). These proportions differed significantly both between different Sparrowhawk pairs ($G = 12.7$, $df = 1$, $P < 0.001$) and

Table 2. Size distribution of the avian prey of Finnish Sparrowhawks: the number of species and individuals in each size class.

Size class	< 15 g	15.1–30 g	30.1–60 g	60.1–120 g	> 120 g	Total
Species	16	27	6	8	5	62
Individuals	356	971	169	161	17	1674
%	21.3	58.0	10.1	9.6	1.0	100

Table 3. Seasonal pattern of predation by Sparrowhawks during the breeding season: numbers and proportions of individuals in each sex and age class (adults and juveniles) identified in the prey samples of Uusimaa.

Period	Males		Females		Total	Adults		Juveniles		Total
	n	%	n	%	n	n	%	n	%	n
May	8	42.1	11	57.9	19	74	89.2	9	10.8	83
June	34	50.0	34	50.0	68	146	50.3	144	49.7	290
July	51	45.1	62	54.9	113	193	39.3	298	60.7	491
Total	93	46.5	107	53.5	200	413	47.8	451	52.2	864

Table 4. Predation by breeding Sparrowhawk pairs and populations on forest birds in southern Finland: proportion of prey individuals taken from forest habitats, density of the available prey community in forests (species weighing less than 200 g as adults), adult prey caught per km^2 forest during the breeding season (three months), and the average predation pressure on adult birds, estimated on the basis of various data sets available. The average density of breeding Sparrowhawks in forests of Uusimaa (first three data sets) has been estimated to be about 0.2 pairs/km^2 (Solonen 1993, 1996), in Ilmajoki 0.1 pairs/km^2 (Sulkava 1972), and the prey requirements of a breeding pair on average as 750 individuals (based on Newton 1978, 1986) (for the proportion of adults in prey, see Table 3).

	Single breeding pairs		Breeding populations	
	Kauniainen	Helsinki	Sipoo–Vantaa	Ilmajoki
Prey taken from forests (%)	69.8	81.6	79.4	88.1
Available prey (pairs/km^2)	518	470	458	340
Adult prey taken (pairs/km^2)	24	28	28	15
Predation pressure on adults (%)	4.7	6.0	6.1	4.5

between the two hawk populations (G = 28.2, $P < 0.001$) studied. For forest birds, the general estimates of the predation pressure on adults during the three months of the breeding season were consistently about 5–6%.

Out of the total 62 prey species, in 24 the vulnerability indices differed significantly from 1 in one or more of the data sets (Tables 5 and 6). In 15 species the values were consistently lower than 1, while in seven species they were, in general, higher than 1. In two species (*M. striata*, *P. cristatus*) the results were inconsistent. Vulnerability values were low especially in *Ph. trochilus*, *Regulus regulus*, *Sylvia borin*, *T. merula*, *Ph. sibilatrix*, and *S. communis*. In two data sets, *F. coelebs*, one of the most important prey species of the Sparrowhawk (Section 3.1.), was taken significantly less often as prey than expected on the basis of its abundance. Especially vulnerable species for Sparrowhawk predation seemed to be *P. caeruleus*, *P. major*, *F. hypoleuca*, *Carduelis chloris* and *T. philomelos*. In general, all these species were taken

Table 5. The effect of predation of single breeding Sparrowhawk pairs on forest birds in two areas in Uusimaa, southern Finland: densities of available prey (D_1) and prey caught (D_2) in pairs/km² (rounded figures), as well as vulnerability ($V = D_2\%/D_1\%$) and predation pressure on adults ($PP = D_2/D_1$) of the available prey species during the breeding season. Vulnerability values significantly higher or lower than 1 (G-test) are marked with asterisks as follows: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Species	Kauniainen 1990				Helsinki 1990			
	D_1	D_2	V	PP%	D_1	D_2	V	PP%
Dendrocopos major	5.8	0	0.00*	0.0	3.6	0	0.00	0.0
Anthus trivialis	7.0	0.1	0.38	1.7	16.7	1.2	1.19	7.2
Prunella modularis	8.1	0	0.00	0.0	9.5	0.6	1.10	6.5
Erithacus rubecula	22.0	1.0	1.00	4.6	22.7	1.6	1.21	7.1
Phoenicurus phoenicurus	7.0	0.3	0.85	3.9	–	–	–	–
Turdus merula	39.4	0.3	0.14***	0.7	21.5	0.2	0.15**	0.9
Turdus pilaris	35.9	1.0	0.61	2.8	19.1	0	0.00***	–
Turdus philomelos	5.8	0.3	1.00	4.7	17.9	0.8	0.76	4.5
Turdus iliacus	18.5	0.1	0.14**	0.6	9.5	0.8	1.45	8.5
Locustella fluviatilis	–	–	–	–	1.2	0	0.00	0.0
Acrocephalus palustris	–	–	–	–	6.0	0	0.00	0.0
Hippolais icterina	3.5	0	0.00	0.0	7.2	0.2	0.47	2.8
Sylvia curruca	4.6	0.1	0.56	2.6	4.8	0.4	1.40	8.1
Sylvia communis	2.3	0	0.00	0.0	11.9	0	0.00**	0.0
Sylvia borin	10.4	0.1	0.25	1.2	15.5	0.2	0.21*	1.3
Sylvia atricapilla	4.6	0	0.00	0.0	9.5	0.4	0.70	4.1
Phylloscopus sibilatrix	17.4	0.1	0.15**	0.7	13.1	0.2	0.25	1.5
Phylloscopus trochilus	92.7	1.3	0.30***	1.4	57.3	0.8	0.24***	1.4
Regulus regulus	18.5	0	0.00***	0.0	16.7	0.6	0.61	3.7
Muscicapa striata	3.5	0.3	1.57	7.8	6.0	1.0	2.77*	16.8
Ficedula hypoleuca	52.1	4.4	1.80**	8.4	8.4	2.0	4.00***	24.0
Parus montanus	2.3	0.4	4.00	16.8	7.2	0.8	1.93	11.3
Parus cristatus	5.8	0.1	0.45	2.1	3.6	0	0.00	0.0
Parus ater	3.5	0.3	1.57	7.8	4.8	0.4	1.40	8.1
Parus caeruleus	5.8	2.7	10.10***	46.8	8.4	2.0	4.00***	24.0
Parus major	38.2	8.1	4.50***	21.3	13.1	5.2	6.68***	40.0
Lanius collurio	–	–	–	–	1.2	0.2	2.33	16.7
Garrulus glandarius	3.5	0.1	0.71	3.4	–	–	–	–
Fringilla coelebs	75.3	1.9	0.54**	2.6	116.9	6.2	0.90	5.3
Carduelis chloris	9.3	0.6	1.44	6.8	7.2	1.4	3.33**	19.4
Carduelis spinus	5.8	0.3	1.00	4.7	15.5	0	0.00**	–
Loxia curvirostra	4.6	0.1	0.56	2.6	3.6	0.2	0.88	5.6
Carpodacus erythrinus	–	–	–	–	8.4	0.4	0.78	4.6
Pyrrhula pyrrhula	1.2	–	–	–	1.2	0	0.00	0.0
Emberiza citrinella	2.3	0.3	2.75	11.6	1.2	0	0.00	0.0

