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Prey selection by sparrowhawks, *Accipiter nisus*: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour

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SUMMARY

Predation is a fundamental ecological process, but there are few studies of predation risk for adult, breeding birds. In this study, we quantified Relative Predation Risk (RPR) for 46 species of passerine birds preyed on by sparrowhawks during the breeding season in south-western Sweden. The sparrowhawk is a major predator of smaller birds in Eurasian forests and woodland. Near nesting hawk pairs, prey abundance was estimated by line transects. From prey remains at hawk nests, we estimated the frequency of prey species in the diet of hawks. For each hawk pair, RPR values for different prey species were calculated. The mean RPR for each prey species, based on hawk pairs as sample units, indicated degree of overrepresentation (positive RPR) or underrepresentation (negative RPR) of the prey in the diet. Prey species with a high positive RPR nested mainly near human habitations (villages or towns), at forest edges and in farmland. However, there were marked seasonal changes in RPR. Forest birds, such as the goldcrest and wren, had the highest RPR in April. Later, the hawks seemed to hunt mainly in the habitats mentioned above, where prey were more abundant or easier to catch, resulting in increasing RPR for the house sparrow, yellowhammer, greenfinch and other species.

RPR values were analysed in relation to prey body size (mass) and relative density, as well as prey foraging height and nest height (categorized from the literature). In addition, the mean perch height and mean exposure of prey species were quantified in the field. Most predation was due to the smaller male hawks, providing food for their mates and young. RPR increased with prey body size up to a mass of about 40 g, then declined with increasing body size (larger prey being more difficult to catch). RPR decreased with increasing relative density of prey species. Nest height was not correlated with RPR, but foraging height seems to be an important factor: RPR decreased with increasing foraging height. A similar result

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was found for mean perch height, when larger prey (over 40 g) and singing individuals were excluded from the field data. RPR increased with mean exposure of prey species when larger prey and singing birds were excluded; a combination of perch height and exposure improved the correlation with RPR. Singing birds were generally perched high in the vegetation and may not suffer high predation risk, contrary to common belief. The results of this study are discussed in relation to temporal and geographical variation in RPR and antipredator adaptations in passerine birds.

1. INTRODUCTION

Predation is an important ecological and evolutionary process, often addressed by theoreticians (Taylor 1984; Endler 1991; Crawley 1992). However, in vertebrates, particularly in birds, it is usually difficult to study predation in the field. There are numerous studies of the behaviour and population ecology of passerine birds, but few studies of predation on different species, sex and age classes (except for nest predation, which is easy to study). Predation on adult passerines is rarely quantified, but probably influences morphology as well as reproductive and other behaviours in different species (Lima & Dill 1990). Certain characteristics of prey species may make them more vulnerable to predation, but what are they? Is it possible to identify ecological and behavioural traits of prey species that are correlated with predation risk? If so, this would improve our understanding of predation as a selection pressure. Moreover, we would be able to make better predictions in comparative studies, where authors often have relied on assumptions about predation that essentially lack empirical support (see, for example, Shutler & Weatherhead 1990; Johnson 1991; Götmark 1994; John 1995).

Recent studies have shown that the mere presence of predators (or the threat of predation) may influence prey behaviour in several ways (Elgar 1989; Lima & Dill 1990; Cresswell 1994*a*). In birds, most work on antipredator behaviour has concerned the non-breeding season, and the benefits and costs of group living. Lima & Dill (1990) emphasized that little is known about predation during the reproductive period. The present study focuses on breeding birds and actual predation rather than on the threat of predation. Predation by sparrowhawks (*Accipiter nisus*) on many common passerines, studied extensively in other respects (for example tits, finches and flycatchers), was examined. The sparrowhawk is the major predator of small and medium-sized passerines in forests throughout Europe and a large part of Asia (see Newton (1986) for a detailed review). Besides forests, it hunts along edges of woods, in farmland, and in towns and villages.

There are many studies of the diet of sparrowhawks (see Newton 1986). Three of them examined prey selection in the breeding season, relating the numbers of different prey species taken to their abundance in the area where the hawks were hunting (Tinbergen 1946; Opdam 1978; Selås 1993; see also Gray (1987) and Cresswell (1995) for winter studies). Tinbergen (1946) focused on population regulation in four prey species, estimating in detail the share of predation in the total mortality. Opdam (1978) and Selås (1993) studied many prey species, but censuses of prey abundance used by them were made for other purposes and not in the years when the hawks were studied (abundance of different prey may vary between years). To quantify the diet of sparrowhawks in the present study, prey remains were collected near hawk nests in two years. The abundance (density) of prey near each hawk nest was estimated from line transects in spring and early summer in both years. On the basis of these data, predation risk for different prey species was estimated. The major contribution of this study is an analysis of factors causing variation in predation risk, such as body size, abundance, foraging, and reproductive behaviour of the prey species.

This study also considers a common problem in studies of diet and prey selection in predators. When comparing prey taken by predators and prey abundance (or 'prey availability'), authors often base their conclusions on the prey as sample units, testing for a difference in relative frequency of species (by χ^2 tests). However, the appropriate units in most cases are the individual predators, which may differ in prey selection. In many earlier studies, few predators were studied (for obvious practical reasons). This study included about 20 pairs of nesting sparrowhawks; the estimates of predation risk were based on these pairs.

2. METHODS

(*a*) *Study area and predators*

The study was done near the city of Göteborg in Sweden during 1994 and 1995, between Hisingen, north of the city, and Onsala, to the south (about 500 km^2). The area is of a mosaic of habitat types: forests, lakes, mires, bedrock, agricultural land, farms, towns and villages (forests predominate). The sparrowhawks had been studied by amateur ornithologists for several years. The hawks usually nested in stands of Norway spruce (*Picea abies*) 30–40 years old, often close to agricultural land or human settlements. Within 1 km of the nest, the areal proportion of town, farms and/or fields was less than 10% for 5 hawk territories, between 10% and 50% for 20 territories and more than 50% for 7 territories.

In early and mid April, a search was made for signs of breeding at sites used by nesting sparrowhawks in earlier years (see Newton 1986). In 1994 23 pairs that laid eggs were found, but 4 of them failed after 4–6 weeks, so prey data are only available for part of the season for these pairs (sample sizes therefore vary over the breeding season). In 1995 there were also 23 nesting pairs located, of which one failed after 6 weeks. Three more pairs failed at a late stage; these failures did not affect the analyses. Twelve of these 23 pairs were also studied in 1994 (the same nest sites, not necessarily the same pairs). The hawks laid eggs mostly in early and mid-May.

(*b*) *Determination of the diet of hawks*

To quantify the diet, prey remains (feathers) were collected near the nests at regular intervals. Earlier workers have concluded that this method gives a relatively reliable estimate of the diet (Tinbergen 1946; Reynolds & Meslow 1984; Newton 1986; Gray 1987; Selås 1993, but see below). The male hawk provides food for the incubating female and for the young. As the food demands of the young increase, the female gradually starts hunting, if additional food is needed (Geer 1981; Newton 1986). Before egg-laying, the male also feeds the female, but most females probably also hunt in April (see below). Thus, from about 1 May to 15 June, the prey were taken almost exclusively by the small male hawks (mass about 150 g). The larger females (about 300 g) (Newton 1986) were probably also involved before and after this period. In the breeding season, prey remains from nests are probably not entirely representative of diet in sparrowhawks. In Scotland, larger prey tended to be more common in prey remains found away from nests than in those found near nests (Newton & Marquiss 1982; Newton 1986). Non-breeding females and females that fail during the breeding season may pluck prey away from nests, as might some breeders.

The hawks remove the feathers of their prey at plucking posts (usually logs or stumps) within about 30 m of the nest. New prey feathers were collected at plucking posts once a week (intervals of 7–10 days) from about mid-April to mid-July. Some hawk nests were not found until early May; if they had begun breeding in April the first prey remains collected were assigned to April in seasonal analyses. All wing and tail feathers and some other characteristic feathers were collected. All collection and identification of prey was done by one person (Jan Olsson) in both years. To identify species, the feathers were compared with the authors' collection of feathers from dead specimens of known species and Vidar Selås' collection from south Norway. For some warblers, identification requires training; prey species determined earlier were re-checked to ensure correct identification. The following species were difficult to separate, and were pooled (for Latin names, see Appendix 1): willow warbler and chiffchaff; tree pipit and meadow pipit; marsh tit and willow tit; crossbill and parrot crossbill; and house sparrow and tree sparrow. The last two species are ecologically similar and were pooled in the line transects; therefore, they were not separated in the prey remains. The chiffchaff and parrot crossbill were rare; the data presented refer largely to the willow warbler and crossbill. The pipits and tits were not very common in the study area (Appendix 1).

Feathers collected at each visit to a hawk nest were lumped; the minimum number of individuals of each prey species taken was then determined (Reynolds & Meslow 1984). This was done by matching wing and, in particular, outermost tail feathers. The hawks may move between plucking posts with a prey item, so posts were not considered independent in sampling. Sometimes only a few feathers from a prey item were found. Before adding it, careful checks were made with species and individuals found at the preceding visit. However, the hawks often arrived at posts with partly or mainly plucked prey (authors' personal observations), so a few feathers may well be evidence of a taken prey. We determined the age of the prey (as 'fledglings' or 'older birds'). Fledglings have feathers that are not fully grown, with sheaths (Newton 1986). Older fledglings with fully grown feathers are difficult to identify, but some prey with new, unworn feathers were also classified as fledglings (about 10% of all fledglings). Only a few nestlings were taken (cf. Newton 1986). Feathers from about 3400 prey, all labelled, are stored in the Department of Zoology at the University of Göteborg. Prey species and number of individuals taken are listed in Appendix 1.

The number of prey items varied between hawk pairs. For two pairs, it was difficult to find prey remains. About 30 prey items from the breeding season (mid-April to mid-July) were required for inclusion of a pair in analyses for 1994 and 1995, resulting in sample sizes of 18 and 21 hawk pairs, respectively. The average number of prey per pair was 88 in 1994 (s.d. = 38.5, range 27–151) and 73 in 1995 (s.d. = 29.5, range 30–132).

(*c*) *Determination of prey abundance*

Some prey species winter in Sweden; short-distance migrants winter in western Europe (arriving from late March to mid-April), and long-distance tropical migrants winter in Africa (mainly arriving in early May). The first two groups were censused in April, the third in mid- and late May. In 1994, the early census began on 7 April; in 1995, the spring was late and the census began on 16 April (the criterion being that most individuals of one common prey, the robin, had arrived).

Birds were censused by line transects near each hawk nest. The nearest-neighbour distance between nests in the study area is usually 1 km or less. The transects were made within about 500 m of each nest. The exact hunting ranges of the hawks were not known; several hawks apparently hunted farther away from the nest than 500 m (see also Newton 1986), but this study probably censused an important part of the hunting area. The line transect covered 2 km, along a square where each side was 500 m, and where the hawk nest was located on one of the sides, midway between the corners. The square was oriented north, east, south, or west of the nest (four options) so that it covered as many habitat types as possible, especially open areas and towns or villages. However, forest dominated along the transects. Where the habitat was relatively homogeneous, orientation of the square was determined by random numbers. For each hawk pair (nest site), exactly the same square was censused by F.G. in both April and May, and in both 1994 and 1995 if hawks nested there in both years.

The census started at sunrise, or about 2 h later. To be able to census at all hawk nests in rather short periods, two line transects per day were done in both April and May, each lasting 1.5–2 h. They were completed within 5 h of sunrise. Singing and other birds of potential prey species, representing breeding pairs, were recorded in two categories; 'close' to observer (within 25 m on each side) or 'distant' (over 25 m away). The species vary in detectability; this variation was corrected for by a Finnish method (Järvinen & Väisänen 1975, 1976, 1983). It assumes that detectability of species decreases linearly with increasing distance from the observer (Järvinen & Väisänen 1975). By use of species-specific correction coefficients (K), 'distant' observations can be converted to values corresponding to 'close' observations (Järvinen & Väisänen 1983). The formula for K is

$$K = 40 - 40\sqrt{(1-p)},$$

where p = proportion of 'close' observations in the total sample (range 0–1). As the sample sizes in this study were relatively large, the K values could be calculated from the census data (see Järvinen & Väisänen 1983). The sum of 'close' and 'distant' observations for each prey species and census (hawk territory) was multiplied by K (Appendix 1), providing an estimate of the relative density of the species (for assumptions, determination of 'breeding pairs', and use of the census method, see the references above).

