

Habitat use under latent predation risk. A case study with wintering forest birds

Luis M. Carrascal and César Luis Alonso

Carrascal, L. M. and Alonso, C. L. 2006. Habitat use under latent predation risk. A case study with wintering forest birds. – *Oikos* 112: 51–62.

We test whether the spatial distribution of birds within a habitat is determined by predation risk and also by interspecific competition. The work was carried out in a montane mixed forest of central Spain with four *Parus* species, the long-tailed tit (*Aegithalos caudatus*) and the nuthatch (*Sitta europaea*). Experimental feeders, that varied in their risk of predation, were used to control the effect of natural variations in food availability and quality on the habitat use patterns of different species. Tree gleaning passerines avoided feeding on dark inner forest places far from edges, distant from protective cover, outside the inner tree canopy and near the ground; they preferred deciduous, relatively clear forest plots. These effects remained invariable across years and weather conditions. There was a common pattern of selection of foraging locations by the four *Parus* species: proximity to cover and height above ground and over the lowest branches of the tree canopy positively influenced the use of feeding places. According to these patterns, the vigilance proportion of species was significantly higher when feeding far from cover than when birds were feeding near pine foliage. This pattern was also common for the four studied *Parus* species. Nevertheless, the interspecific dominance hierarchy of the species was positively correlated with the use of the safest feeders (feeders farther the ground and nearer from protective cover within tree canopy), being the converse with the most exposed ones. Therefore, the results of this paper demonstrate that the selection of feeding locations within habitat follows a pattern minimizing predation risk. Interspecific dominance hierarchies can lead to the exploitation of unfavourable risky patches by subordinate species.

L. M. Carrascal and C. L. Alonso, Dept. Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, ES-28006 Madrid, Spain (mcnc152@mncn.csic.es).

Predation risk is a strong selective pressure influencing many aspects of life history of animals with important implications in the evolution of several morphological and behavioural adaptations, such as the differential use of the habitat (Pulliam and Mills 1977, Lima 1990). As feeding activities are usually incompatible with scanning for predators, animals are especially vulnerable while foraging, being this risk dependent upon the spatial configuration of the habitat providing refuge and concealment against predators. Several studies have shown that animals are able to identify variations in the

perceived predation risk among different locations, and this affects the selection of feeding places (Watts 1991, Suhonen 1993a, Krams 1996, Walther and Gosler 2001, reviewed by Lima and Dill 1990, Lima 1998). Moreover, perceived risk is linked to unambiguous cues available, such as illumination, habitat structure and the escape probability considering the interaction between flight tactics of prey and attack strategies of dominant predators (Lima 1993, Martín and López 1995, Krams 1996, 2000, Lahti et al. 1997, Thorson et al. 1998). The most common cue determining habitat use in birds

Accepted 23 June 2005

Copyright © OIKOS 2006
ISSN 0030-1299

under predation risk is the distance to a potential refuge. Cover functions as both a refuge for prey and as concealment for predators. Thus, birds prefer to feed near vegetation cover and they scan more frequently farther from refuge (Grubb and Greenwald 1982, Ekman 1987, Hinsley et al. 1995, Repasky 1996, Walther and Gosler 2001).

The perception of a higher predation risk entails an increase in time devoted to scan for predators (Caraco et al. 1980, Repasky 1996), vigilance thus compromises feeding activities and gives rise to a conflict in time allocation between different activities (Caraco et al. 1980, McNamara and Houston 1986, Ekman 1987, Houston et al. 1993). Nevertheless, foraging individuals can also compensate for increased predation risk in other ways: they may increase the intensity of feeding with a faster food intake rate, or may shift their activities to other times of the day. Many experimental studies in which prey animals are maintained under low risk and then exposed to a brief "pulse" of high risk, are likely to overestimate the intensity of antipredator behavior expected under field situations or chronic exposure to high risk (Lima and Bednekoff 1999). In this paper we test the role of latent or non-lethal predation risk on habitat use by free-ranging wintering birds (see similar approaches in Brown 1988, Kotler 1997, Thorson et al. 1998). By using specially designed feeders we control for interspecific differences in food preferences and in foraging postures related to ecomorphological constraints, and for differences in natural food availability among foraging substrata.

