

## Prey selection by Sparrowhawks *Accipiter nisus* and characteristics of vulnerable prey

Seppo Rytönen, Panu Kuokkanen, Markku Hukkanen & Kauko Huhtala

*Seppo Rytönen, Department of Biology, University of Oulu, FIN-90570 Oulu, Finland*

*Panu Kuokkanen, Pilkkitie 2 B 15, FIN-90550 Oulu, Finland*

*Markku Hukkanen, Hintantie 84, FIN-90650 Oulu, Finland*

*Kauko Huhtala, FIN-85310 Sievi as., Finland*

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Prey selection of the Sparrowhawk (*Accipiter nisus*) was studied in northern Finland during 1982–1993. A total of 540 prey items (all birds) were recorded from the surroundings of 12 nests. For each prey species a vulnerability index was calculated as the ratio between its proportion in the Sparrowhawk's diet and its proportion in the land bird community (data from the whole of the Oulanka National Park, and spruce forests only). The average prey individual weighed 52 g, whereas the average breeding bird weighed 36 g in the spruce forests and 24 g in the whole of the Oulanka National Park area. Prey vulnerability increased with increasing prey body mass. The result could be interpreted in the light of the optimal foraging theory, large prey being the most profitable among the Sparrowhawks' prey-size range. In the whole of Oulanka data, open habitat species were caught relatively more frequently than forest species, and prey vulnerability correlated negatively with prey abundance. Foraging behaviour and the nest site of the prey species were not related to their vulnerability. Phylogenetic analyses revealed a significant correlation between prey vulnerability and plumage brightness, after the effects of body mass and abundance of prey species were controlled for. Higher relative predation risk of bright species give support to the 'sexual selection' hypothesis but not to the 'unprofitable prey' hypothesis explaining prey vulnerability.

### 1. Introduction

Predation is an important ecological and evolutionary process that affects morphology and behaviour of organisms. From the predator's point of view, it is optimal to maximise the net energy intake by choosing the most worthwhile prey (e.g. Krebs & Davies 1993). However, to understand predation as a selection pressure, it is also important to identify the characteristics of prey species that make them more vulnerable to predation (Göt-

mark & Post 1996).

One of the most important factors influencing prey selection is the size of the prey. Optimal foraging theory predicts that the profitability of a prey depends on the energy gain in relation to the handling time (e.g. Krebs & Davies 1993). In general, both the energy gain and the handling time are greater with increased prey size. With attacking predators, such as birds of prey hunting avian prey, other costs associated with hunting, e.g. the risk of injury, are also greater with increased prey

size (Newton 1986, Krebs & Davies 1993). Therefore, the most profitable prey size would be large but perhaps considerably smaller than the maximum prey size.

The abundance of the most profitable prey would also affect prey selection (Krebs & Davies 1993). Predators should select the most profitable prey as far as it is abundant enough; i.e. the energy gain in relation to searching and handling times exceeds the net energy gain of an alternative prey. The less profitable prey would be hunted only when the abundance of the most profitable prey decreases below a certain level, but still, the most profitable prey is always preferred independent of its abundance. On the other hand, vertebrate predators are thought to adapt their hunting behaviour and prey recognition to the most worthwhile prey, usually an abundant, often encountered species (Ricklefs 1979). Predators may develop a search image (Krebs & Davies 1993), which results in a preference for the common species in prey selection.

Another factor possibly influencing prey selection is the conspicuousness of prey, e.g. plumage colour of avian prey. The 'unprofitable prey' hypothesis suggests that the bright coloured plumage of a bird indicates low vulnerability to predators, i.e. bright coloured birds are more capable of escaping or avoiding predators than dull-coloured birds (Baker & Parker 1979). On the other hand, bright colours, which are assumed to have evolved through sexual selection in dichromatic species, are presumed to be costly for the bearer (Darwin 1871). This classical model of the evolution of plumage colours, or the 'sexual selection' hypothesis, predicts higher predation risk for bright coloured birds (Andersson 1994).

The Sparrowhawk (*Accipiter nisus* L. 1758) is a predator which hunts almost solely on avian prey and is the major predator of small and medium-sized passerines in forests throughout Europe (Newton 1986). Therefore, prey selection of the Sparrowhawk is a good "tool" when studying the characteristics of prey species that make them more vulnerable to predation. In earlier studies of the Sparrowhawk, at least the following factors have been studied: (1) *Size of prey*. A positive correlation has been found between vulnerability and size of Sparrowhawks' prey species (Selås 1993, Cresswell 1995). In Cresswell's (1995) study the most favoured weight of prey was 101–150 g.

