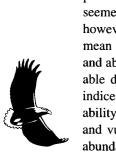
Predation by Sparrowhawks Accipiter nisus and vulnerability of prey

Tapio Solonen

Solonen, T., Luontotutkimus Solonen Oy, Neitsytsaarentie 7b B 147, FIN-00960 Helsinki, Finland. E-mail: tapio.solonen@pp.inet.fi

Received 9 September 1999, accepted 20 December 1999



The relationships between weight, abundance (as a measure of availability), and vulnerability of prey of the Sparrowhawk were studied on the basis of five data sets from the Nordic countries. The purpose of the study was to find out whether the predator showed indications of real prey preference. The mean weight of prey used seemed, in general, to be higher than the mean weight of the available prey. There was, however, no evidence that the average size of prey individuals varied according to the mean size of available prey. The expected negative relationship between the weight and abundance of available prey emerged only in two data sets. There were considerable differences in the relationships between weight, abundance, and vulnerability indices in different data sets. In general, the relationship between weight and vulnerability indices seemed to be not significant. The relationship between the abundance and vulnerability indices was (negatively) significant in two data sets. Weight and abundance factors of prey species together explained 2.2-40.3% of the total variation of vulnerability indices in different data sets. When the effect of the other variable was removed, the contribution of weight was at its highest 21.6%, and that of abundance 39.8% of the total variation. Vulnerability indices of many common species in different data sets varied considerably and the various factors affecting this variation are discussed. It was concluded that the vulnerability of prey of the Sparrowhawk is due to foraging habits of the predator as well as to characteristics of the habitat and those of the prey species itself. The large variability of vulnerability indices in many species suggests that the species-specific characteristics were not important determinants of the predation risk, or that at least some of the indices studied were based on deficient data.

1. Introduction

Predation and prey of the Sparrowhawk Accipiter nisus have been studied frequently in recent decades (Tinbergen 1946, Opdam 1978, Perrins & Geer 1980, Newton & Marquiss 1982, Newton 1986, Frimer 1989, Selås 1993, Götmark & Post 1996, Solonen 1997, Rytkönen et al. 1998, Whitfield et al. 1999). The effect of predation or the vulnerability of prey is usually expressed as the relation between the proportion of the prey species in a prey sample and the proportion of the species in the environment (Tinbergen 1946, Opdam 1978). Though the estimates of prey distributions seem to match relatively well those of the pool of available prey species, it has usually been

concluded that Sparrowhawks do not take their various prey species in proportion to numbers in the environment (e.g. Newton 1986, Götmark & Post 1996). The suggested deviations from the random, opportunistic pattern have been interpreted to indicate prey preference or prey selection by the predator (Selås 1993, Götmark & Post 1996, Rytkönen et al. 1998), or differences in vulnerability between prey species (Tinbergen 1946, Newton 1986).

Some of the studies seem to be in accordance with optimal foraging theory (e.g. Emlen 1968, Krebs & Davies 1993), suggesting that the predator prefers the most profitable prey available, i.e prey in which the energy gain in relation to the foraging effort seemed to be most favourable (Opdam 1978, Selås 1993, Rytkönen et al. 1998). Alternatively, it can be suggested that hawks prey more or less opportunistically upon suitable prey in preferred foraging habitats (cf. Solonen 1997, Whitfield et al. 1999). The habitat preference of the predator, again, is due to the availability (usually indicated by the abundance) of suitable prey. The suitability of prey depends not only on its energetic profitability but also on its accessability (catchability) and manageability (cf. Newton 1986, Selås 1993). In these respects, there are obvious differences between sexes in the Sparrowhawk due to the pronounced sexual size dimorphism of the species (the approximate weight of males being 150 g, and that of females 280 g). Therefore the size distribution of prey brought to nests probably varies according to the participation of the sexes in hunting (see Newton 1986).

Deviations of vulnerability indices from unity may suggest that there are differences in vulnerability between prey species, or that the available and/or used prey populations were inadequately sampled in relation to numbers or area. A major difficulty has been to measure the availability of prey in the real foraging area of the predator (Solonen 1997). The availability of prey has often been measured on the basis of overall density estimates of prey species in the district concerned, and, for simplicity, it has been intuitively assumed that predators forage evenly throughout the area. Thus, the effects of heterogeneity of the environment and uneven prey availability, as well as those of the habitat preference of the predator have been ignored (cf., however, Newton 1986, Götmark & Post 1996, Solonen 1997).