Before calculating relative densities, diurnal and seasonal variation in the census data (for species with sufficient data) was examined. For some species, census efficiency was higher early in the morning; for others it was higher later in the morning. For some species with a significant difference in numbers between early and late morning (tested separately for April and May), diurnal variation was controlled for by multiplying all values in the census with the lowest numbers by the ratio of the mean numbers in the two censuses (greater than 1.0). A correction was also made for seasonal variation in censuses within April and within May, assuming it was caused by changes in song activity due to pairing and nesting or arrival of new migrants. Data for a few species with a significant increase or decrease in numbers in April or in May were corrected by linear regression analysis, by setting the slope to zero (at the highest level) and adding the difference between this and the original slope for the individual census values.

(*d*) *Determination of Relative Predation Risk* (RPR)

Given data on prey taken by hawks and abundance of prey in hunting grounds, it is possible to quantify prey selection. Earlier workers (Opdam 1978; Gray 1987; Selås 1993; Cresswell 1995) calculated the proportion of a prey species in the diet, dividing it by the proportion of the same species in the censuses (Catch–Supply Ratio, CSR; or Vulnerability Index (Newton 1986)). For a ratio greater than unity, the species is overrepresented in the diet of the hawks; for a ratio of about 1, it is taken in relation to abundance; and for a ratio between 0 and 1, it is underrepresented in the diet. As pointed out by Johnson (1980), such ratios have disadvantages. For instance, if a prey species that is common in the census but rare in the diet of the predator is excluded from the analysis, the proportions for all other species in the census will change considerably (see also Crawley 1992, p. 45). CSR ratios are also asymmetrically distributed (species overrepresented in the diet may have high values, whereas all underrepresented ones lie between 0 and 1). Johnson (1980) proposed a ranking procedure, which was used in this study (see also Alldredge & Ratti 1992). For each hawk pair, the prey species recorded in the diet were ranked according to frequency (number of individuals) and so were the potential prey species censused in the hawk territory. For each prey species, the rank for frequency in the diet was subtracted from the rank for abundance in the territory, giving a measure of predation risk for the species in the territory. This gave a relative rather than absolute measure, and we therefore call it Relative Predation Risk (RPR). The procedure was repeated for all hawk pairs; the mean RPR for different prey species was calculated, based on the individual values for all hawk pairs. The rank differences (RPR) for prey species are approximately normally distributed (Johnson 1980), positive if a species is overrepresented in the diet and negative if it is underrepresented.

These data refer to the whole nesting season (mid-April to mid-July). Changes in RPR for prey species within each season, divided into five periods, were also examined. Unfortunately, diet sample sizes were too small for calculating RPR values for each hawk pair and period. Instead, for each period diet data for all pairs were pooled, but first the data for each pair were recalculated as proportions of individuals taken of different prey species, to minimize bias due to variation in sample size for different hawk pairs. If there were fewer than five prey for a pair in a period, the data for that pair were pooled with those from another pair with few prey before proportions were calculated. The prey abundance data were also pooled for all hawk pairs. Diet and abundance data were ranked and RPR values were calculated separately for the following periods: about 15–30 April (referred to as 'April 2' below), about 1–15 May ('May 1'), about 16–31 May ('May 2'), about 1–22 June ('June'), and about 23 June–15 July ('June/July'). These values, referred to as *overall* RPR below, resembled the *mean* RPR values described above. Based on data from whole seasons (mid-April to mid-July), overall and mean RPR values were correlated (Pearson's $r = 0.81$ in 1994, $r = 0.77$ in 1995). Only for the house and tree sparrow did the estimates differ markedly, with lower overall RPR (1994, +8; 1995, +6) than mean RPR (1994, +22.5; 1995, +17.2; see table 2). These species have clumped distributions, making them difficult to census by line transects. Overrepresentation in the diet of many hawk pairs and absence in censuses in several territories explain their high mean RPR; their relatively high pooled abundance (where they occurred, they were often quite common) explains the lower overall RPR.

The five seasonal periods correspond to changes in both prey numbers and breeding stages of hawks. In the period April 2, hawks are defending territories and

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Table 1. *Prey taken by breeding sparrowhawks during five periods in* 1994 *and* 1995

(Data given as number of prey individuals (adult birds and fledglings), identified from feathers collected at plucking posts near hawk nests.)

	period[a]					
year	April 2	May 1	May 2	June	June/July	total
1994	210	171	196	435	624	1636
1995	177	257	237	370	516	1557

[a] Periods are as defined in the text.

building nests, and few tropical migrants have arrived. A few fledglings of species nesting extremely early (crossbills) were taken in April 2 (1994, 0.5% of all prey taken; 1995, 0%; sample sizes in table 1). In the period May 1, female hawks are starting to lay eggs and tropical migrants are arriving. For this period, an average density of tropical migrants was subjectively estimated by multiplying species-specific correction factors to the census figures for (mid- and late) May, taking into account the approximate arrival time of the species in each year (authors' personal observations). A small proportion of fledgling prey was taken in May 1 (1994, 0.6%; 1995, 2.3%). In the period May 2, hawks are incubating and breeding passerines fully established. More fledglings are taken in May 2, but their proportion is still small (1994, 14%; 1995, 3.0%). In 1994, 12 of the 30 fledglings taken in April and May were song thrushes or blackbirds; in 1995, 12 of 13 fledglings taken during these months were song thrushes or blackbirds. In the period June, hawks are hatching and many fledglings are taken (1994, 59%; 1995, 40%) (see also Newton 1986). In the fifth period (June/July), some female hawks are probably also hunting, and fledglings predominate in the diet (1994, 83%; 1995, 71%). From April 2 to June/July, the number of prey items found at the plucking posts increases (table 1).

The high proportion of fledglings in the diet in June and July was a problem, because estimates of RPR, both for seasonal periods and for whole seasons, were based on breeding pairs of the prey species. Ideally, one should also census fledglings, but this is very difficult. In general, across species there should be a correlation between the density of adults and fledglings. Moreover, predation on prey species nesting both early (fledglings in June) and late (fledglings in June/July) was studied. The fledglings are vulnerable mainly during a short period after leaving the nest (Newton 1986) and most predation on late fledglings should be included. To examine the effect of fledglings on RPR, the RPR estimates were compared for May (May 1 + May 2; few fledglings in the diet of hawks) and June–July (June + June/July; fledglings predomating in the diet), still based on breeding pairs of prey species. On the assumption that there is a positive relation between predation risk for fledglings of different species and predation risk for adults of the same species, a correlation is expected between RPR for May and June–July across species. A correlation was found for both 1994 ($r = 0.69$) and 1995 ($r = 0.59$, $n = 46$). Use of mean values for the two years (for May and June–July) improved the correlation ($r = 0.73$; figure 1). It seems that no serious bias is introduced by including fledglings in the diet data; the inclusion of fledglings increases sample sizes considerably. In addition, RPR values for adults are given in seasonal analyses (for April 1, May 1 and May 2).

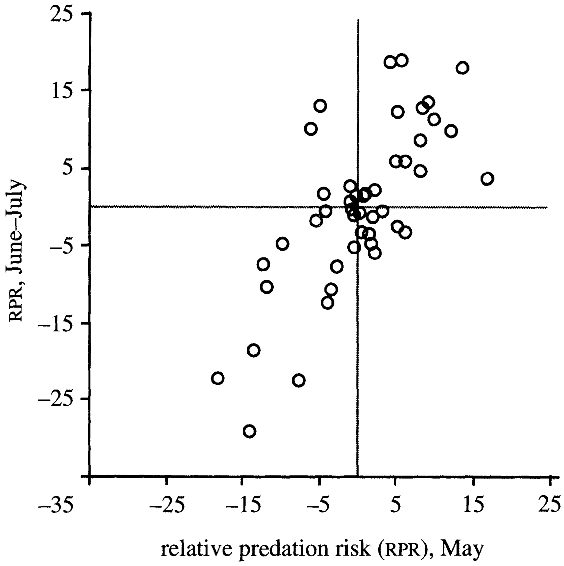

Figure 1. Correlation of Relative Predation Risk (RPR) for 46 prey species taken by sparrowhawks in Sweden during two periods (May and June–July), based on mean values for 1994 and 1995. The circles represent individual species.

The analyses above reflect prey selection across habitats in the hawk territories. Hunting sparrowhawks seem to avoid dense forests, especially spruce forests, instead using mainly deciduous forests (Marquiss & Newton 1981), forest edges, semi-open areas, farms and villages (Tinbergen 1946; Opdam 1978; see also below). To examine RPR in apparently preferred hunting habitats, P.P. made a separate census in each hawk territory in 1995, in both April and May. This census also covered 2 km, along smaller roads or trails in towns or villages, farmland, forest edges and deciduous forests. The exact census route was determined from maps and prior knowledge of each hawk territory. If a town or village, or farm, was located within a maximum of about 1200 m from the hawk nest, it was always included. On average, human habitation made up 25% of the 2 km census (s.d. = 13, range = 5–50%, $n = 21$). The censuses were done at varying distances, from 500 m to about 1200 m (in two cases 1500 and 1800 m) from the hawk nests, but did not overlap with the transect square near the nest. The two censuses, near the nest and in apparently preferred hunting habitats, were done on the same day and during the same hours by F.G. and P.P., making them fully comparable (the latter were also corrected for diurnal and seasonal variation, as above). P.P. noted all birds seen or heard; differences in detectability of species were corrected for by using K values estimated from the censuses near the nests.

In total, 66 bird species were identified in the prey remains; 67 potential prey species were recorded during censuses (Appendix 1). From calculations of RPR, species that were not accurately censused, because they were rare and/or had a patchy distribution, were excluded. Thus, the following were excluded: species recorded only once in the line transects, and also waders and gulls, domestic pigeon, swift, wood lark, house martin, mistle thrush, wheatear, whinchat, red-backed shrike and brambling (see Appendix 1). However, four species were included that were not recorded in the prey remains or recorded only once: cuckoo, green woodpecker, jackdaw and crested tit. These were not rare (Appendix 1) and were within the size range of prey taken by sparrowhawks. In total, RPR was calculated for 46 species (51 if pairs of species that were not distinguished are taken into account; see table 2).

(*e*) *Characteristics of prey species*

During censuses of prey species in areas apparently preferred by hunting hawks, P.P. recorded perch height above the ground, degree of exposure, and vocalization of prey. Hunting sparrowhawks often search for prey from the canopy of trees (Newton 1986; Gray 1987) and may prefer attacking prey that are closer to the ground. Perch height of prey was quantified by assigning each observation to one of five levels: (1) on the ground; (2) above ground but below 1 m; (3) between 1 and 4 m; (4) between 4 and 10 m; and (5) above 10 m. These levels corresponded to the means 0, 0.5 m, 2.5 m, 7.0 m and 15 m (an arbitrary but conservative mean). Exposure was described as follows: C, individual in cover, not permitting attack, or concealed by vegetation; I, intermediate cover or concealment, defined as 'prey being difficult but possible to attack by a sparrowhawk' (as when a bird was surrounded by 3–4 relatively heavy twigs within 1 m); and E, full exposure, 'more or less direct attack possible, without any difficult manoeuvres on the part of the hawk' (the prey could be on the ground, in or on a tree or bush, or on a building). Vocalizations may reveal the position of prey. It was noted whether the bird was silent, singing, or giving other types of call (pooled in one category, including alarm calls and various contact calls; see Catchpole & Slater (1995)). For sexually dichromatic species, the sex of the bird was recorded.