Götmark and Post (1996) found that the vulnerability of Sparrowhawks' prey increased as prey body size increased up to a mass of about 40g, and then declined with increasing body size. (2) *Plumage brightness*. On one hand, Sparrowhawks have been found to avoid bright plumaged birds as prey (supporting the 'unprofitable prey' hypothesis, Götmark & Unger 1994, Götmark 1995) and, on the other hand, to prefer bright plumaged birds as prey (supporting the 'sexual selection' hypothesis, Slagsvold et al. 1995). However, there are also studies in which relative conspicuousness of a prey species was apparently not an important factor in determining vulnerability (Götmark & Unger 1994, Cresswell 1995, see also Huh-ta et al. 1998). (3) *Habitat*. Opdam (1978) concluded that birds of half-open habitats are highly vulnerable: garden villages, agricultural landscapes with woodlots, hedges and human habitations, and open forests and forest edges (see also Götmark & Post 1996). (4) *Abundance*. Götmark and Post (1996) found that the prey vulnerability decreased with increasing relative density of prey species. Rudebeck (1950) and Newton (1986) suggested that the 'search image' did not remarkably affect Sparrowhawks' prey selection. (5) *Breeding and foraging behaviour*. Götmark and Post (1996) showed that nest height was not correlated with vulnerability to Sparrowhawk predation, but foraging height seemed to be an important factor, vulnerability decreased with increasing foraging height. On the other hand, Götmark and Post (1996) did not find that singing birds perched high up suffered higher predation.

In this study we first examine whether Sparrowhawks select the most worthwhile prey, which according to the optimal foraging theory should consist of prey with the best net metabolic value, i.e. most probably relatively large species within Sparrowhawks' prey size range. Second, we inspect the other characteristic of the prey species (listed above) which may make them more vulnerable to Sparrowhawk predation. Special attention is paid to testing of the 'unprofitable prey' and the 'sexual selection' hypotheses by taking into account the phylogenetic relationships of the prey species in the comparative analyses (Felsenstein 1985). Because of the difficulty in restricting the Sparrowhawks' hunting areas, the vulnerability of prey species were based on data from two censuses of the bird community in the study

area: one from the habitats where Sparrowhawks breed and hunt (spruce-dominated forests), and the other from all habitats in the Oulanka National Park.

## 2. Material and methods

Our basic material comes from the Oulanka National Park which lies some 20 km south of the Arctic Circle near the Russian border in northeastern Finland (66°N, 29°E). The study area contains mainly climax coniferous forest (Helle 1985), but also other natural biotopes of the northern boreal taiga zone (see Haila & Järvinen 1990 and references therein).

Prey data of the Sparrowhawk was collected from 12 nests in spruce-dominated forests during 1982–1993. The data include 540 avian prey individuals, which were divided into 28 species or groups of species from the same genera. The genera, processed in groups, were (with the most probable species): *Anthus* spp. (*A. trivialis*, *A. pratensis*), *Turdus* spp. (*T. iliacus*, *T. philomelos*, *T. pilaris*, *T. viscivorus*), *Parus* spp. (*P. montanus*, *P. cinctus*, *P. cristatus*), *Phylloscopus* spp. (*P. trochilus*, *P. collybita*), *Fringilla* spp. (*F. coelebs*, *F. montifringilla*) and *Loxia* spp. (*L. curvirostra*, *L. pytyopsittacus*). The sex and age of the preyed upon birds were not distinguished. Shorebirds (41 ind.) were not considered in this study.

The densities of birds living in the study area were recorded by using the line transect method (Järvinen & Väisänen 1976, 1983) in spruce forests (Helle & Mönkkönen 1986) and in the whole of the Oulanka National Park (Rajasärkkä et al. 1995). Correction coefficients were used to correct the abundance of inconspicuous species (Järvinen & Väisänen 1983). The spruce forest data include census data for six years and the Oulanka data for four years during 1980–1995. The abundance of the species occurring in both data sets were highly correlated ( $r = 0.782$ ,  $n = 21$ ,  $p < 0.001$ ). Thus, we consider that these censuses well describe the forest bird community in Oulanka, and that the vulnerability indices (see below) could reliably be calculated by using these results. The habitat distribution in the Oulanka National Park is 65% forests (of which: 40% spruce dominated forests, 60% pine dominated forests) and 35% open habitats (mainly swamps). Densities in spruce

forest were used because the territories of Sparrowhawks in our study were mainly located in spruce-dominated forests.

The vulnerability index (Newton 1986), which describes the risk of being hunted, was calculated by using the densities of bird species and the numbers of the Sparrowhawks' prey: the proportion of each species/group in prey data was divided by the proportion in the total density of birds in the study area (i.e. catch/supply ratio). This vulnerability index was calculated both from data from the whole of the Oulanka National Park and from data from spruce forests. If vulnerability index of species is 1, the Sparrowhawk catches that species in the same proportion as the species occurs in the area. When the index is greater than 1, the Sparrowhawk prefers that species as a prey and when the index is less than 1, the risk of that species to predation by the Sparrowhawk is smaller than expected. The deviation from 1 was tested by using the  $G^2$ -test.

To describe the size of prey we used the body masses given by Dunning (1993). In calculating the size of an average bird in the area, the species specific body masses were weighed with the abundance of the species. Brightness and colourfulness of plumage of prey species were estimated by five groups of biology students. Each group ranked 43 skins (including males and females of the most dichromatic species) of the birds in descending brightness order. For an index of colourfulness, the average ordinals of the groups' rankings were used (Table 1). Average rank values were calculated for groups of species (see above) and species with different plumage between sexes. Before calculating the average ranks, the similarity of the rankings between the groups was tested with Kendall's concordance analysis. The groups were conformed to be in agreement with each other ( $W = 0.8674$ ,  $\chi^2 = 121.44$ ,  $df = 28$ ,  $p < 0.0001$ ). Thus, we could use the means of estimations as values for the colourfulness of birds in this study (see Baker & Hounscome 1983). In the contrast analyses, the prey species were divided into four (rather distinct) plumage colour groups from 1 (bright) to 4 (dull). This new variable better fits the assumptions of the contrast analysis (see below), since the original ranks were not quantitative measures of plumage colour.