much more frequently than expected on the basis of their abundance. The relationship between the density of available prey and the number of prey remains found for each species (Fig. 1) suggests largely similar results. However, there were also differences in species-specific vulnerability val-

Table 6. Sparrowhawk predation on forest birds in two regions, Uusimaa (Sipoo–Vantaa) and Suomenselkä (Ilmajoki), in southern Finland: densities of available prey (D_1) and prey caught (D_2), in pairs/km² (rounded figures), as well as vulnerability (V) and predation pressure on adults (PP) of the prey species during the breeding season (cf. Table 5). Vulnerability values significantly higher or lower than 1 (G-test) are marked with asterisks as follows: * = P < 0.05, ** = P < 0.01, *** = P < 0.001. Prey data of *Ph. collybita* and *Ph. trochilus* from Suomenselkä are combined. Species scarcer than 0.2 pairs/km² are omitted.

Species	Uusimaa				Suomenselkä			
	D_1	D_2	V	PP%	D_1	D_2	V	PP%
Cuculus canorus	0.3	0	0.00	0.0	0.9	0.0	0.33	2.2
Jynx torquilla	0.4	0	0.00	0.0	–	–	–	–
Dendrocopos major	3.1	0.2	1.14	6.5	0.9	0.0	0.33	2.2
Anthus trivialis	19.9	0.5	0.44*	2.5	33.5	1.7	1.15	5.1
Troglodytes troglodytes	0.7	0	0.00	0.0	–	–	–	–
Prunella modularis	10.8	0.3	0.46	2.8	–	–	–	–
Erithacus rubecula	24.1	1.9	1.32	7.9	7.4	1.6	4.86***	21.6
Luscinia luscinia	0.4	0.1	3.00	25.0	–	–	–	–
Phoenicurus phoenicurus	0.4	0.1	3.00	25.0	2.8	0.2	1.50	6.4
Turdus merula	17.3	1.1	1.05	6.4	–	–	–	–
Turdus pilaris	4.6	0.5	1.90	10.9	5.6	0.3	1.38	5.4
Turdus philomelos	11.0	1.6	2.46***	14.5	3.7	1.4	8.45***	37.8
Turdus iliacus	16.4	0.7	0.67	4.3	6.5	0.2	0.53	2.3
Turdus viscivorus	0.3	0.1	3.00	33.3	0.9	0.0	1.00	5.0
Acrocephalus palustris	0.3	0	0.00	0.0	–	–	–	–
Hippolais icterina	0.6	0	0.00	0.0	–	–	–	–
Sylvia curruca	3.0	0.3	1.57	10.0	2.8	0	0.00***	0.0
Sylvia communis	3.3	0	0.00*	0.0	–	–	–	–
Sylvia borin	11.9	0.2	0.31*	1.7	2.8	0	0.00***	0.0
Sylvia atricapilla	2.8	0.1	0.50	3.6	–	–	–	–
Phylloscopus trochiloides	0.6	0	0.00	0.0	–	–	–	–
Phylloscopus sibilatrix	18.9	0.1	0.07***	0.5	–	–	–	–
Phylloscopus collybita	3.4	0.2	1.14	5.9	13.0	x	x	x
Phylloscopus trochilus	53.2	0.9	0.28***	1.7	99.5	2.3	0.45***	2.0
Regulus regulus	18.5	0.4	0.33**	2.2	8.4	0	0.00***	0.0
Muscicapa striata	24.8	0.4	0.24***	1.6	3.7	0.3	1.64	7.3
Ficedula parva	0.4	0	0.00	0.0	–	–	–	–
Ficedula hypoleuca	8.8	2.4	4.53***	27.3	4.7	0.0	0.21**	1.0
Parus montanus	6.7	0.6	1.47	9.0	17.7	0.6	0.77	3.4
Parus cristatus	2.3	0.4	3.20*	17.4	3.7	0	0.00***	0.0
Parus ater	3.2	0.1	0.43	3.1	–	–	–	–
Parus caeruleus	1.9	1.0	9.50***	52.6	–	–	–	–
Parus major	22.5	5.2	3.90**	23.1	6.5	0.4	1.42	6.2
Certhia familiaris	1.6	0	0.00	0.0	0.9	0.0	0.33	2.2
Lanius collurio	2.2	0.1	0.60	4.3	0.9	0.0	1.00	5.0
Garrulus glandarius	3.3	0.1	0.71	3.0	0.9	0.1	1.33	6.7
Fringilla coelebs	120.1	4.9	0.68**	4.1	80.9	3.9	1.09	4.8
Carduelis chloris	0.7	0.6	11.00***	85.7	–	–	–	–
Carduelis spinus	13.5	0.6	0.76	4.4	3.7	0.2	1.09	4.9
Loxia curvirostra	5.4	0.3	0.92	5.6	0.9	0.0	1.00	5.0
Carpodacus erythrinus	2.5	0	0.00*	0.0	–	–	–	–
Pyrrhula pyrrhula	1.1	0	0.00	0.0	0.9	0.0	1.00	5.0
Emberiza citrinella	8.8	0.6	1.16	6.8	23.3	1.4	1.41*	6.0
Emberiza rustica	0.2	0	0.00	0.0	0.9	0.0	1.00	5.0