To avoid confusion, I define the terms used in the present paper as follows. "Prey abundance" is the relative abundance of the prey species measured in the field. "Availability of prey" is measured by the prey abundance. "Prey use" is measured by the relative abundance of a species in prey remains. "Preference" and "selection" suggest that the predator actively prefers or selects prey from the available alternatives. When such activity is not convincingly indicated, however, the more general term "use" is preferable. "Vulnerability" is the risk of prey to get caught by the predator, measured by the ratio of prey use and availability.

The purpose of this paper is to bring up various factors affecting the relevancy of interpretations of the results of studies concerning prey use and vulnerability of different prey species to predation by Sparrowhawks. I suggest that the "prey preference" or "prey selection" claimed in the literature is largely due to such factors as the accessability of prey, heterogeneity of habitats, and habitat preference of foraging hawks. Though there were no real prey preferences in the Sparrowhawk, some characteristics of its prey (e.g. weight, conspicuousness, abundance) or habitat (e.g. cover, bird density) may make some species more vulnerable to predation than the others. To elucidate these relationships, I examine the data of some recent Nordic studies (Selås 1993, Götmark & Post 1996, Solonen 1997, Rytkönen et al. 1998) and the following predictions:

- In a comparison between regions, the average size of prey individuals varies according to the mean size of available prey (cf., e.g. Newton 1986). The larger sized prey species are less abundant in the diet than the smaller ones, reflecting the general pattern in bird communities (e.g. Solonen 1994a).
- 2. If Sparrowhawks preferred larger sized (e.g. Opdam 1978) or abundant (e.g. Solonen 1997) prey, within the suitable size range of prey for the sexes (see, e.g. Newton 1986), there should be significant positive relationships between size and vulnerability, or between abundance and vulnerability of prey.

2. Material and methods

The data used were derived from five districts in the Nordic countries, including a forest-dominated habitat mosaic near Göteborg, southern (S) Sweden (57°N, 12°E) (Götmark & Post 1996), a forest area in southern (S) Norway (58°N, 08°E) (Selås 1993), rich forests in Uusimaa, southern (S) Finland (60°N, 25°E) (Solonen 1997), poor forests in Suomenselkä, central (C) Finland (62°N, 22°E) (Sulkava 1964, Solonen 1997), and a coniferous forest area in northeastern (N) Finland (66°N, 29°E) (Rytkönen et al. 1998) (Table 1). Prey samples assumed to indicate the composition of the diet of the Sparrowhawk were collected near nests during the breeding season (see, e.g. Newton 1986). In assessing the relative abundance of potential prey populations, assumed to be a measurement of prey availability, line transect or point count methods (see Koskimies & Väisänen 1991) were used.

Because the data in different papers were presented in somewhat different forms, I transformed them to correspond to the presentation of Solonen (1997) as follows. The mean body weights of prey species were taken from a common source (Solonen 1994b). To those prey species with an adult weight of more than 200 g that were preyed upon mostly as young, I arbitrarily assigned a prey mass of half the average adult mass. The vulnerability (V) of potential prey species was estimated by comparing the proportion of each species in the Sparrowhawk's diet by number with their proportion in the total recorded prey community (Tinbergen 1946, Opdam 1978). Indices higher than unity (1) indicate that prey were taken more than expected on the basis of their relative abundance. and indices lower than unity indicate that prey

were taken less often than expected on the basis of their relative abundance. The significance of differences between the proportions was tested with the G-test adjusted by Williams' correction (Sokal & Rohlf 1981). In examining the relationships between the size of the prey species and vulnerability as well as the abundance of the species and vulnerability, I firstly used the original indices regardless of their significance. To minimize the effect of unrealistic indices due to, for instance, small sample size, I also examined the data by replacing those indices that did not deviate significantly from unity by 1. For correlation and regression analyses, the data were normalised by log-transformation.