The simple relationships between the vulnerability index and the size, colourfulness and abun-

dance of prey were tested by using correlation analyses: Pearson's correlation among log-transformed vulnerability index, body mass and abundance, and Spearman's when colour rank was analysed. When the independent factors inter-correlated, the effect of one factor (or more factors, e.g. body mass and abundance) was controlled when analysing the effects of the other factors. This was done by using the residuals of the vulnerability index from the regression of vulnerability on the controlled factor(s) as a new variable describing relative vulnerability. Since species are not independent statistical units, we used an analysis of phylogenetically independent contrasts (Felsenstein 1985) in examining the relationships between the prey plumage colour and vulnerability. The program used was COMPARE 2.0. The topology for the phylogeny used was obtained from Sibley and Ahlquist (1991). We could not obtain "exact" branch lengths for all the prey species studied, and, therefore, the branch lengths were estimated from the number of species in each branch by using the method suggested by Purvis (1991). The relationships were tested by calculating regressions for the linear contrast of one variable on the contrast of one or more independent variables through origin (Garland et al. 1992).

### 3. Results

#### 3.1. Differences in prey vulnerability

Table 1 shows that about half of the prey species were significantly over- or under-represented in the Sparrowhawk's diet. This result gives a good basis with which to study prey selection by the Sparrowhawk and the vulnerability of the prey species. In the following, the factors mentioned in the Introduction are studied separately with the spruce forest data and the whole of Oulanka data, which includes all habitats. Finally, the importance of plumage brightness is analysed with the analysis of phylogenetically independent contrasts.

#### 3.2. Spruce forest data

Prey vulnerability to Sparrowhawk predation increased with increasing prey size ( $r = 0.456$ ,  $n = 21$ ,

$p = 0.019$ , Fig. 1). Similarly, the species which were significantly over-represented in the Sparrowhawks' diet were significantly heavier than those which were significantly under-represented (t-test:  $t = 3.60$ ,  $n = 12$ , 1-tailed  $p = 0.003$ ). The most vulnerable prey species were the group of birds weighing 40–85 g, which was composed of the significantly preferred Crossbills *Loxia* sp., Thrushes *Turdus* sp. and the Great Spotted Woodpecker *Dendrocopos major*. On the other hand, the largest prey species, the Hazel Grouse *Bonasa bonasia*, weighing more than 400 g was also significantly preferred. The weight of an average prey of the studied Sparrowhawks was 52 g, whereas the weight of an average breeding bird (weighed with the abundance of the species) was 36 g in the spruce forests.

After controlling for the effect of prey body mass (see Methods), prey vulnerability was not significantly related to plumage brightness ( $r_s = -0.296$ ,  $n = 21$ ,  $p = 0.193$ ) or prey abundance ( $r_s = -0.247$ ,  $n = 21$ ,  $p = 0.280$ , Fig. 2). Correspondingly, there were no differences in the vulnerability of prey species foraging on the ground and above ground level (t-test:  $t = 0.36$ ,  $n = 21$ ,  $p = 0.722$ ), or nesting on the ground or above ground level ( $t = 1.13$ ,  $n = 21$ ,  $p = 0.272$ ).

#### 3.3. Whole of Oulanka data

In the whole of Oulanka data, which includes all habitats, the species which were significantly over-represented in the Sparrowhawks' diet were significantly heavier than those which were significantly under-represented in the diet (t-test:  $t = 2.42$ ,  $n = 15$ , 1-tailed  $p = 0.017$ ). The average prey (52 g) was much heavier than an average breeding bird in the whole of Oulanka data (24 g). However, the relationship between prey size and vulnerability was not significant ( $r = 0.279$ ,  $n = 28$ ,  $p = 0.075$ , Fig. 3). On the other hand, prey species preferring open habitats (see Table 1) were significantly more vulnerable than forest species (t-test:  $t = 2.81$ ,  $n = 28$ ,  $p = 0.009$ ). Hence, the relationship between prey vulnerability and body mass was significant among the forest species ( $r = 0.419$ ,  $n = 22$ ,  $p = 0.026$ , Fig. 3). As in spruce forest data, the largest prey species, Hazel Grouse, was significantly over-represented in the diet.