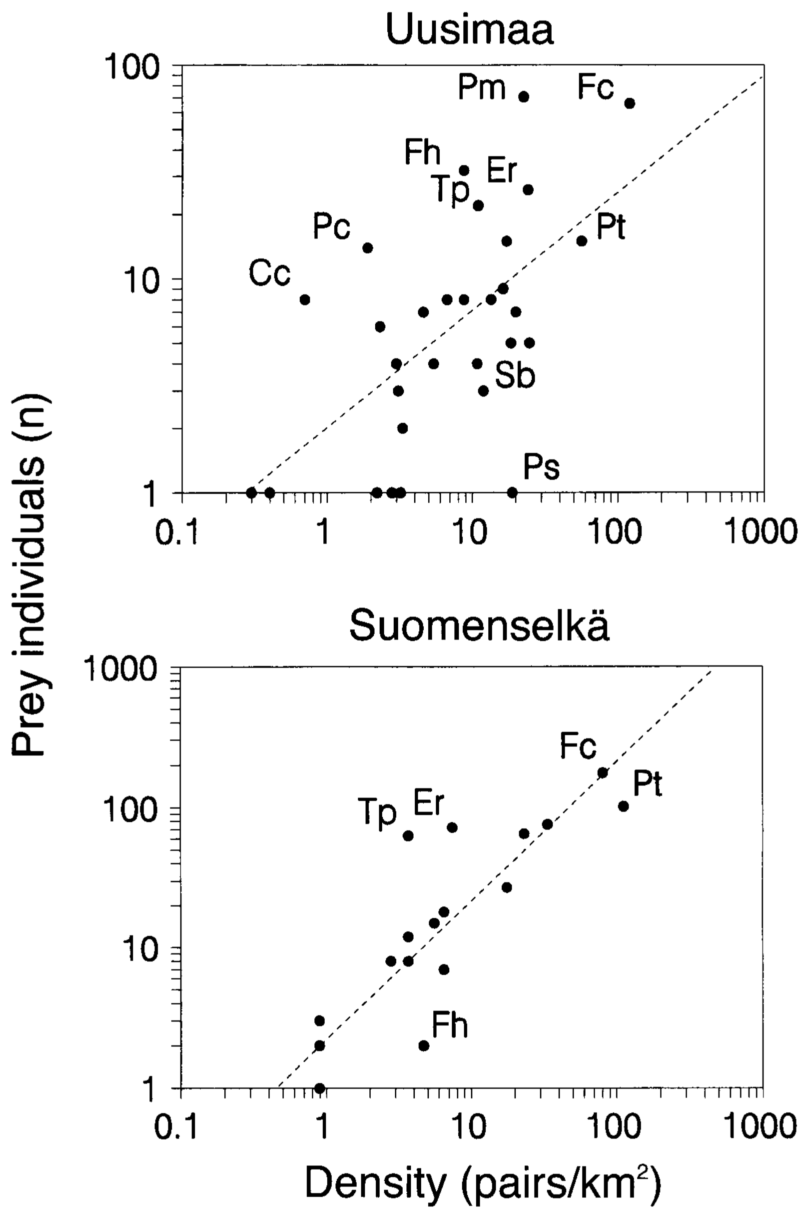

Fig. 1. The relationship between the density of available prey of the Sparrowhawk (pairs/km²) and the number of prey individuals found in remnant samples (n) in the data of Uusimaa and Suomenselkä ($r = 0.63$, $df = 29$, $P < 0.001$, and $r = 0.89$, $df = 21$, $P < 0.001$, respectively). Species coded as follows: Cc = *C. chloris*, Er = *E. rubecula*, Fc = *F. coelebs*, Fh = *F. hypoleuca*, Pc = *P. caeruleus*, Pm = *P. major*, Ps = *Ph. sibilatrix*, Pt = *Ph. trochilus (/collybita)*, Sb = *S. borin*, Tp = *T. philomelos*.

ues between the data sets, in particular between regions. In Uusimaa, forest birds of different size classes, small (weighing less than 15 g), medium-sized (15–30 g), and large (30–120 g), were represented in the prey of Sparrowhawks approximately in proportion of their abundance in the environment (V-values 0.96, 1.04, and 0.96, respectively).

In different data sets, the species-specific predation pressure values of adult birds (Tables 5 and 6) averaged between 5.6% and 9.4%. In total, the abundance of prey taken correlated significantly with the abundance of available prey in each data set ($P < 0.001$). Species composition in (adult) forest bird communities estimated before (density estimates of prey populations, D_1) and after ($D_1 - D_2$) the Sparrowhawk predation, during the three months of breeding, seemed to differ markedly only in the proportions of the few most vulnerable species in each data set (especially *E. rubecula*, *T. philomelos*, *F. hypoleuca*, *P. caeruleus*, *P. major*, and *C. chloris*; see Tables 5 and 6).