3. Results

The mean weight of prey used by the Sparrowhawk seemed, in general, to be higher than the mean weight of the available prey (Table 2, Fig. 1). The significances of differences were not tested because of incomplete lists of available prey in some of the data sets. There was, however, no evidence that the average size of prey individuals varied according to the mean size of available prey ($r_s = -0.30$, n = 5, P > 0.10). No clear regional trends, either in the mean weight of available prey or in that of prey used could be found. In the size range of prey of the Sparrowhawk, the expected negative relationship between the weight and abundance of available prey emerged only in the data of S Sweden and C Finland (P < 0.05) (Fig. 2).

When considering the original vulnerability indices, regardless of their significance, the relationship between the weight and vulnerability of prey was, in general, not significant. There was a

Table 1. Aspects of the data sets examined in this study: the number of prey samples, sampling years, and the method used in estimating the available prey pool in each locality.

| Locality | Prey samples | Sampling years | Census method | Source |
|-----------|--------------|----------------|----------------|----------------------|
| N Finland | 540 | 1982–1993 | Line transect | Rytkönen et al. 1998 |
| C Finland | 772 | 1960-1961 | Main belt | Sulkava 1964 |
| S Finland | 460 | 1989-1990 | Line transect | Solonen 1997 |
| S Norway | 2611 | 1983-1988 | Point counts | Selås 1993 |
| S Sweden | 3193 | 1994–1995 | Line transects | Götmark & Post 1996 |

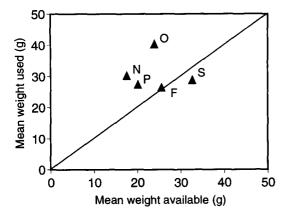


Fig. 1. Relationship between the mean weight of available and used prey of the Sparrowhawk on the basis of the data available: F = S Finland, N = S Norway, O = N Finland, P = C Finland, and S = S Sweden.

significant positive relationship only in the data from C Finland (r = 0.39, df = 25, P < 0.05). When only those indices significantly deviating from unity were considered (and the indices of other species were replaced by 1), a significant relationship emerged in the data of C Finland (r =0.43, df = 25, P < 0.05) and of S Norway (r =0.32, df = 52, P < 0.05) (Fig. 3).

There were significant negative relationships between the abundance of species in the environment and the original vulnerability indices in the data of N Finland (r = -0.79, df = 26, P < 0.001) and S Norway (r = -0.75, df = 52, P < 0.001), and a significant positive relationship in the data of S Finland (r = 0.41, df = 42, P < 0.01). When only those indices that significantly differed from unity were considered (and the others were marked as 1), the significant negative relationships remained in the data of N Finland (r = -0.63, P < 0.001) and S Norway (r = -0.49, P < 0.001), while the positive relationship of S Finland vanished (Fig. 4).

The weight and the abundance of the prey species together explained 2.2–40.3% of the total variation of vulnerability indices in different data sets (Table 3). The percentage contribution of weight alone ranged from 1.2% (N Finland) to 96.8% (C Finland), and that of abundance alone from 3.2% to 98.8%. The contribution of weight was significant only in the data of C Finland, while abundance contributed significantly to the variation of vulnerability indices in the data sets of N Finland, S Norway, and S Sweden. When the effect of the other variable was removed, the contribution of weight was at its highest 21.6%, and that of abundance 39.8% of the total variation of the vulnerability indices.

Vulnerability indices of common species in different data sets varied considerably (Table 4). There were marked differences especially in such species as *Erithacus rubecula*, *Regulus regulus*, *Ficedula hypoleuca*, *Fringilla coelebs*, *Carduelis spinus*, and *Emberiza citrinella*. In contrast, for *Turdus philomelos*, *Phylloscopus trochilus*/sp., and *Garrulus glandarius* the results of different studies were quite consistent with each other.