Many types of bias may influence these data. Only a subset of the individuals of a species might have been recorded, for instance those that were more exposed or were on top of bushes. To minimize bias, P.P. categorized each observation as 'complete visibility in habitat' (CVH) or 'incomplete visibility in habitat' (IVH). CVH meant that P.P. had a good view of potential perches in the habitat up to the point of the focal bird (including ground, bushes and trees). However, if there were hidden perches between P.P. and the bird, for instance dense bushes, it was categorized as 'IVH'. P.P. walked slowly, searching for birds; for CVH observations, few individuals were probably overlooked in the habitat, but for IVH observations more individuals were probably overlooked. Sometimes P.P. walked closer or changed position and was able to record an observation as CVH instead of IVH. For each species, CVH and IVH observations were compared by means of a Mann–Whitney U-test. If a significant difference was found, only CVH observations were used; otherwise the data were pooled.

In May, leafing of bushes and trees made it difficult to observe some birds even near the observer. To avoid a visibility bias, an attempt was made to record all birds within 7 m on both sides of the observer. If a bird was heard but not seen within 7 m, P.P. carefully walked closer to record it. Disturbance was minimized as far as possible by walking slowly and by using small roads and trails where birds were used to people. Moreover, the records were positions where the birds were first seen. If, for instance, a thrush flew up from the ground, P.P. recorded 'ground' and relevant exposure and vocalization. Disturbance was probably not a serious bias, as most birds seemed to ignore P.P. For data from May, CVH and 7 m observations were compared; observations were pooled if they did not differ significantly. For a few species, there were fewer than 10 observations both for CVH and 7 m, and a statistical test was not meaningful. Unless the observations clearly seemed to differ, they were pooled. For each period (April or May), a species was only included in the behavioural analyses if ten or more observations were available. The precision of mean values differs owing to variation in sample size (Appendix 2*a*, *b*), but no systematic bias was expected with respect to sample size.

Perch height and exposure were also combined to construct a 'risk' index. It was assumed that predation risk decreases from the ground to the top of trees, converting the mean heights 0, 0.5, 2.5, 7.0, and 15 m to risk values of 8, 4, 2, 1, and 0.5, respectively. Risk values were then assigned as follows: 0 for individuals in cover (C), 1 for those in intermediate cover (I), and 3 for those that were exposed (E). Finally, for each observation, the perch height value was multiplied by the exposure value. A bird in cover on the ground obtained a value of 0, and an exposed bird in the top of a tree obtained a value of 1.5. The maximal value was 24 (exposed bird on ground; 3×8).

Foraging height of prey species may influence predation risk (Selås 1993). At the spot where the bird was first seen and classified, it was often difficult to determine whether it was foraging or not, and foraging height could not be quantified. Instead, F.G. classified the species, on the basis of experience and the handbook *Birds of the Western Palearctic* (Cramp 1985–1994), into three categories: (1) foraging mainly on the ground; (2) foraging mainly in bushes and lower parts of trees (stem and lowest branches); and (3) foraging mainly in the upper part of (large) trees. Some species, such as finches, forage both on the ground and in trees. By focusing on foraging in early summer, most such cases were resolved (in a few cases, a value of 2 was assigned to species foraging both on ground and in tree tops). Two classifications of the species were also done independently by two other ornithologists, using the same method. The three classifications were highly intercorrelated (Spearman's $r_s = 0.74$–0.86). A mean rank was calculated for each species and used in the analysis.

Some authors have assumed that predation risk decreases with increasing nest height (Shutler & Weatherhead 1990, p. 1969; Johnson 1991, p. 60). As for foraging height, three classifications of nest height of the prey species were made, based on data in Haftorn (1971) and Cramp (1985–1994). The value 1 was used for nests on the ground, 2 mostly for species that mainly use nest boxes in Sweden, and 3 for nests in canopy of trees (the data also allowed use of intermediate values of 1.5 and 2.5). The classifications were highly intercorrelated ($r_s = 0.80$–0.88). A mean rank was calculated for each species.

Size of prey species was estimated by body mass, taken from the literature (Dunning 1993; Cramp 1985–1994). The means of the masses of the two sexes, and the best available data with regard to sample size, season and geographical location, were used. All statistical tests were two-tailed.

3. RESULTS

(*a*) *RPR for prey species*

The sparrowhawks caught mainly birds. Small rodents, taken early in spring in particular, made up 4.3% (1994) and 1.2% (1995) of the prey items (Appendix 1). However, analysis of prey remains may underestimate the frequency of mammalian prey (Bielefeldt *et al.* 1992). Of the 66 bird species recorded, 56 (85%) were passerines. Four passerines, the great tit, blue tit, robin, and house or tree sparrow, together accounted for 49% (1994) and 45% (1995) of all prey items (Appendix 1).

Mean RPR for prey species censused near the hawk nests (table 2) ranged from −13 to +22 in 1994, and from −12 to +17 in 1995. However, most species had values between −6 and +6 (61% in 1994, 76% in 1995). Three species had very low values in both 1994 and 1995: goldcrest, willow warbler, and coal tit. Apart from house or tree sparrow, which had very high mean RPR in both years, several species with high RPR showed marked differences between years, suggesting that predation risk in these species may vary. Mean RPR for individual prey species in 1994 and 1995 were correlated ($r = 0.83$, $n = 46$), but less so if house or tree sparrow, goldcrest, willow warbler, and coal tit are excluded ($r = 0.70$, $n = 42$).

Two species (green woodpecker and crested tit) were not recorded in the prey remains; determination of their exact RPR requires more work. For species with no or few taken individuals, RPR is largely determined by the relative density (relatively uncommon species obtain high RPR, common ones low RPR). For some species that were rare in the census, but where several or many individuals were taken, the risk of predation is probably high (redstart and hawfinch are two examples; table 2, Appendix 1). Owing to its behaviour, the spotted flycatcher may be difficult to detect and census; its RPR value is perhaps overestimated. Prey species common in town or village, farmland and edge habitats were overrepresented in the diet, with high RPR (house or tree sparrow, greenfinch, white wagtail, yellowhammer). Hence, the hawks often hunted in these habitats or had higher attack success there (or both). In 1995, prey species were also censused in these apparently preferred habitats. RPR values based on these censuses (table 3) were correlated with RPR based on censuses near nests

Table 2. *Relative Predation Risk* (RPR) *for avian prey taken by Sparrowhawks in SW Sweden*

(Values are means based on 18 (1994) and 21 (1995) breeding hawk pairs; RPR values were first calculated separately for each hawk pair. For Latin names of species, see Appendix 1.)

species	1994 mean RPR (s.d.)	1995 mean RPR (s.d.)
house/tree sparrow	22.5 (14.0)	17.2 (17.2)
greenfinch	14.2 (8.9)	3.4 (7.6)
hawfinch	12.3 (8.5)	3.2 (11.2)
spotted flycatcher	9.2 (9.5)	3.3 (12.0)
white wagtail	8.2 (12.7)	6.1 (13.7)
reed bunting	7.1 (11.0)	8.6 (8.8)
nuthatch	7.0 (11.3)	2.4 (14.7)
yellowhammer	6.4 (11.3)	4.6 (9.1)
redpoll	5.8 (9.9)	6.2 (10.7)
linnet	5.8 (12.6)	6.6 (11.9)
starling	5.1 (15.0)	5.1 (16.6)
blue tit	4.6 (4.7)	0.2 (9.1)
treecreeper	4.5 (13.2)	−4.6 (13.2)
marsh/willow tit	3.9 (14.7)	0.8 (9.7)
redstart	3.7 (7.8)	8.6 (11.5)
skylark	2.9 (10.2)	4.0 (10.5)
barn swallow	2.7 (6.1)	4.2 (7.1)
song thrush	2.7 (8.7)	1.8 (9.2)
cuckoo	2.7 (4.6)	3.8 (5.5)
jackdaw	2.6 (7.0)	1.4 (7.3)
whitethroat	2.6 (10.2)	−1.1 (11.6)
great spotted woodpecker	2.1 (13.6)	1.2 (8.4)
bullfinch	2.1 (10.2)	0.3 (13.3)
pied flycatcher	1.5 (15.2)	3.0 (10.1)
great tit	1.2 (2.3)	3.4 (2.2)
green woodpecker	0.1 (6.2)	0.2 (5.2)
robin	−1.1 (7.5)	0.1 (3.0)
crossbill/parrot crossbill	−1.6 (9.6)	3.1 (5.0)
fieldfare	−1.9 (13.6)	−3.2 (12.7)
dunnock	−3.1 (13.2)	−2.8 (10.4)
blackbird	−3.2 (12.6)	−1.9 (7.5)
jay	−3.4 (13.6)	0.1 (9.4)
magpie	−3.7 (10.8)	−2.9 (13.3)
crested tit	−5.0 (11.9)	−4.0 (13.3)
wood warbler	−5.2 (14.2)	−4.1 (11.4)
garden warbler	−5.9 (12.2)	−6.9 (12.9)
lesser whitethroat	−6.3 (11.0)	1.4 (11.5)
siskin	−6.5 (10.7)	−0.4 (11.8)
meadow/tree pipit	−6.7 (11.7)	−3.4 (11.9)
wood pigeon	−7.4 (9.9)	−5.3 (9.7)
wren	−7.4 (15.0)	−9.4 (12.0)
chaffinch	−7.5 (6.6)	−4.4 (8.4)
blackcap	−11.4 (9.8)	−0.7 (8.1)
goldcrest	−11.8 (12.3)	−12.2 (13.2)
willow warbler/chiffchaff	−13.1 (10.3)	−9.7 (10.0)
coal tit	−13.2 (11.0)	−8.4 (12.1)

Table 3. *Relative Predation Risk* (RPR) *for avian prey taken by sparrowhawks: comparison of mean* RPR *for apparently preferred hunting habitats (deciduous forest, forest edge, farmland, town/village) and habitats near hawk nests (many habitats, but mostly forest)*

(Based on censuses of prey species in the two types of habitats, conducted in each of the 21 hawk territories in 1995; $n = 21$.)

species	preferred hunting habitat mean RPR (s.d.)	habitats near nests mean RPR (s.d.)
reed bunting	8.8 (9.9)	8.6 (8.9)
white wagtail	8.7 (12.8)	6.1 (13.7)
bullfinch	6.9 (12.0)	0.3 (13.3)
house/tree sparrow	6.8 (12.8)	17.2 (17.2)
song thrush	6.7 (7.5)	1.8 (9.2)
redpoll	6.3 (9.6)	6.2 (10.7)
skylark	6.0 (6.9)	4.0 (10.5)
redstart	5.9 (11.9)	8.6 (11.5)
yellowhammer	5.8 (9.9)	4.6 (9.1)
nuthatch	3.6 (11.0)	2.4 (14.7)
hawfinch	3.1 (10.6)	3.2 (11.2)
cuckoo	3.1 (3.6)	3.8 (5.5)
great tit	2.8 (2.7)	3.4 (2.2)
green woodpecker	2.7 (3.4)	0.2 (5.2)
crested tit	2.4 (6.3)	−4.0 (13.3)
crossbill/parrot crossbill	2.1 (4.1)	3.1 (5.0)
lesser whitethroat	2.0 (12.7)	1.4 (11.5)
greenfinch	1.0 (8.3)	3.4 (7.6)
jackdaw	1.0 (7.7)	1.4 (7.3)
pied flycatcher	0.9 (8.8)	3.0 (10.1)
meadow/tree pipit	0.4 (12.0)	−3.4 (11.9)
siskin	0.4 (11.6)	−0.4 (11.8)
coal tit	0.4 (8.1)	−8.4 (12.1)
robin	0.3 (2.0)	0.1 (3.0)
spotted flycatcher	0.3 (13.8)	3.3 (12.0)
marsh/willow tit	0.2 (11.3)	0.8 (9.7)
barn swallow	−0.1 (9.9)	4.2 (7.1)
blackbird	−0.3 (10.3)	−1.9 (7.5)
dunnock	−1.1 (11.8)	−2.8 (10.4)
jay	−1.4 (17.8)	0.1 (9.4)
whitethroat	−1.7 (10.0)	−1.1 (11.6)
treecreeper	−2.0 (11.5)	−4.6 (13.2)
blackcap	−2.4 (7.3)	−0.7 (8.1)
fieldfare	−2.5 (13.3)	−3.2 (12.7)
blue tit	−3.7 (13.3)	0.2 (9.1)
wood pigeon	−4.1 (8.1)	−5.3 (9.7)
chaffinch	−4.4 (8.1)	−4.4 (8.4)
great spotted woodpecker	−5.9 (9.2)	1.2 (8.4)
garden warbler	−8.3 (11.2)	−6.9 (12.9)
starling	−8.9 (13.2)	5.1 (16.6)
wood warbler	−8.9 (8.7)	−4.1 (11.4)
wren	−9.3 (12.0)	−9.4 (12.0)
willow warbler	−9.4 (10.0)	−9.7 (10.0)
goldcrest	−10.7 (14.4)	−12.2 (13.2)
magpie	−14.0 (9.9)	−2.9 (13.3)

($r = 0.70$), suggesting that sparrowhawks tend to select certain prey also in preferred habitats. Thus, goldcrest, willow warbler, wren and chaffinch were underrepresented, whereas white wagtail, house or tree sparrow, and yellowhammer were overrepresented as prey (table 3). However, compared with the habitat near hawk nests, in apparently preferred habitat RPR for the magpie was low, and RPR for bullfinch and song thrush was high.