After removing the effect of body mass (see

Methods), prey vulnerability correlated significantly with prey abundance ( $r = -0.777$ ,  $n = 28$ ,  $p < 0.001$ ) and the plumage brightness of prey species ( $r_s = -0.547$ ,  $n = 28$ ,  $p = 0.001$ ). When the six open habitat species were removed, these correlations still remained significant ( $r = -0.586$ ,  $n = 22$ ,  $p = 0.004$  and  $r_s = -0.569$ ,  $n = 22$ ,  $p = 0.006$ , respectively). On the other hand, prey abundance and plumage brightness were highly correlated ( $r_s = 0.550$ ), and, therefore, the interpretation of the above results is difficult. Next, we divided the prey species into two plumage brightness groups: dull, colour rank  $< 25$  and bright, colour rank  $\geq 25$

(or 4-class ranks 1–2 and 3–4, see Table 1). Analysis of covariance revealed that both the abundance (as a covariate:  $F_{1,25} = 28.55$ ,  $p < 0.001$ ) and plumage brightness (as a 2-level factor:  $F_{1,25} = 5.18$ ,  $p = 0.032$ ) affected prey vulnerability, i.e. less abundant and brighter prey species were more vulnerable (Fig. 4). However, when the open habitat species were excluded, only the effect of abundance remained significant ( $F_{1,19} = 7.43$ ,  $p = 0.013$  and  $F_{1,19} = 3.32$ ,  $p = 0.084$ , respectively).

Similarly as in the spruce forest data, there were no differences in the vulnerability between prey species foraging on the ground and above

Table 1. The densities (pairs/km<sup>2</sup>) and the vulnerability indices (VI) of the prey species of the Sparrowhawk in Oulanka. In addition, the colour-ranks, body masses, the number of prey items studied (n), the preferred habitat (F = forest, O = open habitat) and foraging and nesting behaviour (A = above and G = on the ground level) are presented. Deviations of VI's from 1 are tested by using the G<sup>2</sup>-test (significance levels are presented as follows: ° =  $p < 0.10$ , \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ ).

	Oulanka, spruce f.		Oulanka, all habitats		Color			n	Habitat/ Foraging/ Nesting
	Density	VI	Density	VI	Mean rank	4-class	Body mass (g)		
1. <i>Bonasa bonasia</i>	1.50	1.54*	.90	5.00***	27.4	3	429.00	24	F/A/G
2. <i>Cuculus canorus</i>	.40	1.45	.50	2.25	27.4	3	113.00	6	F/A/A
3. <i>Dendrocopos major</i>	.20	2.89*	.40	2.81*	3	1	81.60	6	F/A/A
4. <i>Picoides tridactylus</i>			.50	13.1	1.84	1	65.65	5	F/A/A
5. <i>Riparia riparia</i>			.04	37	5.12	1	14.60	1	O/A/A
6. <i>Anthus sp.</i>	3.10	0.96	7.10	0.82	39	4	23.40	31	F/G/G
7. <i>Motacilla flava</i>			4.10	0.77	7.6	1	17.60	17	O/G/G
8. <i>Motacilla alba</i>			.50	1.23	25	3	21.00	3	O/G/G
9. <i>Bombycilla garrulus</i>	.10	2.11	.10	4.09	9.2	1	56.40	2	F/A/A
10. <i>Luscinia svecica</i>			.04	23.02***	5.4	1	18.20	5	O/G/G
11. <i>Erithacus rubecula</i>	3.40	0.23***	.80	1.92	15	2	18.20	8	F/G/G
12. <i>Phoenicurus phoenicurus</i>	2.60	0.71	4.70	0.76	15.4	2	14.60	19	F/A/A
13. <i>Saxicola rubetra</i>			.30	7.50***	19	2	16.60	12	O/G/G
14. <i>Oenanthe oenanthe</i>			.04	48.60***	23.8	2	23.15	10	O/G/G
15. <i>Turdus sp.</i>	2.80	3.37***	3.00	6.14***	29.6	3	81.30	97	F/G/A
16. <i>Phylloscopus sp.</i>	4.70	0.68*	24.90	0.25***	37.8	4	8.70	33	F/A/G
17. <i>Regulus regulus</i>	.80	0.85	.10	13.30***	15.6	2	5.70	7	F/A/A
18. <i>Muscicapa striata</i>	3.30	0.17***	8.90	0.13***	43	4	14.60	6	F/A/A
19. <i>Ficedula hypoleuca</i>	1.50	0.59	2.50	0.70	30	3	11.60	9	F/A/A
20. <i>Parus sp.</i>	2.60	1.23	2.30	2.71***	28.94	3	10.90	33	F/A/A
21. <i>Perisoreus infaustus</i>	.70	0.30*	.60	0.68	27.2	3	84.40	2	F/A/A
22. <i>Fringilla sp.</i>	18.00	0.73***	23.20	1.11	18.7	2	22.70	136	F/A/A
23. <i>Carduelis spinus</i>	1.40	0.82	3.90	0.58*	8.4	1	14.50	12	F/A/A
24. <i>Carduelis flammea</i>	1.00	0.31**	4.60	0.13***	31.2	4	13.00	3	F/A/A
25. <i>Loxia sp.</i>	.60	4.87***	3.90	1.47*	19.2	2	40.05	30	F/A/A
26. <i>Pyrrhula pyrrhula</i>	.50	1.16	.60	1.88	15.8	2	21.80	6	F/A/A
27. <i>Emberiza rustica</i>	2.10	0.75	2.90	1.06	28	3	23.20	16	F/G/G
28. <i>Emberiza schoeniclus</i>	.20	0.53	.70	0.29	31.1	4	18.30	1	F/G/G