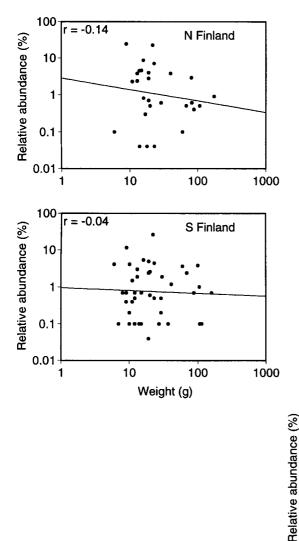
4. Discussion

4.1. Prey size of the Sparrowhawk

There was no evidence that the average size of prey individuals in the diet in different areas varied according to the mean size of available prey in the environment. The general trend of larger species being less abundant than smaller ones (e.g.

| Locality | Latitude °N | Longitude °E | Mean weight of prey (g) | | Prey samples |
|-----------|----------------|-----------------|-------------------------|------|--------------|
| | | | Available | Used | n |
| N Finland | 66 | 29 | 24 | 40.4 | 540 |
| C Finland | 62 | 22 | 20.2 | 27.4 | 766 |
| S Finland | 60 | 25 | 25.6 | 26.5 | 900 |
| S Norway | 58 | 08 | 17.6 | 30.3 | 2611 |
| S Sweden | 57 | 12 | 32.7 | 28.9 | 3234 |

Table 2. Regional variation in the mean size of available and used prey of the Sparrowhawk.



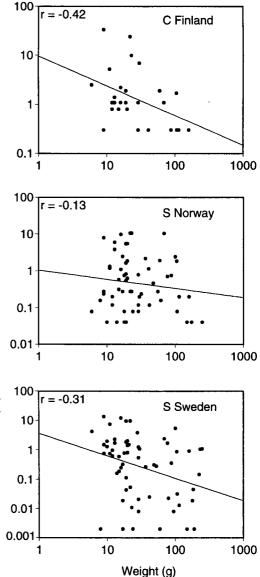
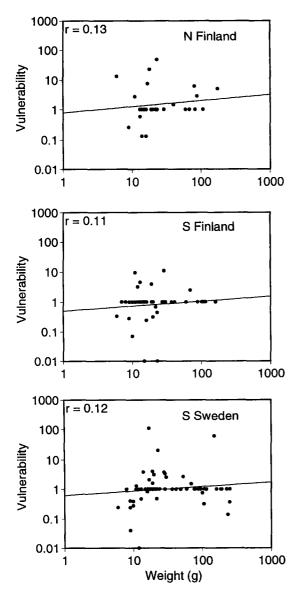


Fig. 2. Relationship between weight (g) and relative abundance (%) of the available potential prey species of the Sparrowhawk according to the different data sets studied.

Solonen 1994a), seemed not to be a common rule in the size range of birds preyed upon by Sparrowhawks. However, the number of large species, and hence their total abundance, was less. Therefore the availability of large (say, weighing more than 50 g) prey individuals was lower than that of smaller ones. The size of Sparrowhawk prey increases during the breeding season due to the growing of the young of prey species and to the participation of the larger female hawk in hunting (e.g. Newton 1986). Sparrowhawks can carry prey as heavy as themselves (Newton 1986) but there are obvious difficulties in carrying the heaviest prey, even for short distances (e.g. Feral Pigeons *Columba livia* weighing about 300 g; T. Solonen, own obs.). Therefore, the largest possible prey species are not very suitable prey for breeding hawks (cf. Rytkönen et al. 1998). Young individuals of larger species of various sizes, however, seem to be commonly preyed upon (e.g. Sulkava 1964, Newton 1986). My provisional estimate was that the mean



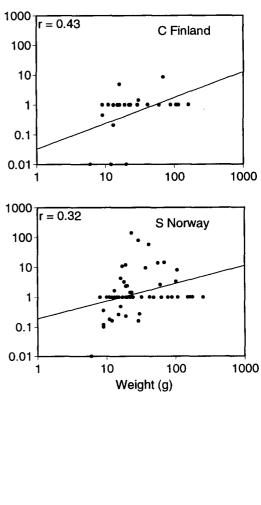


Fig. 3. Relationship between weight (g) and vulnerability (V) of the prey species of the Sparrowhawk in the five data sets studied.

weight of the largest species (adults weighing more than 200 g) of prey was half that of adults (cf. Selås 1993). In any case, I doubt that they all were adult-sized (cf. Götmark & Post 1996, Rytkönen et al. 1998). In altricial species, large nestlings and recently fledged young may be even heavier than adults, while in precocial species young develop to the adult size during a longer period in the field. Sparrowhawks also prey upon nestlings but, not surprisingly, they are under-represented in feather samples collected at plucking posts (e.g. Sulkava 1964, T. Solonen, own obs.). In addition, nestlings are seldom identified in remnant samples.