Two species mainly nesting in deciduous woodland, hawfinch and nuthatch, also had high RPR values (tables 2 and 3). The reed bunting, nesting in smaller wetlands with reeds, was not common. It was difficult to census by the method described above; its RPR (tables 2 and 3) is perhaps overestimated.

It is difficult to evaluate the accuracy of the RPR values, except by comparisons with other, similar studies (see §4). In the great tit, predation rate on fledglings was estimated in 1994 and 1995 by ringing nestlings, later recovering these rings from pellets collected at the hawk nests (Götmark & Olsson 1997). Although probably underestimated, the predation rate was 20% higher in 1995 (5.05%) than in 1994 (4.21%). These values cannot directly be compared with RPR, but mean RPR for the great tit was also higher in 1995 (3.4) than in 1994 (1.2; table 2).

(*b*) *Seasonal changes in* RPR

Below, unless otherwise stated, RPR values are those based on the censuses near the hawk nests, which reflected the average habitat composition of hawk territories. There were marked seasonal changes in RPR for many prey species (figure 2). For one group of species, RPR declined more or less dramatically from April 2 to June/July (figure 2*a*). Most of these were species breeding in forest. The wren and goldcrest were taken in relation to their abundance in April (RPR $\approx$ 0), but predation risk decreased later in the season. For several long-distance migrants, predation risk was relatively high as they arrived in May 1, decreasing to June, and stabilizing or increasing in June/July (figure 2*a*). For a second group of species, RPR increased from April 2 to May 2, remaining high until June/July (figure 2*b*). Most of these species nested in semi-open habitats: farmland, villages and towns. A third group of prey species showed little change or no consistent change in RPR during the season (figure 2*c*). At least three of these (chaffinch, great tit and robin) were widespread species, nesting in all or most habitats in the study area.

The numbers of house or tree sparrows taken in different periods indicate the use of farms, villages, and towns as hunting grounds by the hawks. In 1994, the overall proportions of house or tree sparrows in the diet of all hawk pairs were 6%, 9%, 16%, 23% and 14% in April 2, May 1, May 2, June and June/July, respectively. The corresponding figures from 1995 were 1%, 5%, 11%, 21% and 16%, respectively. For each hawk pair, the correlation was calculated between seasonal period and proportion of house or tree sparrows in the diet. For 1994, this correlation was positive for 16 of 18 pairs ($p = 0.002$, binomial test); for 1995, it was positive for 19 of 21 pairs ($p < 0.001$). Thus, from spring to early summer (at least to June), the hawks hunted increasingly in semi-open habitats near people.

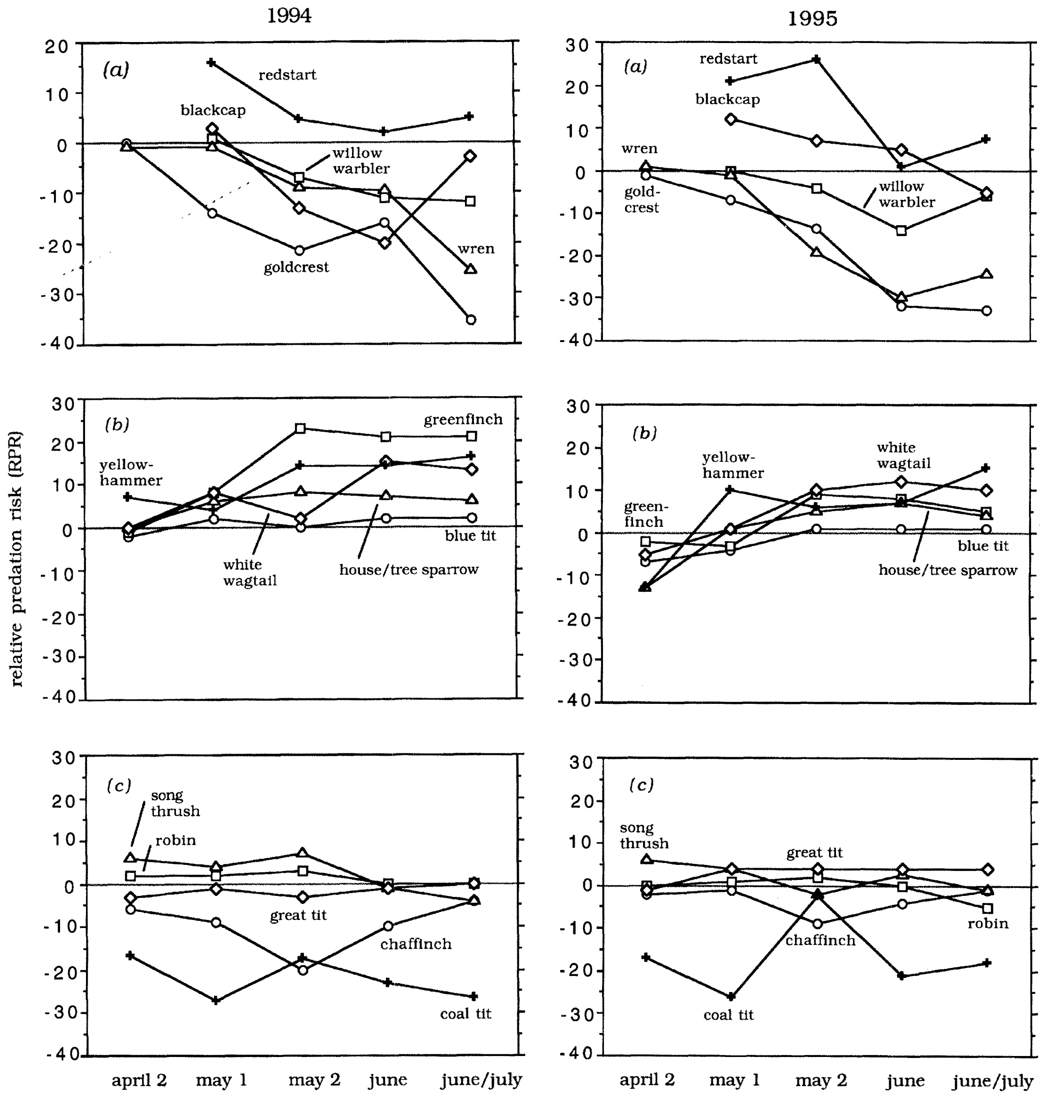

Figure 2. Seasonal pattern of Relative Predation Risk (RPR) for the major prey species of sparrowhawks in 1994 and 1995. (*a*) Prey species showing seasonal decline in RPR; (*b*) prey species showing seasonal increase in RPR; (*c*) Prey species showing no consistent trend in RPR. The seasonal periods were as described in §2*d*. In April 2, 12 tropical migrants had not yet arrived (or only few of them) and RPR is based only on the other 34 species. As there were fewer species to rank, this means that the range of RPR was somewhat more restricted for April 2 than for the other periods (see §2).

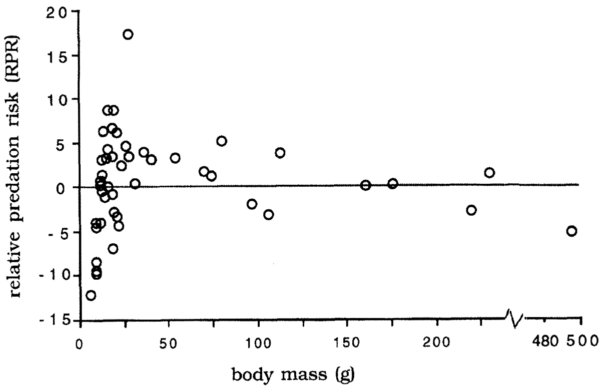

Figure 3. Relative Predation Risk (RPR) in relation to mean body mass (g) of 46 prey species (circles). RPR based on data from 1995 and the whole breeding season (April–July). The result was similar for data from 1994 (see text).

(*c*) *RPR in relation to characteristics of prey species*

(i) *Analyses based on all prey species*

Four factors that may influence RPR were analysed: body size (mass), abundance (relative density), foraging height, and nest height of prey species (Appendix 1). RPR seemed to be positively correlated with body mass in small species, but also seemed to decrease above a body mass of about 40 g (figure 3). For the 14 'larger' prey species (from skylark, 36 g, to wood pigeon, 490 g), RPR decreased significantly with increasing body mass in 1994 ($r_s = -0.60$, $p = 0.030$) and 1995 ($r_s = -0.64$, $p = 0.022$). In contrast, for the 32 'smaller' prey species (from goldcrest, 5.7 g, to bullfinch, 31 g), RPR increased significantly with body mass in 1994 ($r_s = 0.42$, $p = 0.017$) and 1995 ($r_s = 0.53$, $p = 0.003$). Decreased RPR among larger prey is expected, as they should be more difficult to catch or kill, especially for male sparrowhawks (Newton & Marquiss 1982; Newton 1986; Cresswell 1995, p. 386).

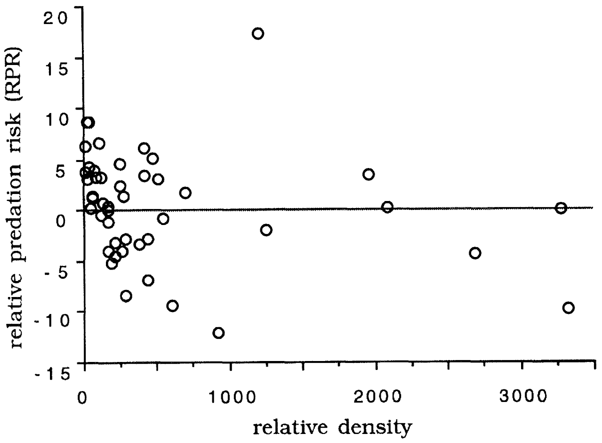

Figure 4. Relative Predation Risk (RPR) in relation to relative breeding density of 46 prey species in 1995 (the result was similar for data from 1994; see §3). Density determined from line transects near hawk nests (see text).

To control for the effect of size below, all 46 species, or only the 32 smaller species, were included in separate analyses.

RPR decreased with increasing relative density when all 46 prey species were included in the analysis (1994, $r_s = -0.49$, $p = 0.001$; 1995, $r_s = -0.41$, $p = 0.006$) (figure 4). The relation was similar when only the smaller prey species were included (1994, $r_s = -0.53$, $p = 0.003$; 1995, $r_s = -0.44$, $p = 0.015$) and when the censuses in apparently preferred hunting areas were used instead to calculate RPR (data not shown).

For 45 species (barn swallow excluded), RPR tended to decrease with increasing foraging height in 1994 (r_s = -0.21, $p = 0.16$) and 1995 ($r_s = -0.24, p = 0.11$) (figure 5*a*). The relation was stronger when only the smaller prey species were included in the analysis (1994, $r_s = -0.36$, $p = 0.047$; 1995, $r_s = -0.42$, $p = 0.021$) (figure 5*b*). The result was almost identical for RPR based on preferred hunting habitats (data not shown).