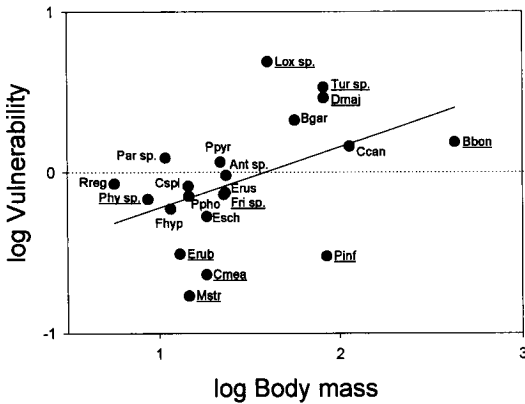


Fig. 1. Relationship between body mass and vulnerability index (VI) of prey species living in spruce forests. Solid line presents the linear regression line, and the dashed line divides the prey species in those over- ( $VI > 1$ , or  $\log VI > 0$ ) and under-represented ( $VI < 1$ ) in the diet (species that differ significantly from  $VI = 1$  are underlined, see Table 1). Scientific name short-cuts: Bbon = Hazel Grouse, Ccan = Cuckoo, Dmaj = Great Spotted Woodpecker, Ant sp. = Pipits, Bgar = Waxwing, Erub = Robin, Ppho = Redstart, Tur sp. = Thrushes, Phyp = Warblers, Rreg = Coldcrest, Mstr = Spotted Flycatcher, Fhyp = Pied Flycatcher, Par sp. = Tits, Pinf = Siberian Jay, Fri sp. = Chaffinch and Brambling, Cspi = Siskin, Cmea = Redpoll, Lox sp. = Crossbills, Ppyr = Bullfinch, Erus = Rustic Bunting, Esch = Reed Bunting.

ground level (t-test:  $t = 0.97$ ,  $n = 28$ ,  $p = 0.343$ ), or nesting on the ground and above ground level ( $t = 0.33$ ,  $n = 28$ ,  $p = 0.747$ ).

### 3.4. Phylogenetic analysis for plumage brightness

Analysis of phylogenetically independent contrasts (Felsenstein 1985) was applied to study the relationships between the evolutionary changes in prey plumage brightness and vulnerability. First, the contrasts were calculated for the log-transformed variables of vulnerability index, body mass and abundance, and for the 4-class variable of plumage brightness (see Table 1). In the spruce forest data, after controlling for the effect of body size contrast (see Methods), there was a significant negative relationship between the evolutionary changes in prey plumage brightness and relative vulnerability ( $b \pm S.E. = -0.132 \pm 0.054$ ,  $t = 2.44$ ,

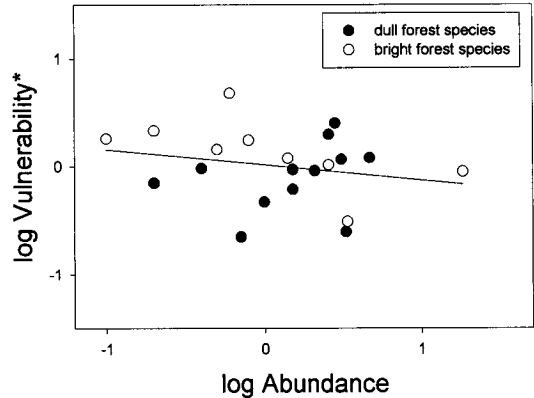


Fig. 2. Relationship between abundance and vulnerability of the spruce forest species in relation to their plumage brightness. In the vulnerability\*-variable the effect of body mass was controlled for (see Methods).

$p = 0.025$ ,  $R^2 = 0.238$ ; Fig. 5), suggesting that bright plumage coloration was associated with higher predation risk. The corresponding relationship was significant also in the whole of Oulanka data ( $b \pm S.E. = -0.193 \pm 0.057$ ,  $t = 3.35$ ,  $p = 0.003$ ,  $R^2 = 0.302$ ; Fig. 6), after controlling for the effects of prey body mass and abundance (see Methods).

The non-parametric plumage brightness variable did not properly fit the assumptions of the contrast analysis of two continuous traits (Felsenstein 1985). However, a conservative method resulted in the same. The effect of plumage brightness was significant, when the changes in vulnerability were compared with the directions of changes in plumage brightness (brighter: contrast  $< 0$  and duller: contrast  $> 0$ , zero-contrasts omitted, see Fig. 5 and 6). In the spruce forest data, the average change in relative VI for brighter and duller contrasts were  $-0.08 \pm 0.08$  (S.D.) and  $0.07 \pm 0.16$ , respectively (Mann-Whitney U-test:  $z = 2.31$ ,  $n = 17$ ,  $p = 0.021$ ). In the whole of Oulanka data, the corresponding values were  $-0.14 \pm 0.25$  and  $0.10 \pm 0.16$ , respectively ( $z = 2.27$ ,  $n = 23$ ,  $p = 0.023$ ).