4.2. Factors causing deviations in vulnerability indices

The vulnerability indices of Sparrowhawk prey species varied both within and between the data sets studied. Many factors can cause deviations from unity in vulnerability indices — see Table 5, which considers characteristics of the predator as

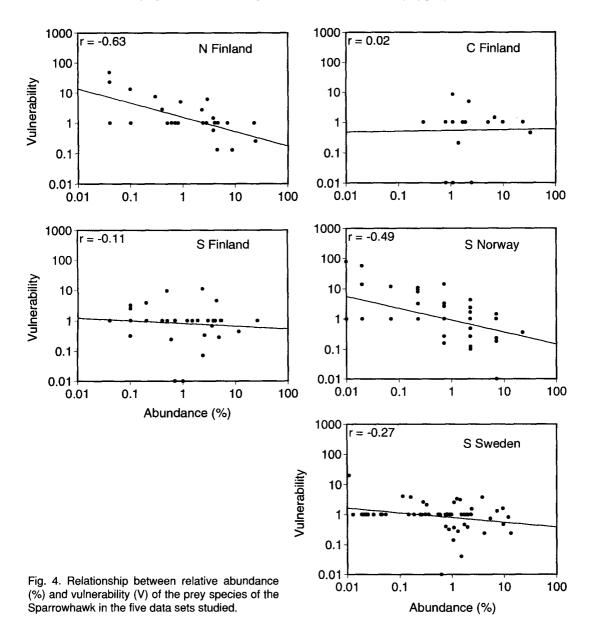


Table 3. Summary of the multiple regression analyses explaining the variation in vulnerability indices of prey species of the Sparrowhawk in terms of their weight and abundance. Significance levels: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

| | Data | | | | |
|--------------------|------------|-----------|-----------|-----------|----------|
| | N Finland | C Finland | S Finland | S Norway | S Sweden |
| F explained, total | 8.427 ** | 3.537 * | 0.461 | 7.381 ** | 4.210 * |
| F weight | 0.052 | 7.051 ** | 0.326 | 2.794 | 0.033 |
| F abundance | 16.193 *** | 1.547 | 0.559 | 8.188 *** | 7.297 ** |
| R ² | 0.403 | 0.228 | 0.022 | 0.224 | 0.125 |

well as those of potential prey. For prey the deviations may be due to either real or seeming differences in vulnerability.

A habitat may be actively preferred or selected by the predator for the resources it provides. Because of observational restrictions (see, e.g. Newton 1986), it is, however, rather difficult to know if hunting Sparrowhawks attack when opportunity offers for all suitable prey, or if they actively select between various alternatives encountered (see, however, Whitfield et al. 1999). Though there were no general preferences for certain kinds of prey, single individual predators can learn about or specialize in using some locally tempting resources such as accessible broods or dense urban populations as a consequence of good hunting success (cf. Newton 1986, Götmark & Post 1996, Solonen 1997).

Though Sparrowhawk nests were mainly situated in spruce forests, the birds foraged largely in other habitats (see Götmark & Post 1996, Solonen 1997, Rytkönen et al. 1998). The hunting methods of Sparrowhawks require opportunities for surprise attack from cover; consequently, preferred foraging habitats are usually linked with woodland edges and continuous or adjacent lines and clusters of cover in partly open terrain adjoining blocks of woodland (Cramp & Simmons 1980, Newton 1986).

Species-specific characteristics of prey might be important determinants of their predation risk. There were, however, considerable differences in the relationships between weight, abundance, and vulnerability indices in different data sets studied. The data of S Norway deviated most from the expected patterns but there were also various differences in the other data sets (especially in those of N Finland and C Finland). In general, the relationship between weight and vulnerability seemed not to be significant. The relationship between abundance and vulnerability was significant in three or two of the five data sets studied, depending on the derivation of the indices. In general weight and abundance explained only a mi-

Table 4. Vulnerability indices (V) of common prey species of the Sparrowhawk in different data sets. Significant deviations from 1 (unity) are presented as follows: * = P < 0.05, ** = P < 0.01, *** = P < 0.001. Other explanations: $\S = V$ calculated for a group of species from the same genus; + = species present in prey but V not calculated; - = species not present, # = Perisoreus infaustus, & = Emberiza rustica.