No relation was found between RPR and nest height in either 1994 or 1995 ($p > 0.90$, $n = 46$). This was also true when only the smaller species were included in the dataset (1994, $p = 0.48$; 1995, $p = 0.27$).

RPR values in the analyses above reflected predation risk during the breeding season for the prey species (table 2), but did not take into account differences in the total time that species were at risk. For instance, garden warblers, arriving mainly in mid-May, were present for a shorter period than were great tits. It is difficult to calculate predation per time unit, because the species arrive gradually in sequence and delimitation of exposure period is rather subjective. Moreover, predation by sparrowhawks increases with food demand during the season. Relatively few prey were recorded as taken in April 2 (table 1). Nevertheless, controlling for exposure time is important in the analyses above; the data were therefore reanalysed based on overall RPR values from the 15 day period May 2, when all breeding species were established and few fledglings had appeared. The results were essentially the same, as regards levels of significance. For the smaller species, similar or stronger negative correlations between RPR and foraging height were found for 1994 ($p = 0.017$) and 1995 ($p = 0.036$). The results of this reanalysis indicate a weak influence of exposure time on RPR, compared with other characteristics of the prey species.

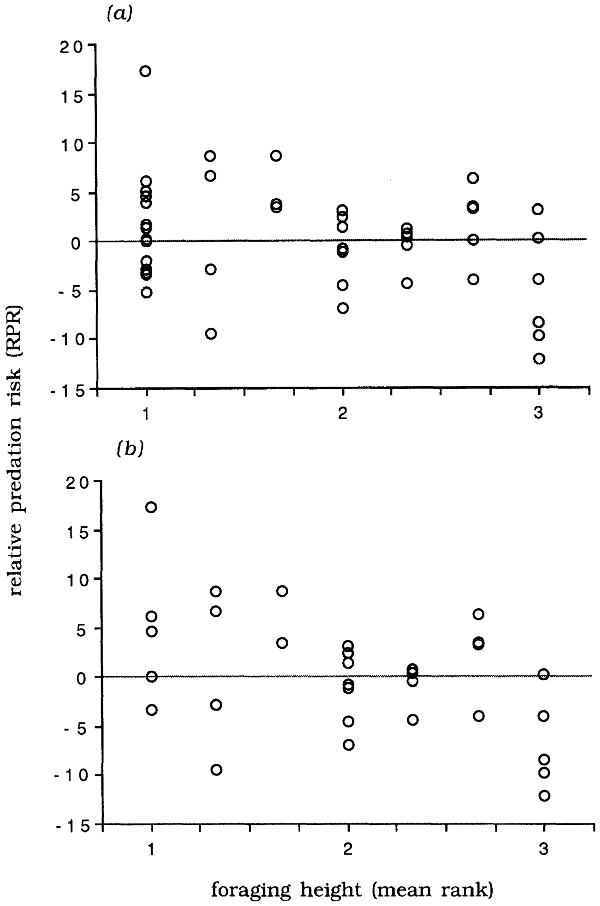

Figure 5. Relative Predation Risk (RPR) in relation to foraging height in the prey species. (*a*) All prey species ($n = 45$) included; (*b*) smaller prey species only (with body mass up to 31 g). Foraging heights of prey species were judged from handbooks; they correspond to mainly ground foraging (1), mainly foraging in bushes or in lower parts of trees (2), and mainly foraging in upper parts of trees (3) (mean rank was calculated from three classifications; see text). RPR data were from 1995; the results were similar for 1994 (see text).

Finally, covariation between body mass, relative density, foraging height, and nest height was examined. There was a strong negative correlation between foraging height and body mass, for all 45 species ($r_s = -0.56$, $p = 0.0002$) and for the smaller species ($r_s = -0.59$, $p = 0.001$). Thus, larger species more often foraged on the ground. Because of the strong collinearity between these variables, the authors followed the advice of James & McCulloch (1990) and did not use partial correlation analysis. In addition, nest height and body mass were positively correlated for all 46 species ($r_s = 0.37$, $p = 0.013$), but not for smaller species only ($p = 0.99$).

(ii) *Analyses based on behaviour of prey species in the field*

Prey behaviour was studied during the periods 16–30 April and 13–31 May 1995. Because behaviour may vary seasonally and annually (Morrison *et al.*

1990), overall RPR values from the same periods, i.e. April 2 and May 2 1995, were used. Three factors that may influence RPR were analysed: mean perch height of prey species, mean exposure in relation to vegetation, and mean risk index. Mean perch height was based on the mean height of the interval where the bird was recorded (see Methods); values for mean exposure were 0 (in cover), 1 (intermediate cover) and 2 (exposed) (see §2). Data were available for 23 and 27 species in April 2 and May 2, respectively (Appendix 2*a*, *b*).

For April 2, no significant relations were found between RPR and the three variables ($p \geqslant 0.78$). To take prey size into account, the data were reanalysed and nine larger species (> 40 g) were removed in three steps: wood pigeon, magpie, jay and jackdaw (the largest ones) in the first step; blackbird and fieldfare in the second step; and great spotted woodpecker, song thrush and starling in the third step (smallest). Singing, calling, and silent birds were included. There were no significant correlations ($0.93 \geqslant p \geqslant 0.17$), with the exception of two tendencies; RPR × exposure ($p = 0.06$) and risk index ($p = 0.08$) in step three. However, these two correlations were negative, contrary to what one would expect. If singing birds are excluded from the data, the observations would reflect foraging birds to a greater extent. Because foraging position seemed to influence RPR, the data were reanalysed to include only calling and silent birds. Again, when all 23 species were included, there were no significant correlations ($p \geqslant 0.31$). When steps 1–3 above were repeated, only one significant correlation was found, between RPR and exposure (step 3; $p = 0.03$). However, this correlation was also negative ($r_s = -0.63$).

In April 2, before egg laying, both male and female hawks probably hunted in the territory and contributed to the prey remains. Seasonal changes in RPR (figure 2) suggested that they mostly hunted near the nest in forest (see also Tinbergen 1946, and changes in range size in Newton 1986). Species with high RPR over most of the breeding season, such as house or tree sparrow, white wagtail and yellowhammer, had low RPR in April 2, apparently because the hawks did not come into contact with them. This may explain the negative correlations above. In May 2, however, only male hawks are hunting, and over a gradually expanding area.

For May 2, when all 27 species and all observations were included, no relations were found between RPR and mean perch height, mean exposure, or mean risk index ($p \geqslant 0.59$). The following species were excluded in three steps: (1) magpie and wood pigeon; (2) blackbird and fieldfare; and (3) song thrush and starling (species in the analyses differed in April and May; Appendix 2). The value of p decreased for each step of the analysis (from 1 to 3), but no significant relations were detected between RPR and perch height ($p \geqslant 0.24$), exposure ($p \geqslant 0.19$) or risk index ($p \geqslant 0.15$). When singing individuals were excluded, four species for which the sample sizes were too small (wren, whitethroat, lesser whitethroat and garden warbler) also had to be excluded. For calling and silent birds (23 species), no relations were found between RPR and the three variables ($0.78 \geqslant p \geqslant 0.26$). However, for each step in the analysis (1–3), the value of p decreased. For step 3, there were significant correlations between RPR and perch height ($p = 0.047$) (figure 6*a*) and between RPR and exposure ($p = 0.041$) (figure 6*b*). For the risk index, a correlation was found in both step 2 ($p = 0.048$) and step 3 ($p = 0.014$) (figure 6*c*).

Body mass covaried with exposure, with perch height, and in particular with risk index (May 2). Body mass and exposure were positively correlated, for all observations ($r_s = 0.63$, $p = 0.001$, $n = 27$), for non-singing birds ($r_s = 0.64$, $p = 0.003$, $n = 23$), and for non-singing small species ($r_s = 0.48$, $p = 0.056$, $n = 17$). Body mass and perch height were less well

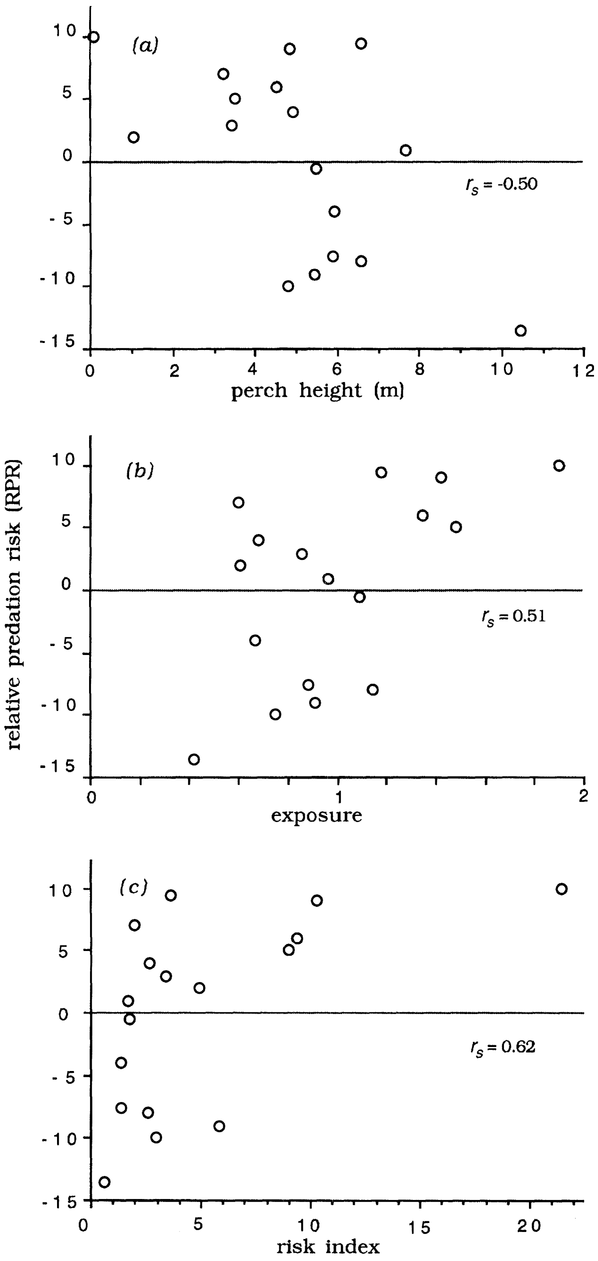

Figure 6. Relative Predation Risk (RPR) in May 2 1995 (see figure 2, and text) in relation to (*a*) mean perch height, (*b*) mean exposure, and (*c*) mean risk index in prey species (recorded during line transects in the latter part of May 1995). Only calling (non-singing) and silent birds were included in this analysis (see text).

Table 4. *Comparison of mean perch height (m) of singing and non-singing birds (silent, or giving various calls, but no typical song) during censuses in hawk territories in April and May 1995 (preferred hunting habitats)*

(Several species for which it was difficult to separate song from calls, such as house/tree sparrow and jackdaw, were not included; *n* is number of individuals.)