## 4. Discussion

### 4.1. Size of Prey

One quite straightforward result of this study was that large prey species (weighing over 30 g) were

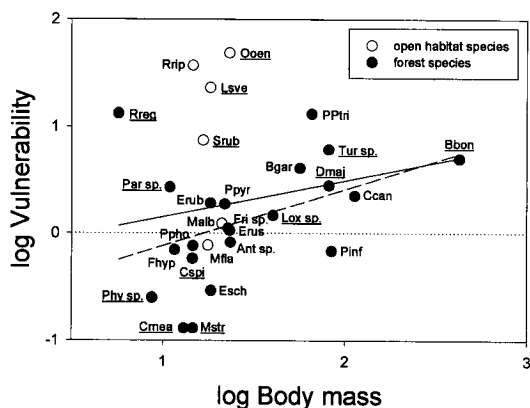


Fig. 3. Relationship between body mass and vulnerability index (VI) of prey species living in all habitats in the Oulanka National Park. Solid line presents the linear regression line for all species, and the broken line the same when open habitat species (open circles) were excluded. For more information see Fig. 1. Scientific name shortcuts for species not mentioned in Fig. 1: Lsve = Bluethroat, Malb = Pied Wagtail, Mfla = Yellow Wagtail, Ooen = Wheatear, Ptri = Three-toed Woodpecker, Rrip = Sand Martin, Srub = Whinchat.

over-represented in the Sparrowhawks' diet, and that the prey vulnerability increased with increasing prey size. The result is in line with the earlier studies on the Sparrowhawk by Selås (1993) and Creswell (1995). However, our result differs from that of Götmark and Post (1996), who found that vulnerability increased with increased prey body size up to a mass of about 40 g, and then declined with increasing body size. We could not find a clear decrease in prey vulnerability at the maximum end of the Sparrowhawks' prey size range. The largest prey species, the Hazel Grouse, was significantly over-represented in the Sparrowhawks' diet. On the other hand, the number of large prey species was quite low in our data. The average prey size (52 g) in northern Finland seems to be larger than that in southern Finland, where the average prey weight was determined at 26.6 g by Solonen (1997).

The main reason for the preference for large prey may be that it is more profitable for the Sparrowhawk to prefer larger prey species, which offer a better profit to the energy lost in hunting (Opdam 1978), i.e. the result supports the prediction of the optimal foraging theory (see Krebs & Davis 1993). Moreover, the Sparrowhawk hunt-

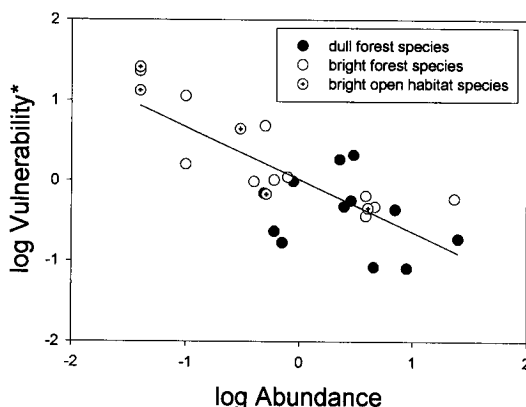


Fig. 4. Relationship between abundance and vulnerability of the prey species in relation to their plumage brightness and preferred habitat in the whole of Oulanka data. In the vulnerability\*-variable the effect of body mass was controlled for (see Methods).

ing in forests can take advantage of the clumsiness and lesser hiding ability of larger bird species. The Sparrowhawk has no similar advantage over smaller species, for which the most common escape tactic is hiding in dense woody vegetation (Newton 1986, Lima 1993). An interesting exception in the group of thrush-sized birds, which were the most preferred in the Sparrowhawk's diet, is the Siberian Jay *Perisoreus infaustus* because of its significantly low vulnerability to predation by the Sparrowhawk (spruce forest data). The low vulnerability might be explained by the early breeding season and, especially, the family-oriented social life of the Siberian Jay (Ekman et al. 1994).

The methods used in the collection of prey remains around the Sparrowhawk nests might have caused some bias towards the above results. It has been argued that large prey items are found better than small ones (Sulkava 1964). Therefore, the vulnerability indices of small prey might remain lower than what they really are. However, we think that the results for some easily distinguishable small passerines (Redstart *Phoenicurus phoenicurus*, *Fringilla* sp. and Bullfinch *Pyrrhula pyrrhula*, see Figs. 1 and 2) showed that this possible bias was not serious. Another problem would be that small prey are likely to be under-represented in prey collections from the nest sites because they are more often eaten in the hunting

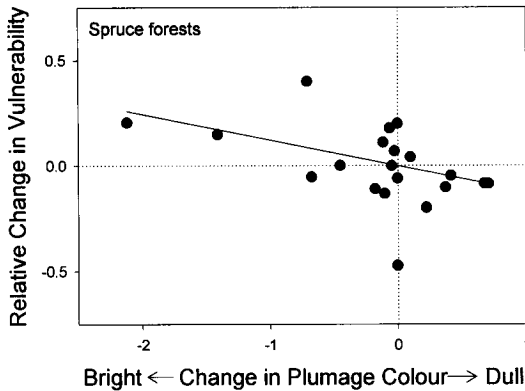


Fig. 5. Relationship between the evolutionary changes in plumage brightness and relative vulnerability of prey species living in spruce forests, when the phylogenetic relationships of the prey species and the effect of body mass on vulnerability were controlled for (see Methods). Solid line presents the linear regression line through origin.

area than large prey (e.g. Sonerud 1989). Third, we do not know how many Sparrowhawks' diet we did study. Our data consisted of yearly checked nests in the same area, and it is obvious that the same birds had bred there over several years. Data from few individuals could bias the results, since individual predators may have specific characteristics in their hunting behaviour (Newton 1986).