| Species | Data sets | | | | | |
|-------------------------|-------------|------------|-----------|-----------|-----------|--|
| | N Finland | C Finland | S Finland | S Norway | S Sweden | |
| Cuculus canorus | 2.25 | 0.33 | 0 | 4.00 | 0.94 | |
| Dendrocopos major | 2.81 * | 0.33 | 1.14 | 1.03 | 1.11 | |
| Anthus trivialis | § 0.82 | 1.15 | 0.44 * | 1.45 * | § 0.80 | |
| Motacilla alba | 1.23 | + | + | 2.40 *** | 3.09 *** | |
| Erithacus rubecula | 1.92 | 4.86 *** | 1.32 | 4.25 *** | 0.82 ** | |
| Phoenicurus phoenicurus | 0.76 | 1.50 | 3.00 | 0.26 *** | 2.28 | |
| Turdus philomelos | § 6.14 *** | 8.45 *** | 2.46 *** | 14.26 *** | 1.52 ** | |
| Sylvia curruca | - | 0.00 *** | 1.57 | 0.87 | 0.89 | |
| Sylvia borin | - | 0.00 *** | 0.31 * | 0.82 | 1.29 | |
| Phylloscopus trochilus | § 0.25 *** | § 0.45 *** | 0.28 *** | 0.35 *** | § 0.24*** | |
| Regulus regulus | 13.30 *** | 0.00 *** | 0.33 ** | 0.01 *** | 0.24 *** | |
| Muscicapa striata | 0.13 *** | 1.64 | 0.24 *** | 0.48 *** | 1.60 | |
| Ficedula hypoleuca | 0.70 | 0.21 ** | 4.53 *** | 0.82 | 1.14 | |
| Parus cristatus | - | 0.00 *** | 3.20 * | 0.16 *** | 0.00 *** | |
| Parus major | § 2.71 *** | 1.42 | 3.90 ** | 2.38 *** | 1.58 *** | |
| Garrulus glandarius | (#0.68) | 1.33 | 0.71 | 2.86 | 0.59 | |
| Fringilla coelebs | § 1.11 | 1.01 | 0.68 ** | 1.44 *** | 0.48 *** | |
| Carduelis spinus | 0.58 * | 1.09 | 0.76 | 1.66 ** | 0.47 *** | |
| Loxia curvirostra | § 1.47 * | 1.00 | 0.92 | 57.50 *** | § 0.90 | |
| Pyrrhula pyrrhula | <u>1.88</u> | 1.00 | 0.00 | 0.16 *** | 0.90 | |
| Emberiza citrinella | (&1.06) | 1.41 * | 1.16 | 0.27 ** | 2.49 *** | |

nor proportion of the variation of the vulnerability indices.

The conspicuousness and habits of a species may cause real differences in vulnerability as well as apparent differences in vulnerability indices due to sampling errors. This applies to samples of available prey and those of prey used (e.g. Sulkava 1964, Solonen 1997). Species that seemed to be the most vulnerable were also relatively conspicuous in the field. Conspicuousness of species is affected by many independent factors. Brightness is a subjective measure but obviously a determinant of conspicuousness. However, the effects of background and behaviour must additionally be taken into account (cf. Huhta et al. 1998). The interpretation of the effects of conspicuousness may also be complicated (see Götmark 1993, Götmark & Post 1996, Huhta et al. 1998). Close relatives may include very different kind of species with respect to conspicuousness, so that vulnerability indices derived by clumping species into groups (Rytkönen et al. 1998) must be interpreted with caution.

Estimates of the relative abundance of prey using line transects and (especially) point counts (S Norway), tend to underestimate the proportions of large species and those that are crepuscular (such as Turdidae, see Solonen 1997). Large and conspicuous species are, in general, over-represented in prey samples (e.g. Sulkava 1964, Newton 1986). Species that lead a skulking way of life, again, even when abundant in the field, were usually rare in the prey of the Sparrowhawk (cf., however, Selås 1993).