	April				May			
	Singing		Non-singing		Singing		Non – singing	
species	mean (s.d.)	*n*	mean (s.d.)	*n*	mean (s.d.)	*n*	mean (s.d.)	*n*
great spotted woodpecker	9.7 (4.6)	3	8.2 (5.4)	19	—		—	
great tit	6.7 (4.5)	18	3.3 (3.9)	187	6.4 (4.0)	24	4.9 (4.7)	103
blue tit	8.7 (4.3)	25	8.2 (4.8)	161	9.7 (5.4)	13	7.7(4.9)	87
nuthatch	11.8 (4.4)	5	5.7 (3.7)	15	—		6.6 (5.4)	21
wren	4.9 (4.7)	9	2.3 (4.5)	12	5.9 (4.8)	7	0.3 (0.3)	5
song thrush	13.7 (3.1)	12	1.6 (4.3)	27	15.0 —	1	0 (0)	12
blackbird	8.2 (6.3)	3	1.8 (3.4)	83	6.1 (5.0)	12	1.6 (3.5)	97
redstart	—		—		8.0 (5.2)	7	0.2 (0.4)	2
robin	7.0 (5.2)	95	1.0 (2.2)	61	4.6 (5.5)	7	1.1 (1.5)	58
blackcap	—		—		5.4 (4.7)	22	3.2 (3.3)	35
garden warbler	—		—		8.0 (5.6)	17	4.3 (2.5)	5
whitethroat	—		—		5.5 (4.6)	8	1.2 (1.8)	2
lesser whitethroat	—		—		3.4 (2.3)	8	1.5 (1.2)	4
chiffchaff/willow warbler	9.1 (4.3)	13	6.4 (5.3)	10	9.5 (4.3)	31	5.9 (4.6)	87
wood warbler	—		—		5.6 (4.7)	14	5.9 (3.2)	17
goldcrest	6.8 (5.1)	5	8.0 (4.4)	33	11.0 (5.7)	2	10.5 (5.1)	12
spotted flycatcher	—		—		15.0 —	1	6.6 (6.0)	17
pied flycatcher	—		—		5.6 (4.0)	22	3.4 (3.7)	35
dunnock	8.6 (5.6)	6	0 (0)	4	—			
starling	11.7 (4.1)	12	5.4 (6.3)	239	—		1.7 (3.7)	27
hawfinch	—		—		15.0 —	1	14.0 (2.8)	8
greenfinch	11.0 (5.1)	24	6.8 (5.3)	23	13.2 (3.5)	9	4.9 (5.4)	38
redpoll	—		—		15.0 (0)	2	12.8 (5.3)	12
bullfinch	—		—		15.0 —	1	4.8 (5.5)	12
chaffinch	8.9 (4.4)	33	3.7 (4.0)	173	6.8 (3.7)	25	5.5 (5.5)	98
yellowhammer	13.0 (4.0)	4	5.5 (5.4)	40	7 (0)	5	4.5 (5.1)	26

correlated for all observations ($p = 0.09$), for non-singing birds ($r_s = -0.45$, $p = 0.036$), and for non-singing small species ($r_s = -0.49$, $p = 0.051$). Body mass and risk index were strongly correlated for all observations ($r_s = 0.75$, $p = 0.0001$), for non-singing birds ($r_s = 0.79, p = 0.0002$), and for non-singing small species ($r_s = 0.73$, $p = 0.003$).

In April and May, singing birds were perched higher above the ground than non-singing birds in 24 of 26 species (table 4, $p < 0.001$, sign test). If species with small sample sizes (fewer than 10 individuals in a category) are excluded, singing birds were perched higher in 11 of 12 species ($p = 0.006$). In many cases, there were substantial differences in height between singing and non-singing birds (table 4) (see also Kouki *et al.* 1992). The data did not simply reflect a difference between males and females: in four dichromatic species: there was a high proportion of males (43–64%) among the non-singing birds.

4. DISCUSSION

(*a*) *Variation in* RPR

The diet of the sparrowhawks in this study did not simply reflect the abundance of the prey species: proportions of different species taken did not correspond to proportions of the same species censused near hawk nests. Instead, many prey species were over- or underrepresented in the diet. Of course, these conclusions depend on the reliability of the study methods. Line-transect censuses, including the Finnish method, give only relatively crude estimates of the densities of different species (see discussion and references in Verner (1985)). It is therefore appropriate to use ranks for the species when calculating RPR (see Johnson 1980). Nevertheless, larger diet and census samples are desirable for more accurate estimates of mean RPR for rare species and for adult birds in April and May.

The results for habitats surrounding the hawk nests and for apparently preferred hunting habitats were generally similar, indicating that some prey species face higher predation risk than others in most habitats used by the hawks. However, marked seasonal changes in RPR were also found. In April 2, the hawks seemed to hunt mainly in forest near the nests. From May 1 to June, more open habitats (forest edge, farmland, village or town) at some distance from the nests apparently increased in importance as hunting grounds. In a similar type of landscape in Holland, the sparrowhawks seemed to shift hunting grounds in the same way (Tinbergen 1946; see also Opdam 1978). In Britain, radio-tracking of breeding hawks demonstrated that hunting ranges increase from early spring to late summer (Marquiss & Newton 1981; Newton 1986). These changes coincide with changes in the composition of the prey community and marked changes in the environment (in the area of the present study, the trees are leafless and there is little vegetation on the ground in April; leafing and ground vegetation are not fully developed until early June).

There are several explanations for the seasonal change in sparrowhawk predation. In April, territory defence, nest building and mate guarding may restrict the hunting to areas close to the nests. However, as soon as the females start incubating, the males can use all parts of the territory. Although the food demand does not increase, the males seem to expand the hunting grounds in May (from May 1 to May 2) (figure 2). By exploring the surroundings, the males may identify sites with the highest prey density (Tinbergen 1946). In addition, leafing and growing ground vegetation in May probably makes it more difficult to catch prey in woodland and other natural habitats. Several prey species, such as finches, forage more in trees in May and June (see Cramp 1985–1994), where they should be more difficult to catch.

More work is needed to clarify the seasonal changes in sparrowhawk predation. These changes are important, as they imply that the prey species face different predation risks during different parts of the breeding season. For example, several tropical migrants seemed to face higher predation risk on arrival (in May 1) than later on (figure 2*a*) (see also table 41 in Tinbergen (1946)). It is possible that they were easier to catch in trees before than after leafing, or foraged more on the ground early in the season. Widespread species occurring in most types of habitat experienced little change in RPR (figure 2*c*) (Tinbergen 1946), but populations within these species (in forests compared with villages) may differ in RPR.

(*b*) *Characteristics of prey species and* RPR

(i) *Analyses based on all prey species*

The size of prey species obviously influences predation risk from sparrowhawks (van Beusekom 1972; Opdam 1975; Newton & Marquiss 1982; Newton 1986; Selås 1993; Cresswell 1995). As expected, among the larger prey (from skylark to wood pigeon), RPR decreased with increasing body mass. Increasing RPR with body size among the small prey species (from goldcrest to bullfinch) may be explained in at least two ways. First, owing to size *per se* or to other traits, the larger finches and sparrows may be easier for male hawks to catch than the smaller warblers are. Second, finches and sparrows may be more profitable as prey, because they provide more meat for the hawk than the smaller species.

Body size was strongly correlated with foraging height, however, for all prey species and for the smaller ones. Selås (1993) suggested that predation risk from sparrowhawks decreases with increasing foraging height of prey species (see also Gray (1987), pp. 74–75). In general, prey should be vulnerable to predation while foraging, as they can devote little time to vigilance (Lima & Dill 1990). Hunting sparrowhawks, which usually search for prey from trees (Newton 1986; Gray 1987), probably prefer attacking prey that are below them, for which the approach would be easier and more concealed. On the ground, the chance that a foraging prey detects the hawk may be relatively low, and there are fewer directions for escape than in bushes and trees. In addition, exposed prey on the ground are usually further from cover than are exposed prey on bushes and trees. In this study, a correlation was found between foraging height and RPR; this correlation was significant when the larger species were excluded. Thus, foraging height may be an important factor (see also Selås 1993) but given covariation with body mass, the causal relations remain to be clarified. Body size *per se* is probably involved, but we suggest that foraging height, especially in combination with exposure, are more important for predation risk in the smaller passerines. Unfortunately, there is little evidence on this point. Gray (1987, p. 66) reported higher success for attacks on prey on the ground (21 %, $n = 19$) than for prey in the shrub layer (8 %, $n = 13$). Only four attacks were seen in the canopy (one successful). Of 37 attacks seen, 32 were directed at the ground or shrub layer (Gray 1987); however, attacks in trees may be more difficult to detect. To evaluate the role of foraging height, more data of this type are needed.

This study found no support for the assumption that nest height influences predation risk (Shutler & Weatherhead 1990; Johnson 1991). Sparrowhawks probably rarely find nests (Newton 1986) and the total time parents feed young in nests is small compared to the total foraging time. Moreover, nest and foraging heights were not correlated. Species nesting on the ground, such as the willow warbler, may forage in trees, and ground foragers may nest above the ground (for example, house or tree sparrow, song thrush).

In the winter in Scotland, predation risk (CSR; see §2) for species taken by sparrowhawks was not related to relative density of the prey (Cresswell 1995). In the present study, it was found that less abundant species suffered higher predation from sparrowhawks than common ones. Several models predict the reverse; that predators should concentrate on common species or varieties of prey (Holling 1965; Allen 1988; Crawley 1992), except in flocks where odd individuals may be at risk (Allen 1988; see also Cresswell 1995). In sparrowhawks, a response to overall prey density is likely, as the hawks nest at a higher density in areas with more prey (Newton 1986). However, as sparrowhawks rely on surprise to catch prey (Newton 1986), they may select them more on the basis of vulnerability than on species abundance. In this study, the hawks seemed to hunt mostly in deciduous groves, farmland, and villages or towns, where prey were more abundant or easier to catch (or both) than in forest. Most prey species with high RPR nested in these types of habitat. They were also relatively uncommon compared with abundant species in forest (chaffinch, willow warbler and great tit); this difference may explain the negative correlation between abundance and RPR. Alternatively, common species may have evolved better defence against sparrowhawks, or low RPR may be due to dilution of predation risk (Foster & Treherne 1981). Finally, the type of landscape in a study may influence RPR values; the results might have been different in continuous forest, as discussed below.

(*ii*) *Analyses based on behaviour of prey species in the field*

These analyses involved fewer prey species, but detailed field data. For April 2, no relations were found between RPR and exposure, perch height or risk index. Judging from prey selection, the hawks hunted mostly near the nests in forest (see also Tinbergen 1946; Newton 1986). In April 2, it would have been more relevant to study prey behaviour in the forest habitat only. Species of more open habitats were also excluded from the analyses, but no significant relations were found (data not shown; sample sizes were small, about 10 species). More work on RPR and prey behaviour is needed for this period.

In May 2, all prey species have arrived at the breeding grounds and male hawks are hunting in many types of habitat. May 2 is the period for which the best estimates of RPR are available. For prey species smaller than thrushes, relations were found between RPR and perch height, exposure, and risk index. Thrushes and larger prey may have low RPR at this time not only because of their size, but also because smaller, more easily caught prey are relatively abundant in our study area (see Newton 1986, and below). We therefore considered exclusion of the larger species in the analyses to be justified, at least for periods when only male hawks are hunting. When singing birds were excluded, so that the data contained more foraging birds, RPR increased with increasing exposure of the prey species. A negative relation between predation risk and cover was emphasized by Tinbergen (1946) and Newton (1986), and is supported by this result (see also Sodhi & Oliphant 1993; Suhonen 1993; and references therein). Prey species in farmland and villages may be more exposed (because there are fewer trees and less ground vegetation) than prey species in forest. For non-singing and silent birds, RPR was also correlated with perch height, presumably a reflection of the importance of foraging height. If our risk index accurately combined perch height and exposure into an overall risk for the prey species, one should expect a stronger correlation with RPR for this index than for height and exposure alone. Judging from the correlations (figure 6), this seemed to be true.

No relations with predation risk were found when singing birds were included in the data set in May 2. Many authors seem to assume that singing in males increases the risk of predation (Tinbergen 1946, pp. 196, 202; Opdam 1978, p. 142; Newton 1986, p. 125; Lima & Dill 1990, p. 631; Götmark 1993, p. 145; Catchpole & Slater 1995, pp. 76–77; but see Slagsvold *et al.* 1995, p. 1118; Cresswell 1994*b*). This assumption may not be true, however. Singing birds were generally perched higher above the ground than non-singing birds. Some birds, such as yellowhammer, robin and thrushes, forage on the ground but usually sing from the tops of bushes or trees. If a position on the ground or low in the vegetation increases predation risk in prey, as our results suggest, singing from a higher position would reduce the risk of predation. Moreover, singing birds, compared with foraging birds, may be more vigilant for predators. Communication theory suggests that males optimize vocal transmission in the environment by singing at some distance above the ground (Catchpole & Slater 1995), but reduced predation risk may also select for high singing position. In a detailed (unpublished) study of the chaffinch, F.G. and P.P. found that sparrowhawks caught more adult females than adult males in April and May, although females, but not males, incubate for part of this time. The hawks showed no preference for males or females, because they were attacked equally often in experiments with mounts near hawk nests (see Götmark (1995) for methods). However, males, especially singing ones, were generally perched higher in the vegetation than females.