#### 4.2. Habitat

The size of prey seemed to have less of an effect on the Sparrowhawk's prey selection when the supply data were calculated from the whole of the Oulanka National Park area. On the other hand, some less abundant prey species that live in open habitats biased the result. The Sparrowhawk often catches species that are very visible, vulnerable because of their behaviour or foraging in open places or in half-open habitats (Opdam 1978, Newton 1986). This is also supported by our results on birds breeding or foraging in open places but not in spruce forests. Especially the Wheatear *Oenanthe oenanthe*, the Whinchat *Saxicola rubetra* and the Bluethroat *Luscinia svecica* were found to be very vulnerable. These birds are small and less abundant, and, therefore, the relationship between vulnerability and size of prey found in pure

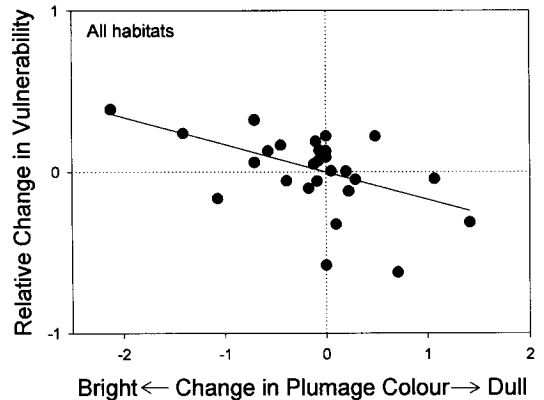


Fig. 6. Relationship between the evolutionary changes in plumage brightness and relative vulnerability of prey species living in all habitats in the Oulanka National Park, when the phylogenetic relationships of the prey species and the effects of body mass and abundance on vulnerability were controlled for (see Methods). Solid line presents the linear regression line through origin.

spruce forests could not be found in the mixed habitat data; however, the relationship was found when these species were excluded in the analysis.

One problem in this study is that we could not exactly restrict the analyses to the hunting areas or habitats of the studied Sparrowhawks. The importance of the size, colour and abundance of prey may differ in different habitats (e.g. Selås 1993). In the Oulanka National Park, there are large areas where Sparrowhawks do not hunt at all, and a variety of different habitats in which the Sparrowhawks' hunting effort may differ spatially and temporally.

#### 4.3. Plumage colour

The plumage colour of the prey species had a significant effect on the prey vulnerability when the phylogeny of the prey species was taken into account in the comparative analyses. Thus, the evolution of bright colours in the Sparrowhawks' prey species seems to be associated with higher vulnerability to Sparrowhawk predation. The result gives support to the 'sexual selection' hypothesis, which predicts a higher predation risk for bright plumaged birds (Andersson 1994). On the other hand, the result gives no support to the 'unprofit-



able prey' hypothesis, which predicts lower predation on bright coloured birds (Baker & Parker 1979). Earlier studies of the importance of prey coloration to the predation of the Sparrowhawk have been conflicting. Götmark (1995) found evidence that the black-and-white plumage of male Pied Flycatchers *Ficedula hypoleuca* reduces the risk of predation from Sparrowhawks, thus supporting the 'unprofitable prey' hypothesis (see also Götmark & Unger 1994). On the other hand, the study by Slagsvold et al. (1995) suggests that the Sparrowhawk favours cryptic coloration in Pied Flycatchers (see also Dale & Slagsvold 1996). In addition, prey colourfulness has been found to be of low importance in prey selection of Sparrowhawks (Creswell 1995), Merlins *Falco columbarius* (Baker & Bibby 1987) and Kestrels *Falco tinnunculus* (Huhta et al. 1998).

When the vulnerability indices of single prey species are compared, the high vulnerability of the Great Spotted Woodpecker arouses attention. The result is in contrast to the results of the study carried out in open places in experimental conditions by Götmark and Unger (1994), which (concerning the Great Spotted Woodpecker) supported the 'unprofitable prey' hypothesis. Another example indirectly rejecting the 'unprofitable prey' hypothesis is the Spotted Flycatcher *Muscicapa striata*, which was the best at avoiding predation by the Sparrowhawk despite its unpretentious plumage. However, the small size, unassuming behaviour and vigilant foraging habits of the Spotted Flycatcher may also reduce its vulnerability.