Another pressure affecting habitat use while foraging is competition, both interspecific and intraspecific, specially when resources are limiting (Wiens 1989). Several studies have shown that dominant individuals/species select the preferred, most rewarding feeding patches, while the subordinates are usually displaced to less profitable and/or riskier substrata (Alatalo et al. 1985, Ekman 1987, Hogstad 1988b, Suhonen 1993a, 1993b, Koivula et al. 1994, Krams 1996). Therefore, if habitat use by species is affected by other species, the within-habitat selection of foraging patches should be the result of minimizing predation risk and reducing competitive interferences between species.

In this paper we test whether the spatial distribution of birds within a habitat is determined by predation risk: we predict that the safest feeding patches will be used. If birds exhibit antipredator behavior only during brief and infrequent high-risk situations, no spatial differences should be in food obtained from feeders depending on their locations. We use experimental feeders that vary in their risk of predation but that control for amount and type of available food, thus controlling for the confounding effects of natural food availability and interspecific differences in foraging. Use of the feeders that minimise predation risk may also be affected by

interspecific competition: we predict the least dominant species will be found more often on the most dangerous feeders.

Material and methods

Study area and species

Field work was carried out at 'El Ventorrillo' field station (1450 m a.s.l., Sierra de Guadarrama, Madrid, 40°45'N, 4°00'W) during four winters (January to February 1998, December 1998, November 2000 to February 2001 and in December 2001). The study area is a mixed forest of 6 ha, where *Pinus sylvestris* L., *Castanea sativa* Miller, *Quercus pyrenaica* Willd., *Acer* sp., and *Populus* sp. are the most frequent species. The northern part of this area is dominated by a dense pinewood, while the southern part is dominated by a relatively clear deciduous woodland mainly composed by *Q. pyrenaica* and *Populus* sp. trees. In the middle of these two sectors there is a transition where deciduous and coniferous trees are intermingled.

The study species are those belonging to the tree gleaning guild of the mountainous forests of central Spain (Carrascal et al. 1987) that have omnivorous diets (Perrins 1998). They use hanging postures while foraging, allowing them to forage on feeders: nuthatch (*Sitta europaea* L.), great tit (*Parus major* L.), crested tit (*Parus cristatus* L.), blue tit (*Parus caeruleus* L.), coal tit (*Parus ater* L.) and long-tailed tit (*Aegithalos caudatus* L.). These small-sized species mainly forage in the foliage, twigs and branches of trees, although they can also use the forest floor or trunks as foraging substrates (especially nuthatch). Other members of this guild (*Certhia brachydactyla* Brehm, *Regulus regulus* L., *R. ignicapillus* Temminck and *Phylloscopus collybita/ibericus* Vieillot/Ticehurst) were not considered because their strictly insectivorous diets (Perrins 1998) preclude their use the artificial feeders.

Potential predators of small birds in the study area are the sparrowhawk (*Accipiter nisus* L.) and the tawny owl (*Strix aluco* L.). Sparrowhawks were observed on nine occasions passing by the feeders throughout 136 h of sampling sessions (0.7 attacks to birds at feeders per 10 h of observation). Birds reacted to predator presence by flying towards vegetation cover within tree canopy and by emitting series of chirps (short, high-pitched sounds; pers. obs.). Although we did not see any attack by tawny owls on birds foraging on feeders, this species is a potential risk to these small birds, specially at dawn and at dusk under dim light conditions. Moreover, birds reacted to the presence of a stuffed tawny owl fleeing to vegetation cover and producing alarm calls in dense flocks around the stuffed bird (pers. obs. obtained in a pilot study when a stuffed owl was placed in a natural

position on a branch 2–3 m near the feeders; see Naguib et al. 1999, for a similar approach).

To determine the approximate population size of study species, we trapped birds using especially designed funnel-traps (Senar et al. 1997) after sampling periods of feeders use (five days in February 1998 and eight days in December 1998). Five funnel-traps were located in the study area suspended from low pine branches approximately 1.5 m above ground. Funnel-traps were baited with husked peanuts and were opened uninterruptedly from 7:30 to 17:00 h GMT. They were checked for bird captures every 30–50 min. The cumulative number of different individual birds per species nearly approached the asymptotic population size for these four species in both sampling periods. We caught 28–46 different coal tits, 32–43 great tits, 18–27 blue tits and 8–10 crested tits in the two capturing periods. For the long-tailed tit and the nuthatch the funnel-traps did not provide reliable population estimations (Senar et al. 1997), although the average number of individual birds of these species were 10–14 and 8–10 individuals respectively in previous years (trapped with mist-nets; pers. obs.).