These species were, in general, intermediate in abundance. Summarizing, at a large scale, the effect of Sparrowhawk predation on total prey communities did not seem very drastic, neither qualitatively nor quantitatively. Locally, however, the predation pressure on some species may be quite heavy.

4. Discussion

4.1. Predator density, prey availability, and predation rate

For reliable estimates of the effect of Sparrowhawk predation on bird communities, representative samples of the density and foraging area of the predator, as well as those of available prey, are needed, together with information on the diet of the predator. The accuracy and comparability of the density estimates are of utmost importance. The deviations of the results from the opportunistic predation pattern may more or less be due to inaccuracies in the data (biases in the estimates of numbers of prey and in prey remnant sampling), to scaling problems (estimates of available and consumed prey do not match reality or each other, i. e., the foraging area of the predator, adequately) and, especially in heterogeneous environments, to chance, and consequently to a temporally and spatially varying prey pool (chance largely determines the individuals of prey that really are taken by predators in a particular area).

In southern Finland, suitable (preferred) nesting habitats of the Sparrowhawk are generally not continuous even in forests, but occur as small plots distributed more or less unevenly among other habitats (Solonen 1993). Overlap in ranges of different Sparrowhawk pairs does not seem to be very great in Finland, where general breeding densities (habitats other than forest also included) are relatively low (6–10 pairs/100km^2; P. Sulkava 1964, Forsman & Solonen 1984, Solonen 1984, 1993, 1994b; see also Saurola 1985) as compared with the situation in some other areas (Newton 1979, 1986, Perrins & Geer 1980). In Britain, the availability of suitable woods, in conjunction with the spacing of territories, limited density over large areas, resulting in much lower densities than in continuous nesting habitats (at 14–96 pairs/100 km^2; Newton et al. 1977, see also Newton 1986). If pairs are evenly distributed, as it seems in general to be the case (Newton 1986, Solonen 1993), the potential free range for each pair (without overlap) in Finland would be at least 10 km^2. Locally, however, within a suitable habitat even Finnish densities of Sparrowhawks may be much higher (at least up to 26 pairs/100 km^2; Solonen 1993).

On the basis of the spacing of territories in suitable habitats (Solonen 1993), the home range size of Sparrowhawks in southern Finland was estimated at about 5 km^2. This corresponds well to the results of other studies. According to Marquiss and Newton (1981), the home range size of the Sparrowhawk can be estimated to be around 3–30 km^2, depending on the phase of the breeding season, habitat and local food availability. In rich habitats (prey density 1 500 pairs/km^2), the hunting range was 0.5–1.5 km^2, and in poor ones (prey density 600 pairs/km^2) 1.5–5.0 km^2. Birds hunted mainly within a radius of 1–2 km from the nest site. Most prey are killed relatively near to the nest site but, in poor habitats, hunting ranges can be much larger if prey are by chance not encountered nearer the nest. In general, home range sizes of birds of prey seem to depend largely on habitat and local food availability (Newton 1979).

The rate at which the male can provide food for the brood will depend partly on the abundance of prey within his hunting range (Snyder & Snyder 1973, Perrins & Geer 1980). Possibly the female only starts to hunt when the male can no longer adequately provide for his family (Newton 1978, Perrins & Geer 1980). The rate of predation on adult birds appears to vary both with the overall density of prey species and with their behaviour (Perrins & Geer 1980). Breeding Sparrowhawks, at least males, hunt at a more or less constant and probably nearly maximal effort, and kill rate is largely determined by the density of prey populations, as is also the hunting range (Newton 1978, 1986).

4.2. Vulnerability of species

Results on the vulnerability of different species could have two general interpretations. Firstly, the differences in vulnerability may be real and caused by differences in catchability due to structural or behavioural differences between species. Secondly, the results may be biased by methodological shortcomings (cf. Section 4.1.).

There were no differences in vulnerability between the three broad size categories of prey studied, but in some cases, some largest (large *Turdus* species, *Dendrocopos major*) and smallest (*R. regulus*, *Phylloscopus* spp.) species seemed to be less vulnerable to Sparrowhawk predation than expected on the basis of their abundance. According to Pertti Sulkava (1964, 1972), during the breeding season, Sparrowhawks prey on birds weighing 15–105 g in approximately the ratio in which they are present, but prey less on lighter and heavier species (see also Opdam 1978, Perrins & Geer 1980). In southern Norway, birds weighing 51–80 g have been suggested as the most vulnerable (Selås 1993).

Species that lead a skulking way of life (e.g., *Sylvia* spp., *Prunella modularis*), even though abundant in the field, were rare in the prey of the Sparrowhawk (cf. Selås 1993). Those species that seemed to be the most vulnerable ones were also relatively conspicuous in the field. It has been argued that the low energetic profitability of small *Phylloscopus* warblers is the reason for their rarity as prey of the Sparrowhawk, in spite of their great abundance (Tiainen 1983). I rather suggest that differences in the habitat use of prey species and the hunting behaviour of the predator were more likely decisive factors modifying the prey composition of the predator (see also Newton 1986). According to Tinbergen (1946), *Phylloscopus* warblers were preyed upon more frequently than expected on the basis of their numbers, probably because of the exposed singing posts of the males.