(*c*) *Comparison with earlier studies*: *the importance of prey composition and type of landscape*

The study areas in Holland (Tinbergen 1946; Opdam 1978) and Sweden (present study) are similar with respect to habitat and prey composition. Tinbergen (1946) studied four prey species in detail, estimating the share of predation in the total mortality. Other factors being equal, this share should be correlated with RPR. Tinbergen's data were collected mainly in spring and late summer, and a direct comparison is difficult. However, from his study area with the most accurate data and 'theoretical values' of predation during the whole summer (table 50 in Tinbergen 1946), it is clear that predation share and RPR were similar for the house sparrow, great tit, chaffinch and coal tit. Predation accounted for 79%, 44%, 30% and 15% of the total mortality, respectively; the corresponding mean RPR values from this study were 20, 2, −6, and −11, respectively (overall RPR: 7, 2, −3, and −24; all values are means for the two years).

Because CSR (see §2) and RPR were correlated (this study: 1994, $r = 0.84$; 1995, $r = 0.73$), comparisons are also possible with other studies. In Opdam's (1978) study (in an area rich in prey, with much farmland), CSR values were presented for April and May; they are in good agreement with our RPR values for whole seasons. Species in agricultural and suburban areas suffered the highest predation risk; house sparrow, white wagtail and redstart had high CSR values (> 2.0), whereas chaffinch and robin were taken less than expected from their abundance (CSR = 0.5–1.0) and coal tit, goldcrest and willow warbler much less than expected (CSR = 0–0.5). The redstart was also vulnerable in the present study and in that of Tinbergen (in May; his figure 11), presumably because it forages much on the ground (Hogstad 1977) and often nests near human habitations.

For sparrowhawks nesting in continuous forests, or where prey density in villages and farmland is low, the diet consisted mainly of chaffinches, song thrushes, pipits and robins (tables 17 and 18 in Newton 1986; Selås 1993). In contrast, near prey-rich agricultural and suburban areas, house or tree sparrows and tits predominate as prey. A different suite of prey species is available to sparrowhawks in the former areas, and consequently predation risk for the prey species may be different. Selås' study, in a forest area with only 2% agricultural land, provides evidence for such a difference. For the breeding season (early May to late August), predation risk was high for song thrush, robin and whinchat (CSR > 4.0); relatively high for great tit, blackbird, white wagtail and siskin (1.7–3.3); somewhat lower for chaffinch and tree pipit (both 1.4); and low for pied flycatcher and willow warbler (0.8 and 0.3, respectively) (Selås 1993; V. Selås, personal communication). Predation risk was considerably higher for the song thrush and robin than in the present study or in that of Opdam, whereas the risk for chaffinch and willow warbler seemed to be similar (both the song thrush and robin are ground foragers).

Thus, as suggested by Newton (1986, p. 127), the type of landscape may influence relative predation risk for breeding passerine birds, at least where sparrowhawks are the major predators. Heterogeneous, partly open ecosystems, such as those where people have created farmland and settlements, may be characterized by relatively low predation risk for adult birds in forest patches. Newton (1986, p. 117) also suggested that in areas where small prey (tits, sparrows) are less abundant, predation risk for larger birds such as thrushes may increase. The high CSR for song thrush and blackbird in Selås' study supports this idea; they had high CSR (greater than 10) even early in the season when only male hawks were hunting (May–June) (V. Selås, personal communication).

(*d*) *Future studies*

The results of the present study suggest some predictions that may be tested in future work. First, for breeding passerines of approximately similar size, one should expect morphological antipredator adaptations, such as cryptic coloration, to a higher degree in species foraging low in the vegetation and especially on the ground. Note that crypsis needs to be studied in the field, and may occur in different forms (see Endler 1978, 1990; and for birds Götmark & Unger 1994; Götmark & Hohlfält 1995). Not only sparrowhawks, but also owls (see, for example, Suhonen 1993; Kullberg 1995) and buzzards are expected to prefer attacking prey on the ground. In addition, mammalian predators are more common on the ground than in trees (but all these predators take mainly mammalian prey). Second, behavioural antipredator adaptations should be more marked in passerines foraging closer to the ground. Examples of potential adaptations are increased vigilance, more time spent in vegetation, singing in vegetation, and more cryptic movements. Species nesting and foraging on the ground in partly open habitat, such as yellowhammer and meadow pipit, should avoid forest edges where sparrowhawks (and nest predators) may search for and attack prey. Forest edges are very rich in passerine birds (Hansson 1983) and may attract sparrowhawks. For discussion of habitat selection, behaviour of prey, and attack success of raptors, see Lima *et al.* (1987), Lima (1993) and Cresswell (1994*a*).

Detailed observational and comparative studies are needed to test these predictions. Caution is needed, however, in extrapolating the present findings to geographical areas other than Europe and parts of Asia. For instance, in North America there are three different-sized *Accipiter* hawks. The smallest species, the sharp-shinned hawk (*A. striatus*), appears to prey on birds mainly in the canopy of trees (Reynolds & Meslow 1984; but see Joy *et al.* 1994). The intermediate Cooper's hawk (*A. cooperii*), however, takes mainly ground-foraging birds and mammals (Bielefeldt *et al.* 1992). More work on predation risk in relation to the ecology and behaviour of breeding passerines is needed, especially in areas with predators other than sparrowhawks.

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Appendix 1. *Total number of prey identified in prey remains from breeding sparrowhawks, total number of birds (pairs) censused in all hawk territories during line transects, species-specific correction coefficients* (K) *for line transects estimated from our data (see Järvinen & Väisänen 1975, 1976, 1983), and foraging height, nest height and body mass for each prey species (see Methods for explanations)*

(*K* is given only for species included in the analyses. A total of 23 and 25 hawk pairs were studied during 1994 and 1995, respectively, but 4 (1994) and 2 (1995) pairs failed and produced prey remains only during part of the breeding season. In addition, in both years one pair produced few prey remains near the nest. Twelve hawk nest sites (territories) were common to both years. Rare, sparse or other species that could not be used in the analyses are also listed below. The line transects were done close to nests, covering many habitat types in each hawk territory (1995: 1), or in apparently preferred hunting habitat of sparrowhawks in each territory (1995: 2), that is, in deciduous forest, forest edge, farmland, and town or village. Data for line transects given below are raw data, not corrected for differences in detectability of species and effects of time of day or season (see text). An asterisk (*) denote species that were censused in May (for all other species, line transect numbers were based on the April census). In 1994, a total of 23 hawk territories censused in April, and 22 censused in May were included (one hawk pair failed early in May and was not studied in May). In 1995, in total 23 hawk territories, censused in both April and May, were included. A dash (—) means that the species was not censused or used in the analyses.)

species	no. in prey remains		no. in line transects			*K*	foraging height^{a}	nest height^{a}	body mass (g)
	1994	1995	1994	1995: 1	1995: 2				
sparrowhawk *Accipiter nisus*	1	0	—	—	—	—	—	—	—
snipe *Gallinago gallinago*	2	1	1	3	0	—	—	—	—
woodcock *Scolopax rusticola*	3	1	1	0	0	—	—	—	—
green sandpiper *Tringa ochropus*	0	0	5	6	4	—	—	—	—
black-headed gull *Larus ridibundus*	1	0	—	—	—	—	—	—	—
wood pigeon *Columba palumbus*	9	4	84	49	60	3.90	1.0	2.7	490
domestic pigeon *C. livia domesticus*	0	2	6	3	12	—	—	—	—
collared turtle dove *Streptopelia decaocto*	0	0	0	1	0	—	—	—	—
cuckoo *Cuculus canorus**	0	1	12	10	2	0.70^{b}	1.7	1.2	115
swift *Apus apus**	0	2	1	11	22	—	—	—	—
great spotted woodpecker *Dendrocopus major*	10	3	21	14	37	4.90	2.3	2.5	74
lesser spotted woodpecker *D. minor*	0	0	1	0	0	—	—	—	—
green woodpecker *Picus viridis*	0	0	10	12	4	—	1.0	2.5	195
skylark *Alauda arvensis*	3	11	18	30	14	2.65	1.0	1.0	36
wood lark *Lullula arborea*	1	1	7	3	0	—	—	—	—
barn swallow *Hirundo rustica**	1	3	7	14	24	—	—	—	—
house martin *Delichon urbica**	1	6	1	0	5	—	—	—	—
jay *Garrulus glandarius*	8	9	32	22	28	8.08	2.7	2.5	161
magpie *Pica pica*	1	4	22	32	95	9.42	1.0	2.8	220
jackdaw *Corvus monedula*	0	1	3	22	24	2.82	1.0	2.8	230
great tit *Parus major*	265	220	238	201	234	10.3	2.7	2.0	18.2
blue tit *P. caeruleus*	175	133	99	169	232	13.1	3.0	2.0	11.8
crested tit *P. cristatus*	0	0	13	14	3	11.0	2.7	1.8	11.5
coal tit *P. ater*	1	1	43	38	10	8.91	3.0	1.7	9.5
marsh/willow tit *P. palustris/montanus*	14	6	6/28	9/8	12/2	7.00	2.3	1.8	11.5
long-tailed tit *Aegithalos caudatus*	3	0	0	1	1	—	—	—	—
nuthatch *Sitta europaea*	21	19	28	58	40	4.36	2.0	1.8	23
treecreeper *Certhia familiaris*	7	3	9	17	12	14.0	2.0	1.8	8.9
waxwing *Bombycilla garrulus*	0	1	1	0	0	—	—	—	—
wren *Troglodytes troglodytes*	10	15	69	99	91	5.64	1.3	1.3	9.3
fieldfare *Turdus pilaris*	4	5	31	39	71	5.96	1.0	2.7	106
song thrush *T. philomelos*	55	63	127	156	72	4.04	1.0	2.2	70
blackbird *T. merula*	60	71	172	180	160	7.30^{c}	1.0	1.5	97
mistle thrush *T. viscivorus*	3	0	1	5	0	—	—	—	—
wheatear *Oenanthe oenanthe**	2	5	0	5	0	—	—	—	—
whinchat *Saxicola rubetra**	1	1	1	8	4	—	—	—	—
redstart *Phoenicurus phoenicurus**	5	9	15	10	13	3.60	1.3	2.2	15.9
robin *Erithacus rubecula*	151	164	327	415	301	7.66	1.0	1.0	16.3
blackcap *Sylvia atricapilla**	22	42	108	94	118	4.78	2.0	1.7	18.5
garden warbler *S. borin**	16	18	35	34	49	5.64	2.0	1.7	18.7
whitethroat *S. communis**	4	5	17	28	28	6.30	2.0	1.5	14.5
lesser whitethroat *S. curruca**	6	22	32	40	47	6.48	2.0	1.7	12.4
willow warbler *Phylloscopus trochilus**/chiffchaff *P. collybita**	43	60	463/9	541/8	480/15	6.27	3.0	1.0	8.9
wood warbler *P. sibilatrix**	5	7	57	58	90	5.41	3.0	1.0	9.5