Interspecific dominance relationships were determined by recording hostile interactions between species at feeders. We observed 346 hostile interactions among the six studied species during 42 h of observation while birds were foraging at feeders. We considered a bird to have won when it supplanted another bird or chased it from feeders.

Feeders

Artificial feeders were used to experimentally control the effect of food characteristics on the patterns of space utilization by forest birds. They provided the same kind of food resource, with constant availability and accessibility. Feeders were metallic cylinders (20 × 5 cm) made up by a 4.8 mm mesh net allowing birds access to food. They were baited with peeled raw peanuts. To gather food, birds handled the peanuts through the metallic net to obtain small pieces. Feeders were placed on tree canopy by hanging them on branches and foliage by means of special hooks. In order to experimentally modify the distance from the ground, a wire was used to separate them 3–5 meters from the hooks. This type of feeders had been used the previous five years at the study site, and thus were easily identifiable as a food source by birds.

To analyze general preferences regarding the use of different feeding sites by birds, feeders were distributed in an attempt to cover all the natural foraging sites in the forest (according to position in the vertical and horizontal tree axis, distance to cover, proximity to forest edge, luminosity of the location and tree species). Vegetation cover functions as both a refuge for prey

and as concealment for predators. Thus, we refer hereafter to cover as “protective cover” or refuge against predators. Sixty feeders were placed in a first study period (January 16–22, 1998; 60 h of exposure) and other 44 feeders in a second period (January 23–30, 1998; 68 h). The two study periods differed both in the amount of snow cover (lacking in the first period) and in average temperature at midday ($6.6 \pm 1.4^\circ\text{C}$ vs $2.0 \pm 2.3^\circ\text{C}$, Mann–Whitney U-test, $Z = 2.64$; $p = 0.008$). Thus, metabolic demands for thermoregulation were higher and natural food availability was lower in the second study period.

Another 50 feeders were placed during a third study period the following winter (12–18 December, 1998; 60 h) in an attempt to estimate the reliability and between-year consistency of habitat use patterns obtained during the two periods of the previous winter. Weather conditions were very similar to those observed in the first period of 1998. In this third study period we also determined interspecific differences in feeder use according to their spatial location within habitat. The 50 feeders were randomly spread throughout the study area in ten groups of five feeders, with a minimum separation of 40 m between the two nearest groups. The ten feeding points were established in coniferous, deciduous and mixed forest plots. Within each point, the feeders were placed at different locations from trunk to branch tips, and from 0.5 to 6.7 m in height. From each feeder, the remaining four feeders were visible, so birds could exert simultaneous choices of the feeding place according to their preferences, perceived predation risk or competition pressure. The maximum separation between any two feeders in each point was ten meters, so all of the points had approximately the same density of feeders.

The location of each feeder within the forest was characterized through variables related to the foraging choices made by forest birds (i.e. habitat and substrate use). The types of tree in which the feeder was placed were categorized as coniferous (which was assigned a value of 1) and deciduous (value = 0). The predominant cover of deciduous trees at each point was characterized by counting the number of deciduous trees among the five closest trees to the feeder and the tree in which the feeder was placed. The density of tree trunks was estimated by using the five minimum distances from the tree in which the feeder was placed to the five closest trees; this density was expressed in trees per hectare through the following formula: $[100/(\text{average distance between trunks})]^2$. The distance to the border of the forest was measured with the telemeter of a reflex camera (Nikon F90) equipped with a mirror 500 mm lens (precision of 1 m). The border of the forest (mainly clearings) was defined by the convex polygon that joined the edges of the canopy of the most external trees. It measures how far inside the deep forest the feeders are.

This distance ranged between 0 (placed just in the edge) and 45 m.

The minimum distance from the center of the feeder to the trunk and above ground was measured using a metric tape (precision of 1 cm). Due to obvious logistic problems with feeders located high above ground level, the minimal distances to foliage cover and to the lower edge of tree canopy in which the feeder was placed were estimated by two observers, using the average value of the observations (precision of less than 25 cm). The distance to the foliage was defined as the minimum distance to the needles or dense groups of small branches and twigs (less than one centimeter in diameter), that could offer refuge to the birds when attacked by a predator. The lower edge of the canopy was defined by the lower branch or group of branches. Feeders above the imaginary plane defined by these branches had positive distances, while those below the canopy edge had negative values.