As pointed out in the previous paragraphs, the prey of the Sparrowhawk do not seem to represent a random sample from the local avifauna. This pattern seems to be common in many predators. It is due to various factors. Firstly, predator size determines prey size to a considerable extent (e.g., Opdam 1975, Andersson & Norberg 1981). Secondly, hunting technique is closely related to the vulnerability of potential prey species. When relatively vulnerable species are present, predators do not practice preying on less vulnerable ones — in spite of their abundance or availability (e.g., Lindén & Wikman 1983, Ekman 1986, Suhonen 1993).

Estimates of the abundance of available prey and those of prey taken by Sparrowhawks may, however, be variously biased due to differences in the conspicuousness of the prey species in the field or in remnant samples (cf. P. Sulkava 1964, Newton 1986). Too low density estimates of available prey cause high vulnerability values, while too high density estimates have an opposite effect. For instance, *T. philomelos* and *E. rubecula*, the numbers of which are probably often underestimated (e.g., Tomialoijć & Lontkowski 1989; but cf. also Sulkava 1995), especially in one visit censuses (such as line transect and point counts; e.g., Tiainen et al. 1980), showed high vulnerability values only on the basis of those prey data that were compared with density values based on the line transect method. The numbers of secondary hole-nesters may also be, at least to some extent, underestimated (cf., e.g., Morozov 1994). Sometimes, exceptionally high (but not significant) vulnerability and predation pressure values were obviously biased by small sample size (Tables 5 and 6).

Results may also be affected if samples of the available and consumed prey compared do not represent the same geographical areas. Important food sources of the Sparrowhawk may have been located outside the area monitored for the estimates of abundance of available prey. Thus, unevenly distributed forest bird species that, for one reason or another, concentrate in forest-like habitats near human settlements (parks, gardens, yards) and that are heavily exploited by hawks, may have been estimated to be more vulnerable than they really are (species using resources provided by man, e.g., secondary hole-nesters nesting in nestboxes). Such species (*P. major*, *P. caeruleus*, *F. hypoleuca*, *C. chloris*) were estimated to be especially vulnerable in the data sets of Uusimaa. There, Sparrowhawks commonly hunt in rural and urban habitats, as indicated by the abundance of *Passer domesticus*, a species clearly restricted to the neighbourhood of man, in their prey (Appendix). Thus, conspicuously uneven distribution among habitats of some forest bird species, and similar exploitation patterns of Sparrowhawks, may make the vulnerability estimates based on average densities of prey unreliable. This is more probable in the data sets of single pairs than in those of local populations. The density estimates of prey of single Sparrowhawk pairs are relatively accurate but of restricted geographical cover, while those of local populations are less accurate but they represent better various habitats of the hawks' foraging area. Local, heavily exploited food resources (such as concentrations of unevenly distributed species) may reduce predation pressure on some other, evenly distributed species. This might, in some cases, explain the low vulnerability values, for instance those of *F. coelebs* in Uusimaa.

The prey composition of the Sparrowhawk, determined from prey remains, corresponded rather well to the structure of the surrounding bird community, especially when only species of appropriate size were considered (cf., e.g., Newton 1986, Selås 1993). Trophic diversity depends closely on the diversity of the available food (e.g., P. Sulkava 1964, Kellomäki 1977). Bias in prey remains is well acknowledged (see, e.g., P. Sulkava 1964, 1972, Newton 1978, 1986), with larger-sized and brightly coloured species overrepresented and small and dull-coloured species underrepresented with respect to numbers in the environment. For example, observations have shown that more *Ph. trochilus* than *F. coelebs* were consumed by hawks, in contrast to the picture given by prey remains (P. Sulkava 1964, 1972).

4.3. Effects of predation

The results of this study suggest that the Sparrowhawk may consume considerable proportions of available prey species during the breeding period. In earlier studies, the Sparrowhawk has been estimated to reduce the number of breeding adult birds in its hunting area by 3–14%, and birds made up 90–97% of its food (Tinbergen 1946, Sulkava 1972, Opdam 1978, Perrins & Geer 1980, Newton 1986, Selås 1993). There seems, however, to be no clear evidence that Sparrowhawks, in spite of taking large numbers of birds, are having a serious effect on their overall numbers (Tinbergen 1946, Perrins & Geer 1980, Newton 1986). They might, however, be altering the pattern of adult survival and movements (cf. also Mönkkönen 1990), and immigration may play a more important role in maintaining the numbers of birds in areas where predation is heavy (Perrins & Geer 1980). The Goshawk predation on Hazel Grouse during the breeding season (12%) was considered to be a rather high figure, especially when predation was directed at the adults, which comprise the most productive part of the prey population (Lindén & Wikman 1983).

The species that seemed to be most heavily affected by Sparrowhawk predation in this study were mainly intermediate in abundance. Selective predation can affect diversity either by lowering the status of the most vulnerable species, especially sparse or restricted ones, thereby decreasing diversity, or by concentrating on dominant species, thus increasing the evenness of prey communities leading to an increase in diversity. If, however, predators exploit prey resources in proportion of their availability, which might be assumed to correspond roughly to their abundance, there would be no drastic change in diversity. Peregrines *Falco peregrinus* could not account for more than a small part of the mortality of their principal prey taken by breeding birds (see Ratcliffe 1980). Prey species might be significantly reduced or checked by predation if predators preyed preferentially on a species but without actually being dependent on that species as a staple item of diet; or in situations where they could move on to other species or other areas when they had exhausted the first one (Ratcliffe 1980, cf. also Lindén & Wikman 1983, Newton 1993).