Appendix 1 (*cont.*)

species	no. in prey remains 1994	1995	no. in line transects 1994	1995: 1	1995: 2	*K*	foraging height[a]	nest height[a]	body mass (g)
goldcrest *Regulus regulus*	21	12	75	77	90	13.1	3.0	2.8	5.7
spotted flycatcher *Muscicapa striata**	9	4	3	8	18	10.8	2.7	2.2	15.2
pied flycatcher *Ficedula hypoleuca**	44	42	99	89	119	5.90	2.0	2.0	12.5
dunnock *Prunella modularis*	31	24	99	85	43	4.85	1.3	1.7	19.7
meadow pipit *Anthus pratensis*/tree pipit *A. trivialis**	11	28	26/63	37/55	13/58	4.00	1.0	1.0	21
white wagtail *Motacilla alba*	56	87	40	60	63	6.82	1.0	1.3	21
red-backed shrike *Lanius collurio**	0	1	0	4	4	—	—	—	—
starling *Sturnus vulgaris*	40	30	62	63	190	6.52	1.0	2.2	80
hawfinch *Coccothraustes coccothraustes*	14	10	5	17	30	6.09	2.7	2.7	54
greenfinch *Carduelis chloris*	84	49	108	157	154	2.24	1.7	1.8	28
siskin *C. spinus*	21	5	158	31	27	4.33	2.3	2.3	13.0
linnet *C. cannabina*	7	15	12	15	(4)[d]	5.80	1.3	1.8	18.2
redpoll *C. flammea*	13	7	53	14	7	1.16	2.7	2.3	13.5
bullfinch *Pyrrhula pyrrhula*	6	10	19	31	9	5.20	2.3	2.2	31
crossbill *Loxia curvirostra*/parrot crossbill *L. pityopsittacus*	9	0	55	7	3	2.39	3.0	2.8	41
chaffinch *Fringilla coelebs*	62	87	454	461	341	5.01	2.3	2.5	22
brambling *F. montifringilla*	1	0	13	13	3	—	—	—	—
yellowhammer *Emberiza citrinella*	51	37	84	84	78	3.10	1.0	1.0	26
reed bunting *E. schoeniclus*	5	10	5	4	1	6.08	1.7	1.0	19.0
house sparrow *Passer domesticus*/tree sparrow *P. montanus*	258	202	52	73	179	14.5	1.0	2.2	28
budgerigar *Melopsittacus undulatus*	0	1	0	0	0	—	—	—	—
unidentified birds	4	2	0	0	0	—	—	—	—
unidentified small rodents	75	20	—	—	—	—	—	—	—
total	1736	1602	3646	3852					

[a] Mean rank based on three independent scorings of foraging and nest height (1 corresponding to ground; see Methods).
[b] *K* value taken from Järvinen & Väisänen (numbers in census too small for estimation of *K* from present study).
[c] *K* is a mean value of estimate from present study and that of Järvinen & Väisänen.
[d] Census inaccurate for this species (not included in table 3).

Appendix 2. *Behavioural data for prey species studied during censuses in* (a) *April and* (b) *May 1995 in habitats apparently preferred by hunting hawks*

(Values are mean, s.d. (in parentheses), and *n* (number of individuals). Calculations are given for all observations, and for non-singing birds only (those that were silent or gave calls, but no song). When sample sizes were smaller than 10, the data were not used in the analyses (indicated by dashes).)

species	perch height (m)[a] all birds	no song	exposure[b] all birds	no song	risk index[c] all birds	no song
(*a*) April data						
wood pigeon	3.2 (5.2) 50	3.2 (5.2) 50	1.6 (0.8) 60	1.6 (0.8) 60	16.6 (10.9) 50	16.6 (10.9) 50
great spotted woodpecker	8.4 (5.2) 22	8.2 (5.4) 19	1.0 (1.0) 22	1.2 (1.0) 19	3.8 (7.1) 22	4.4 (7.5) 19
jay	5.2 (7.1) 10	5.2 (7.1) 10	1.1 (1.0) 10	1.1 (1.0) 10	10.6 (11.8) 10	10.6 (11.8) 10
magpie	4.9 (5.3) 83	4.9 (5.3) 83	1.3 (0.9) 108	1.3 (0.9) 108	9.3 (10.6)83	9.3 (10.6) 83
jackdaw	10.3 (5.9) 16	10.3 (5.9) 16	1.9 (0.2) 16	1.9 (0.2) 16	4.7 (7.6) 16	4.7 (7.6) 16
great tit	3.6 (4.1) 208	3.3 (3.9) 187	0.9 (0.8) 209	0.9 (0.8) 188	4.1 (6.7) 206	4.4 (6.9) 185
blue tit	8.3 (4.7) 186	8.2 (4.8) 161	1.3 (0.8) 186	1.2 (0.8) 161	2.1 (2.7) 186	2.1 (2.8) 161
marsh/willow tit	5.7 (3.5) 16	4.9 (2.5) 14	0.8 (0.9) 16	0.6 (0.8) 14	1.7 (3.2) 16	1.8 (3.4) 14
nuthatch	7.6 (4.8) 21	5.7 (3.7) 15	1.0 (0.8) 21	1.0 (0.7) 15	2.5 (5.1) 21	3.0 (6.0) 15
tree creeper	4.7 (4.9) 15	4.7 (4.9) 15	0.8 (0.7) 15	0.8 (0.7) 15	2.3 (3.1) 15	2.3 (3.1)) 15
wren	3.4 (4.6) 21	2.3 (4.5) 12	0.9 (0.8) 21	0.5 (0.7) 12	3.5 (4.1) 21	2.8 (4.2) 12
fieldfare	8.7 (6.0) 51	8.6 (6.0) 50	0.9 (0.8) 51	0.9 (0.8) 50	4.2 (8.6) 51	4.3 (8.7) 50
song thrush	5.3 (6.8) 39	1.6 (4.3) 27	1.0 (0.8) 29	0.7 (0.8) 23	6.0 (8.9) 39	8.0 (10.1) 27
blackbird	2.1 (3.7) 86	1.9 (3.4) 83	1.1 (0.8) 110	1.0 (0.8) 102	9.0 (10.1) 86	9.2 (10.2) 83
robin	4.7 (5.2) 157	1.0 (2.2) 61	1.1 (0.8) 157	0.8 (0.9) 61	4.1 (6.9) 157	6.8 (9.5) 61
goldcrest	7.8 (4.4) 38	8.0 (4.4) 33	0.8 (0.8) 38	0.8 (0.8) 33	1.0 (1.5) 38	1.0 (1.5) 33
dunnock	5.2 (6.1) 10	—	0.9 (1.0) 10	—	1.0 (1.2) 10	—
white wagtail	2.6 (3.3) 52	2.6 (3.3) 52	2.0 (0.1) 52	2.0 (0.1) 52	15.0 (10.3) 52	15.0 (10.3) 52

Appendix 2 (*cont.*)

	perch height (m)[a]		exposure[b]		risk index[c]	
species	all birds	no song	all birds	no song	all birds	no song
starling	5.8 (6.4) 255	5.4 (6.3) 239	1.8 (0.6) 255	1.8 (0.6) 239	12.3 (11.2) 255	13.0 (11.2) 239
greenfinch	8.9 (5.6) 47	6.8 (5.3) 23	1.6 (0.7) 78	1.5 (0.8) 36	2.4 (3.1) 78	2.7 (4.0) 36
chaffinch	4.5 (4.4) 209	3.7 (4.0) 173	1.1 (0.8) 209	1.1 (0.8) 173	6.5 (9.3) 209	7.6 (9.9) 173
yellowhammer	6.2 (5.6) 44	5.5 (5.4) 40	1.6 (0.7) 44	1.6 (0.7) 40	8.4 (10.3) 44	9.1 (10.5) 40
house/tree sparrow	3.6 (4.1) 212	3.6 (4.1) 199	1.3 (0.9) 201	1.3 (0.9) 199	6.8 (9.0) 201	6.8 (9.0) 199
(*b*) May data						
wood pigeon	7.0 (5.4) 17	7.0 (5.4) 17	1.5 (0.9) 17	1.5 (0.9) 17	7.0 (9.8) 17	6.9 (9.8) 17
magpie	2.8 (4.6) 72	2.8 (4.6) 72	1.6 (0.7) 72	1.6 (0.7) 72	15.9 (10.9) 72	15.9 (10.9) 72
great tit	5.2 (4.6) 127	4.9 (4.7) 103	0.6 (0.8) 127	0.7 (0.8) 103	2.4 (5.3) 127	2.7 (5.7) 103
blue tit	7.9 (5.0) 101	7.7 (4.9) 87	1.0 (0.9) 101	1.0 (0.9) 87	1.7 (2.8) 101	1.7 (3.0) 87
nuthatch	6.6 (5.4) 21	6.6 (5.4) 21	1.1 (0.9) 21	1.4 (0.9) 21	2.5 (3.0) 21	2.5 (3.0) 21
treecreeper	5.5 (4.0) 11	5.5 (4.0) 11	1.1 (1.0) 11	1.1 (1.0) 11	1.8 (2.0) 11	1.8 (2.0) 11
wren	3.7 (4.8) 12	0.3 (0.3) 5	0.8 (0.9) 12	0.8 (0.8) 5	4.4 (7.2) 12	6.4 (10.0) 5
fieldfare	4.0 (6.0) 26	4.0 (6.0) 26	1.7 (0.6) 26	1.7 (0.6) 26	16.0 (11.2) 26	16.0 (11.2) 26
song thrush	1.2 (4.2) 13	0.0 (0.0) 12	1.2 (0.9) 24	1.1 (0.9) 19	9.8 (10.6) 24	11.8 (11.1) 19
blackbird	2.1 (3.9) 109	1.6 (3.5) 97	1.1 (0.9) 109	1.1 (0.9) 97	10.0 (11.0) 109	10.8 (11.2) 97
robin	1.4 (2.4) 65	1.1 (1.5) 58	0.6 (0.9) 66	0.6 (0.9) 58	4.9 (8.5) 65	4.9 (8.5) 58
blackcap	4.1 (4.0) 57	3.2 (3.3) 35	0.5 (0.7) 57	0.6 (0.8) 35	1.4 (3.8) 57	2.0 (4.6) 35
garden warbler	7.1 (5.3) 22	4.3 (2.5) 5	0.5 (0.7) 21	—	0.6 (0.9) 21	1.0 (1.0) 5
whitethroat	4.6 (4.5) 10	—	1.3(0.9) 10	—	3.4 (3.8) 10	—
lesser whitethroat	2.8 (2.2) 12	—	0.2 (0.6) 12	—	0.4 (1.0) 12	—
willow warbler	6.9 (4.8) 118	5.9 (4.6) 87	0.7 (0.8) 116	0.7 (0.8) 87	1.3 (2.7) 116	1.4 (3.1) 87
wood warbler	5.8 (3.9) 30	5.9 (3.2) 17	1.0 (0.7) 31	0.9 (0.8) 17	2.4 (4.4) 31	1.4 (1.6) 17
goldcrest	10.5 (4.9) 14	10.5 (5.1) 12	0.4 (0.5) 14	0.4 (0.5) 12	0.5 (1.1) 14	0.6 (1.1) 12
spotted flycatcher	7.1 (6.1) 18	6.6 (6.0) 17	1.2 (0.8) 18	1.2 (0.8) 17	3.5 (5.9) 18	3.6 (6.1) 17
pied flycatcher	4.3 (3.9) 57	3.4 (3.7) 35	0.8 (0.8) 57	0.9 (0.8) 35	2.8 (5.1) 57	3.4 (6.0) 35
white wagtail	2.1 (3.1) 29	2.1 (3.1) 29	1.9 (0.4) 29	1.9 (0.4) 29	21.4 (6.9) 14	21.4 (6.9) 14
starling	1.7 (3.7) 27	1.7 (3.7) 27	1.8 (0.6) 129	1.8 (0.6) 129	15.6 (10.8) 129	15.6 (10.8) 129
greenfinch	6.5 (6.0) 47	4.9 (5.4) 38	1.4 (0.8) 18	1.4 (0.8) 17	8.6 (10.7) 47	10.3 (11.3) 38
bullfinch	5.6 (6.0) 13	4.8 (5.5) 12	0.8 (0.7) 13	0.8 (0.6) 12	2.8 (6.5) 13	3.0 (6.7) 12
chaffinch	5.8 (5.2) 124	5.5 (5.4) 98	1.0 (0.8) 122	0.9 (0.9) 96	5.0 (8.6) 122	5.8 (9.5) 96
yellowhammer	4.8 (4.7) 32	4.5 (5.1) 26	1.3 (0.9) 32	1.3 (0.8) 26	8.0 (10.3) 32	9.4 (11.0) 26
house/tree sparrow	3.5 (4.0) 123	3.5 (4.0) 123	1.5 (0.8) 123	1.5 (0.8) 123	9.0 (10.1) 123	9.0 (10.1) 123

[a] Height above the ground in five intervals; the mean for each interval was used for calculations.

[b] 0 = individual in cover; 1 = partly exposed; 2 = fully exposed.

[c] Combination of perch height and exposure to risk index (high value = high predation risk; see Methods).