Vulnerability indices based on small samples may be unrealistically high or low. If potential prey species not found in prey samples were not included when calculating vulnerability indices (e.g. Rytkönen et al. 1998), the average indices became too high. The high vulnerability indices also suggest inadequate sampling of the real foraging area of the predators (Solonen 1997). Vulnerability indices are not very informative if there is a poor numerical or geographical correspondence between the data representing available and used prey (cf. Solonen 1997, Rytkönen et al. 1998). Such a correspondence is most likely good in abundant and evenly distributed species. In larger samples, the effects of heterogeneity of both the environment and prey pool will probably be taken better into account (e.g. in studying local populations rather than single territories; Solonen 1997).

No census method accurately measures the size of prey populations, or even the relative abundance of different prey species, because some species are easier to record than others. All we can record is the difference between Sparrowhawk sampling of prey (as reflected in the diet) and the sampling of a human observer (as reflected in birds detected in censuses). In the data sets used, there were also some general deficiences and differences that may have affected the results. The estimates of prey populations referred to breeding adults, but they did not always adequately corre-

| Table 5. Factors affecting | deviations in vulner | ability indices. |
|----------------------------|----------------------|------------------|
|----------------------------|----------------------|------------------|

| Factors | Effects |
|---|----------------------|
| Real differences in vulnerability | |
| Prey preference of the predator | Higher vulnerability |
| Conspicuousness of prey | Higher vulnerability |
| Skulking habits of prey | Lower vulnerability |
| Seeming differences in vulnerability | |
| Bias in assessing potential prey pool: | |
| Underestimates | Higher indices |
| Overestimates | Lower indices |
| Deficient areal representativeness | |
| (preferred areas not included) | Higher indices |
| Bias in assessing the abundance of prey used: | - |
| Underestimates | Lower indices |
| Overestimates | Higher indices |

spond, locally or temporally, to the respective diet samples. The diet samples concerned a longer period of time than the censuses of breeding birds, and they included both adult and young birds.

4.3. Conclusions

The vulnerability of prey of the Sparrowhawk is due to the foraging habits of the predator as well as to characteristics of the habitat and those of the prey species itself. It also depends on the number of other prey in the same area, and this will vary from one locality to another (Newton 1986) as well as seasonally (Götmark & Post 1996, Solonen 1997). The prey lists of the Sparrowhawk (e.g. Newton 1986, data of this study) suggest that size is the only characteristic of a bird species that may absolutely restrict the hawks using them as prey. Remnants of the largest prey species, however, have not been found commonly near nests due to the restricted carrying capabilities of the predator.

The large variation of the vulnerability indices in many species suggests that species-specific characteristics were not important determinants of predation risk, or that at least some of the indices were based on deficient data. The environment may also have differed between studies, making some species very vulnerable in some study areas and less vulnerable in others.

The seemingly vulnerable species in the prey of the Sparrowhawk may be (a) locally abundant, or species that have been concentrated in habitats in which the bird density is higher than the general bird density of the district, or in which the hunting is easier due to some structural characteristics (openness) of habitat (habitat preference hypothesis), or (b) they may be inadequately sampled for density estimates due to some speciesspecific behavioural or ecological characteristics (sampling bias hypothesis) (cf. Solonen 1997). Low vulnerability indices of species can be explained by the morphological, behavioural and/ or ecological characteristics of the species concerned, or by the species being under-represented in prey samples.

script and made useful suggestions. Marcus Walsh checked the English. Esa Lammi kindly improved the figures.