For local breeding bird communities, in general, the effect of predation on the numbers of breeding adults is apparently slight in early spring (especially during the prelaying period) because migrants and surplus birds (floaters, immigrants) probably readily compensate the losses (Newton 1993). Later in the season, however, there may be a marked reduction in nesting success because of predation on both adults and juveniles (Perrins & Geer 1980). Cade (1960) suggested that removing most of a prey species from an area by predators was best regarded in terms of habitat marginality for the prey, rather than as regulation of prey numbers. Where the predators preyed only on a limited part of the total breeding distribution of prey, surplus individuals from other areas could move in to fill vacated territories. Locally heavy predation may keep the production of young low, but in the next breeding season prey populations may be "balanced" by immigration (e.g., Solonen

1979). Thus, the effects of predation on populations are probably seen in marginal habitats, rather than in those that are very attractive for the prey species and where the actual predation might be heavy (cf. also Solonen 1979, Newton 1986, Martin 1996). Predators often seem to live on the expendable surpluses of their prey populations, and do not themselves exert any serious limiting effect on the annual numbers of prey (see Cade 1960, Errington 1963, Ratcliffe 1980; but see also Korpimäki 1985, Newton 1986, Korpimäki & Norrdahl 1991). However, the spatial structure of bird communities may be modified by birds avoiding potential predation risk (Solonen 1993, Suhonen et al. 1994).

Acknowledgements I thank M. Mönkkönen, I. Newton, H. Pietiäinen and J. Suhonen for comments on the manuscript, J. Simula for help in the field work and R. A. Väisänen for access to the collections of the Finnish Museum of Natural History. The study was partly supported by the Finnish Cultural Foundation.

Selostus: **Varpushaukan saalistuksen vaikutus eteläsuomalaiseen metsälinnustoon**

Varpushaukan saalista ja eri lintulajien alttiutta joutua haukan saaliiksi tutkittiin pesien lähistöltä kerättyjen saalisnäytteiden ja saalistusalueella tehtyjen lintulaskentojen avulla neljän pesimäaikaisen aineiston perusteella. Saalistuksen voimakkuutta arvioitiin lintujen runsausarvioiden ja haukan saaliintarpeen pohjalta. Pesimäaikaan 17,2% saalislintuyksilöistä (n = 1 674; 62 lajia) oli peräisin muualta kuin metsäympäristöstä. Runsaimmin saaliissa oli peippoja (17,1%), talitiaisia (10,7%), pajulintuja (7,8%), varpusia (7,2%), punarintoja (6,9%), metsäkirvisiä (5,4%) ja laulurastaita (5,4%). Saalislinnut painoivat tavallisimmin 15–30 g keskipainon ollessa 26,6 g (n = 1 666). Painon perusteella tärkeimmät saalislajit olivat peippo (13,4%), laulurastas (13,4%), varpunen (8,2%), talitiainen (7,3%) ja räkättirastas (6,6%). Viidentoista lajin yksilöitä oli varpushaukan saaliissa merkitsevästi vähemmän ja seitsemän lajin yksilöitä merkitsevästi enemmän kuin niiden runsausarvioiden perusteella oli odotettavissa. Pajulintu, hippiäinen, lehtokerttu, mustarastas, sirittäjä ja pensaskerttu esiintyivät saaliissa harvemmin, sinitiainen, talitiainen, kirjosieppo, viherpeippo ja laulurastas taas useammin kuin niiden runsaus olisi edellyttänyt yhdessä tai useammassa tutkituista aineistoista. Aikuislintuihin kohdistuva saalistuspaine oli pesimäkauden kolmen kuukauden aikana noin 5–6%.

References

Andersson, M. & Norberg, R. Å. 1981: Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. — Biol. J. Linnean Soc. 15: 105–130.

Angelstam, P. 1986: Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. — Oikos 47: 365–373.

Cade, T. J. 1960: Ecology of the Peregrine and Gyrfalcon populations in Alaska. — Univ. Calif. Publ. Zool. 63: 151–290.

Connell, J. H. 1975: Some mechanisms producing structure in natural communities: a model and evidence from field experiments. — In: Cody, M. L. & Diamond, J. M. (eds.), Ecology and evolution of communities: 460–490. Belknap Harvard, Cambridge, Mass. & London.

Diamond, J. & Case, T. J. (eds.) 1986: Community ecology. — Harper & Row, New York. 665 pp.

Ekman, J. 1986: Tree use and predator vulnerability of wintering passerines. — Ornis Scand. 17: 261–267.

Errington, P. L. 1963: The phenomenon of predation. — Am. Sci. 51: 180–192.

Forsman, D. & Solonen, T. 1984: Censusing breeding raptors in southern Finland: methods and results. — Ann. Zool. Fennici 21: 317–320.

Frimer, O. 1989: Food and predation in suburban Sparrowhawks Accipiter nisus during the breeding season. — Dansk Orn. Foren. Tidsskr. 83: 35–44.

Glasser, J. W. 1979: The role of predation in shaping and maintaining the structure of communities. — Am. Nat. 113: 631–641.

Hanski, I. K. & Laurila, A. 1993: High nest predation rate in the Chaffinch. — Ornis Fennica 70: 65–70.

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

Korpimäki, E. 1985: Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. — Oikos 45: 281–284.

Korpimäki, E. & Norrdahl, K. 1991: Do breeding nomadic avian predators dampen population fluctuations of small mammals? — Oikos 62: 195–208.

Koskimies, P. & Väisänen, R. A. 1991: Monitoring bird populations. — Zoological Museum, Finnish Museum of Natural History, Helsinki. 144 pp.