In studying the importance of plumage colours of the prey species we faced two difficulties. First, we should have estimated the colourfulness of prey species on the same basis as predators do, and we should have known which factors of colourfulness (e.g. contrast, brightness or location of colour, etc.) make a predator notice and take interest in a potential prey. Avian predators often notice their prey from the backside, where colour usually differs from the front side and a cryptic coloration is displayed. This is one of the commonest adaptations of avoiding predation (Kettlewell 1955, Endler 1978). In addition, the determination of plumage brightness of birds by humans is perhaps different from that by avian predators, since several birds see in the ultraviolet light (e.g. Bennet et al. 1994) to which humans are

blind. This problem remained unsolved in this study. Another problem is the unknown number of juvenile birds in the Sparrowhawks' prey data. The plumage brightness of fledglings differs from that of adult birds in many species. We tried to dilute this bias by calculating the colour rank of dichromatic species as the average of male and female ranks, and by dividing the plumage colour ranks into fewer (four) more or less distinct brightness categories for the comparative analyses.

#### 4.4. Prey abundance

Prey vulnerability to Sparrowhawk predation proved to be independent of prey abundance in the spruce forest data. In the whole of Oulanka data, however, less abundant species suffered higher predation from Sparrowhawks than common ones. The latter result is the same as that of Götmark and Post (1996). Several models predict the reverse (Allen 1988, see also Götmark & Post 1996). However, as Sparrowhawks rely on surprise to catch prey (Newton 1986), they may select their prey more on the basis of vulnerability than on species abundance (Götmark & Post 1996). The most preferred prey species in this study lived in the most risky habitats, open and edge habitats. These species were also less abundant than most of the forest species, which may explain the negative correlation between prey vulnerability and abundance (see also Götmark & Post 1996). On the other hand, when the open habitat species were excluded, the above correlation still remained significant. One explanation for this might be the Sparrowhawks' preference for large prey, since large species tend to be less abundant in Oulanka. Another explanation would be that common species might have evolved better defences against Sparrowhawks (see Götmark & Post 1996).

The number of some small passerines can vary quite a lot between years (e.g. *Loxia* species, Helle & Mönkkönen 1986). This might bias the results, if the prey item collections and bird density censuses have been done in different years. We did not have bird census data from all the study years; however, the censuses of two areas, which were from different years and together covered seven study years, gave very similar results for the breeding bird community in Oulanka (see Methods).

Thus, both the prey item data and bird census data balanced the annual variation in the results.

## Conclusions

Our conclusion is that the Sparrowhawk is mainly a generalist (see also Rudebeck 1950, Newton 1986) with a preference for larger than average prey species within its prey-size range, which is in accordance with the predictions of the optimal foraging theory. On the other hand, some other characteristics of prey species also increased the vulnerability to Sparrowhawk predation. The most at risk species seemed to be open habitat species, which were bright-coloured and less abundant, whereas the least at risk were common, dull-coloured species living in forests (when size was controlled for). When considering the hypotheses explaining the evolution of plumage coloration in birds, the results give support to the 'sexual selection' hypothesis, but no support to the 'unprofitable prey' hypothesis. On the other hand, field studies of prey selection always have many difficulties in controlling for errors in some parameters (as our study did), which must be remembered when considering the results. Better controllable experiments would give more reliable insight into the factors affecting prey selection and the characteristics of vulnerable prey.

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## Selostus: Varpushaukan saaliinvalinta ja saalislajien predaatoririski

Varpushaukan saaliinvalintaa tutkittiin Oulangan kansallispuistossa Pohjois-Suomessa vuosina 1982–1993 12 pesältä kerätyn 540 yksilöä sisältävän saalislintuaineiston pohjalta. Saalislintujen osuutta ravintoaineistossa verrattiin niiden osuuksiin kokonaislinnustossa. Näin saatuja lajikohtaisia saaliksijoutumisriskejä tutkittiin suhteessa saaliin kokoon, väriin ja runsauteen sekä ruokailuttä pesintäkäyttäytymiseen. Vertailu tehtiin erikseen kuusimetsien ja koko kansallispuiston linnus-

ton osalta. Varsinkin kuusimetsissä varpushaukan saaliinvalintaan vaikutti saaliin koko varpushaukan suosiessa keskimääräistä suurempia, yli 30 g painavia lintulajeja (kuvat 1 ja 3). Saalisaineistossa keskimääräinen saaliin paino oli 52 g, eli enemmän kuin keskimääräinen pesivän linnun paino kuusimetsässä (36 g) tai koko Oulangan alueella (24 g). Tulos on optimaalisen saalistusteorian mukainen, eli varpushaukka näyttäisi suosivan energettisesti edullista saaliskokoa. Koko kansallispuiston alueella alttiimpia joutumaan varpushaukan saaliiksi olivat avomaalajit, samoin vähälukuiset lajit olivat suuremmissa vaarassa (kuva 4). Ruokailutavalla tai pesäpaikalla ei havaittu yhteyttä varpushaukan saaliksijoutumisen alttiuteen. Kun analyysissä otettiin huomioon saalislajien fylogeneettiset sukulaisuussuhteet, ja saaliin massa ja runsaus kontrolloitiin, havaittiin merkitsevä korrelaatio saaliksijoutumisriskin ja höyhenpuvun värikyyden välillä (kuvat 5 ja 6). Tämä tukee hypoteesia, jonka mukaan seksuaalisen valinnan suosima höyhenpuvun värikkyys lisää kantajansa predaatoririskiä. Tulos ei tue ns. epäsopeva saalis-hypoteesia, jonka mukaan pedot välttäisivät höyhenpuvultaan värikkäitä saaliita.

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