Selostus: Lintujen alttiudesta joutua varpushaukan saaliiksi

Varpushaukan ravintonaan käyttämien lintujen painon, runsauden ja saaliiksijoutumisalttiuden (käytetyn ja käytettävissä olevan saaliin välisen suhteen) välisiä riippuvuuksia tutkittiin viiden pohjoismaisen aineiston valossa. Työn tarkoituksena oli etsiä mahdollisia viitteitä haukan suosimista saalistuskohteista. Haukkojen ravinnoksi käyttämien lintujen keskipaino näytti yleensä olevan korkeampi kuin maastossa linja- tai pistelaskentojen perusteella arvioitu tarjolla olevien lintujen keskipaino. Mikään ei kuitenkaan viitannut siihen, että saalisyksilöiden keskipaino vaihtelisi tarjolla olevien lintujen keskipainon mukaan. Odotettu käänteinen riippuvuus lintulajin painon ja runsauden välillä todettiin vain kahdessa aineistossa. Eri aineistoissa oli huomattavia eroja lintujen painon, runsauden ja saaliiksijoutumisen välisissä riippuvuussuhteissa. Painon ja saaliiksijoutumisen välillä ei yleensä ollut merkitsevää riippuvuutta. Runsauden ja saaliiksijoutumisen välillä oli merkitsevä käänteinen riippuvuus kahdessa aineistoista. Saalislajin paino ja runsaus yhdessä selittivät 2.2-40.3% eri aineistojen saaliiksijoutumisalttiuden vaihtelusta. Kun toisen muuttujan vaikutus poistettiin, selitti paino enintään 21.6% ja runsaus 39.8% kokonaisvaihtelusta. Lintujen saaliiksijoutumisalttiuden katsottiin johtuvan paitsi saalislajien ominaisuuksista myös haukan saalistustavoista ja tietyistä ympäristön piirteistä. Monien eri aineistoissa yhteisten lajien saaliiksijoutumisalttius näytti vaihtelevan huomattavasti aineistojen välillä. Tämä viittaa siihen, että lintujen lajityypilliset ominaisuudet eivät olisi kovin tärkeitä saaliiksijoutumisriskin kannalta tai riskiä on arvioitu puutteellisten aineistojen perusteella.

References

- Cramp, S. & Simmons, K. E. L. (eds.) 1980: The Birds of the Western Palearctic. Vol. II. — Oxford Univ. Press, Oxford.
- Emlen, J. M. 1968: Optimal choice in animals. Am.

Acknowledgements: Harri Högmander, Hannu Pietiäinen and some anonymous referees read drafts of the manu-

Nat. 102: 385-389.

- Frimer, O. 1989: Food and predation in suburban Sparrowhawks Accipiter nisus during the breeding season. — Dansk Orn. Foren. Tidsskr. 83: 35–44.
- Götmark, F. 1993: Conspicuous coloration in male birds is favoured by predation in some species and disfavoured in others. — Proc. R. Soc. Lond. B. 253: 143–146.
- Götmark, F. & Post, P. 1996: Prey selection by sparrowhawks, Accipiter nisus: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. — Phil. Trans. R. Soc. Lond. B 351: 1559–1577.
- Huhta, E., Hakkarainen, H. & Lundvall, P. 1998: Bright colours and predation risk in passerines. — Ornis Fennica 75: 89–93.
- Koskimies, P. & Väisänen, R. A. 1991: Monitoring bird populations. — Zoological Museum, Finnish Museum of Natural History, Helsinki.
- Krebs, J. R. & Davies, N. B. 1993: Behavioural Ecology. — Blackwell, Oxford.
- Newton, I. 1986: The Sparrowhawk. Poyser, Calton.
- Newton, I. & Marquiss, M. 1982: Food, predation and breeding season in Sparrowhawks (Accipiter nisus). — J. Zool., Lond. 197: 221–240.
- 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.
- Rytkönen, S., Kuokkanen, P., Hukkanen, M. & Huhtala, K.

1998: Prey selection by Sparrowhawks Accipiter nisus and characteristics of vulnerable prey. — Ornis Fennica 75: 77–87.

- 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.
- Sokal, R. R. & Rohlf, F. J. 1981: Biometry. Freeman, New York.
- Solonen, T. 1994a: Finnish bird fauna species dynamics and adaptive constraints. — Ornis Fennica 71: 81– 94.
- Solonen, T. 1994b: Structure and dynamics of the Finnish avifauna. — Memoranda Soc. Fauna Flora Fennica 70: 1–22.
- Solonen, T. 1997: Effect of Sparrowhawk Accipiter nisus predation on forest birds in southern Finland. — Ornis Fennica 74: 1–14.
- 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.)
- Tinbergen, L. 1946: The Sparrowhawk (Accipiter nisus L.) as a predator of passerine birds. — Ardea 34: 1– 123. (In Dutch with summary in English.)
- Whitfield, D. P., Cresswell, W., Ashmole, N. P., Clark, N. A. & Evans, A. D. 1999: No evidence for Sparrowhawks selecting Redshanks according to size or condition. — J. Avian Biol. 30: 31–39.