Lindén, H. & Wikman, M. 1983: Goshawk predation on tetraonids: availability of prey and diet of the predator

in the breeding season. — J. Anim. Ecol. 52: 953–968.
Ludwig, J. A. & Reynolds, J. F. 1988: Statistical ecology. — Wiley, New York. 337 pp.
MacArthur, R. H. 1972: Geographical ecology. — Harper & Row, New York. 269 pp.
Marquiss, M. & Newton, I. 1981: A radio-tracking study of the ranging behaviour and dispersion of European Sparrowhawks Accipiter nisus. — J. Anim. Ecol. 51: 111–133.
Martin, E. T. 1996: Fitness cost of resource overlap among coexisting bird species. — Nature 380: 338–340.
Mönkkönen, M. 1990: Removal of territory holders causes influx of small-sized intruders in passerine bird communities in northern Finland. — Oikos 57: 281–288.
Morozov, N. S. 1994: Inter-analyst variation in the combined version of the mapping method: the role of experience. — Acta Orn. 29: 89–99.
Murdoch, W. W. & Oaten, A. 1975: Predation and population stability. — Adv. Ecol. Res. 9: 2–131.
Newton, I. 1978: Feeding and development of Sparrowhawk Accipiter nisus nestlings. — J. Zool., Lond. 184: 465–487.
Newton, I. 1979: Population ecology of raptors. — Poyser, Berkhamsted. 339 pp.
Newton, I. 1986: The Sparrowhawk. — Poyser, Calton. 396 pp.
Newton, I. 1993: Predation and limitation of bird numbers. — Current Ornithology 11: 143–194.
Newton, I., Marquiss, M., Weir, D. N. & Moss, D. 1977: Spacing of Sparrowhawk nesting territories. — J. Anim. Ecol. 46: 425–441.
Opdam, P. 1975: Inter- and intraspecific differentiation with respect to feeding ecology in two sympatric species of the genus Accipiter. — Ardea 63: 30–54.
Opdam, P. 1978: Feeding ecology of a Sparrowhawk population (Accipiter nisus). — Ardea 66: 137–155.
Perrins, C. M. & Geer, T. A. 1980: The effect of Sparrowhawks on tit populations. — Ardea 68: 133–142.
Ratcliffe, D. A. 1980: The Peregrine Falcon. — Poyser, Calton. 416 pp.
Saurola, P. 1985: Finnish birds of prey: status and population changes. — Ornis Fennica 62: 64–72.
Selås, V. 1993: Selection of avian prey by breeding Sparrowhawks Accipiter nisus in southern Norway: The importance of size and foraging behaviour of prey. — Ornis Fennica 70: 144–154.
Sih, A., Crowley, P., McPeek, M., Petranka, J. & Strohmeier, K. 1985: Predation, competition, and prey communities: a review of field experiments. — Annu. Rev. Ecol. Syst. 16: 269–311.
Snyder, N. F. & Snyder, H. A. 1973: Experimental study of feeding rates of nesting Cooper's Hawks. — Condor 75: 461–463.
Sokal, R. R. & Rohlf, F. J. 1981: Biometry. — Freeman, New York. 859 pp.
Solonen, T. 1979: Population dynamics of the Garden Warbler Sylvia borin in southern Finland. — Ornis Fennica 56: 3–12.
Solonen, T. 1984: Raptors and owls of Uusimaa, southern Finland. — Tringa 11(5): 82–101. (In Finnish with summary in English.)
Solonen, T. 1993: Spacing of birds of prey in southern Finland. — Ornis Fennica 70: 129–143.
Solonen, T. 1994a: Structure and dynamics of the Finnish avifauna. — Memoranda Soc. Fauna Flora Fennica 70: 1–22.
Solonen, T. 1994b: Factors affecting the structure of Finnish birds of prey communities. — Ornis Fennica 71: 156–169.
Solonen, T. 1996: Patterns and variations in the structure of forest bird communities in southern Finland. — Ornis Fennica 73: 12–26.
Suhonen, J. 1993: Predation risk influences the use of foraging sites by tits. — Ecology 74: 1197–1203.
Suhonen, J., Norrdahl, K. & Korpimäki, E. 1994: Avian predation risk modifies breeding bird communities on a farmland area. — Ecology 75: 1626–1634.
Sulkava, P. 1964: On the behaviour and food habits of the Sparrowhawk (Accipiter nisus) during the nesting season. — Suomen Riista 17: 93–105. (In Finnish with summary in English.)
Sulkava, P. 1972: Varpushaukan, Accipiter nisus (L.), pesimisbiologiasta ja pesimisaikaisesta ravinnosta. — Manuscript, Dept. Zool., Univ. Helsinki.
Sulkava, P. 1995: Mitenkäs siinä näin kävi? Linjalaskentaa Ilmajoella 1960–61 ja 1984–87. — Suomenselän Linnut 30: 84–85.
Sulkava, S. 1964: Zur Nahrungsbiologie des Habichts Accipiter gentilis (L.). — Aquilo, Ser. Zool. 3: 1–103.
Tiainen, J. 1983: Dynamics of a local population of the Willow Warbler Phylloscopus trochilus in southern Finland. — Ornis Scand. 14: 1–15.
Tiainen, J., Martin, J.-L., Pakkala, T., Piiroinen, J., Solonen, T., Vickholm, M. & Virolainen, E. 1980: Efficiency of the line transect and point count methods in a South Finnish forest area. — Proc. VI Int. Con. Bird Census Work, Göttingen, 24.–28.09.1979: 107–113.
Tinbergen, L. 1946: The Sparrowhawk (Accipiter nisus L.) as a predator of passerine birds. — Ardea 34: 1–123. (In Dutch with English summary.)
Tomialojć, L. & Lontkowski, J. 1989: A technique for censusing territorial song thrushes Turdus philomelos. — Ann. Zool. Fennici 26: 235–243.
Wiens, J. A. 1989: The ecology of bird communities. — Cambridge Univ. Press, Cambridge. Vols. 1 & 2, 539 + 316 pp.

Appendix. Composition of the avian prey of Sparrowhawks during the breeding season in Uusimaa (this study) and in Suomenselkä (Sulkava 1972). Biomass values in parentheses refer to probable maximum estimates for juvenile birds of those large-sized species that were not preyed upon as adults. * Data for *Ph. collybita* and *Ph. trochilus* are combined.

Species	Biomass	Uusimaa		Suomenselkä		Total		
	g	n	%	n	%	n	%	Biomass %
Bonasa bonasia	(175)	3	0.3	2	0.3	5	0.3	1.8
Lagopus lagopus	(175)	–	–	1	0.1	1	0.1	0.4
Charadrius dubius	40	1	0.1	–	–	1	0.1	0.1
Scolopax rusticola	(150)	–	–	1	0.1	1	0.1	0.3
Actitis hypoleucos	48	1	0.1	–	–	1	0.1	0.1
Sterna hirundo	120	1	0.1	–	–	1	0.1	0.3
Columba palumbus	(250)	1	0.1	2	0.3	3	0.2	1.6
Cuculus canorus	107	–	–	1	0.1	1	0.1	0.2
Dendrocopos major	88	3	0.3	1	0.1	4	0.2	0.8
Alauda arvensis	37	8	0.9	10	1.3	18	1.1	1.4
Riparia riparia	14	1	0.1	–	–	1	0.1	0.0
Hirundo rustica	19	1	0.1	–	–	1	0.1	0.0
Anthus trivialis	23	14	1.6	76	9.8	90	5.4	4.4
Motacilla flava	19	–	–	3	0.4	3	0.2	0.1
Motacilla alba	20	55	6.1	17	2.2	72	4.3	3.1
Prunella modularis	19	7	0.8	–	–	7	0.4	0.3
Erithacus rubecula	16	43	4.8	72	9.3	115	6.9	3.9
Luscinia luscinia	27	1	0.1	–	–	1	0.1	0.1
Luscinia svecica	18	1	0.1	–	–	1	0.1	0.0
Phoenicurus phoenicurus	15	3	0.3	8	1.0	11	0.7	0.4
Saxicola rubetra	17	–	–	33	4.3	33	2.0	1.2
Oenanthe oenanthe	23	14	1.6	18	2.3	32	1.9	1.6
Turdus merula	101	18	2.0	–	–	18	1.1	3.9
Turdus pilaris	106	14	1.6	15	1.9	29	1.7	6.6
Turdus philomelos	69	28	3.1	63	8.2	91	5.4	13.4
Turdus iliacus	60	14	1.6	7	0.9	21	1.3	2.7
Turdus viscivorus	115	1	0.1	2	0.3	3	0.2	0.7
Hippolais icterina	14	1	0.1	–	–	1	0.1	0.0
Sylvia nisoria	30	1	0.1	–	–	1	0.1	0.1
Sylvia curruca	12	7	0.8	–	–	7	0.4	0.2
Sylvia borin	20	5	0.6	–	–	5	0.3	0.2
Sylvia atricapilla	20	3	0.3	–	–	3	0.2	0.1
Phylloscopus sibilatrix	10	3	0.3	–	–	3	0.2	0.1
*Phylloscopus collybita**	8	x	..	x	..	x	..	..
*Phylloscopus trochilus**	9	29	3.2	101	13.1	130	7.8	2.5
Regulus regulus	6	8	0.9	–	–	8	0.5	0.1
Muscicapa striata	16	12	1.3	12	1.6	24	1.4	0.8
Ficedula hypoleuca	13	74	8.2	2	0.3	76	4.5	2.1
Parus montanus	11	15	1.7	27	3.5	42	2.5	1.0
Parus cristatus	12	7	0.8	–	–	7	0.4	0.2
Parus ater	9	5	0.6	–	–	5	0.3	0.1
Parus caeruleus	11	44	4.9	–	–	44	2.6	1.0
Parus major	19	161	17.8	18	2.3	179	10.7	7.3
Certhia familiaris	9	–	–	1	0.1	1	0.1	0.0
Lanius collurio	29	2	0.2	2	0.3	4	0.2	0.2
Garrulus glandarius	160	4	0.4	3	0.4	7	0.4	2.4
Sturnus vulgaris	77	5	0.6	9	1.2	14	0.8	2.3
Passer domesticus	32	110	12.2	10	1.3	120	7.2	8.2
Fringilla coelebs	22	111	12.2	175	22.7	286	17.1	13.4

(continues ...)

Appendix. Continued.

Species	Biomass g	Uusimaa n	Uusimaa %	Suomenselkä n	Suomenselkä %	Total n	Total %	Total Biomass %
Fringilla montifringilla	22	1	0.1	–	–	1	0.1	0.0
Carduelis chloris	29	21	2.3	–	–	21	1.3	1.3
Carduelis carduelis	18	5	0.6	–	–	5	0.3	0.2
Carduelis spinus	13	10	1.1	8	1.0	18	1.1	0.5
Carduelis cannabina	17	1	0.1	–	–	1	0.1	0.0
Carduelis flammea	14	2	0.2	–	–	2	0.1	0.1
Loxia curvirostra	41	6	0.7	2	0.3	8	0.5	0.7
Carpodacus erythrinus	23	2	0.2	–	–	2	0.1	0.1
Pyrrhula pyrrhula	29	–	–	2	0.3	2	0.1	0.1
Emberiza citrinella	30	10	1.1	65	8.4	75	4.5	4.8
Emberiza hortulana	24	–	–	1	0.1	1	0.1	0.1
Emberiza rustica	19	–	–	2	0.3	2	0.1	0.1
Emberiza schoeniclus	19	4	0.4	–	–	4	0.2	0.2
Total		902	100	772	100	1 674	100	100