The luminosity of each location was measured with the center weighted light meter of the reflex camera equipped with a wide angle lens (17 mm) and loaded with 100 ASA film at an aperture of f8. Exposure values obtained (EV, precision of 1/3 EV) are directly related to the luminosity of the surroundings at each feeder location. The measurements were made from the ground exactly below each feeder, with the feeder centered in the viewfinder of the camera. All light measurements were made on completely cloudless days between 10:00 and 14:00 GMT. Light estimations were re-scaled dividing the values of EV obtained by the maximum EV measured.

Each feeder was located on a map of the field station (spatial resolution of 1:1000), locating the 0,0 coordinate at the southwestern most feeder.

Feeder use by birds

Two approaches were used in order to determine feeder use by birds: weight loss of the feeders (all study periods), and observation of the visits made by each bird species to feeders (only in the third period). The weight loss of each feeder was obtained through the difference between the dry weight of the feeders at the beginning and the end of each sampling period. This difference in feeder weight is an index of the degree of utilization of each of the feeders (i.e. food consumed). Before placing the feeders in the field, they were dried in a stove at 40°C for 48 h. Immediately after, they were weighed with an electronic balance (precision of 0.01 g). At the end of the study periods we measured the final weight of feeders. Feeders never ran out of peanuts during the study periods, so feeder use was not confounded by depletion (i.e. they were never empty). The amount of peanuts consumed in each period was

standardized dividing by the time the feeders had been exposed to birds (expressed in grams of peanuts consumed per daytime hour; day length = 10 h).

From 14–18 December, 1998, direct observations were made of feeder use by birds. An immobile observer, sited at a distance of 20 m from each one of the 10 groups of feeders, recorded the number and duration of visits each bird species made at each feeder. Four observers participated in the sampling rotating among the 10 groups of feeders. The sampling period spanned from 8:30 to 16:30 GMT. An attempt was made to cover each feeding point (five feeders) throughout this time period. The average cumulative sample effort was 7 h 11 min per feeder (range: 6 h 33 min – 7 h 45 min). Thus, each feeder was sampled approximately 12% of diurnal time available (60 h in 6 days). The cumulative sum of time spent at each feeder (expressed in seconds per hour of observation) shows the utilization of that location (globally or by each species).

The most exposed and the safest feeders were selected from the five feeders composing each one of the ten groups. This selection was made according to the distance to vegetation cover and above the lower edge of canopy (safest: near cover and the highest above the lower canopy edge; most exposed: below canopy edge and the most distant to cover). Within each group of five feeders, the percentage of time devoted to their exploitation by each species was calculated, dividing the time spent in each feeder by the total amount of time the species was in that group of five feeders. Feeders were usually used by only one bird at the same time. Only on very few occasions (<3% of feeder visits depending on the species) they were simultaneously used by two or, more rarely, three birds. We did not find any pattern in simultaneous visits to feeders when comparing the safest and most exposed positions.

Vigilance

Field work on scanning behaviour was carried out from November 2000 to February 2001 and in December 2001. Within the area, five feeding points were established at least 50 m apart from one another. Each consisted of one feeder filled with husked peanuts and suspended from pine branches. Two experimental situations were designed to simulate low and high risk positions. The low risk position (NEAR hereafter) consisted of one feeder suspended 0.5 m below the canopy, whereas the high risk position (FAR hereafter) consisted of one feeder suspended 2 m below the canopy (in both positions feeders were at least 2 m above ground). Although all the species were chosen as focal species, enough data for different individual birds could be obtained only for the four *Parus* species.

Vigilance at feeders was recorded at each feeding point for sampling periods of 40–60 minutes. Behavioural data were collected with the Psion Organiser II computer program as an event recorder using The Observer (Noldus Information Technology, Wageningen, the Netherlands). We observed the individual activity by sitting immobile in front of the feeders at a distance of 10–15 m. Sampling began when one individual arrived to a feeder and began to eat. Time spent at feeders (the duration of a single visit), number of scans and duration of each individual scan were recorded. To avoid flock size effects, only records of solitary birds lasting more than 15 seconds were used for statistical analyses. We considered operationally that birds were scanning when birds interrupted feeding making lateral head movements or rising the tip of the bill up to the back level or higher. Because birds had been trapped and colour-ringed, we were able to identify them when they used the feeders. Vigilance proportion was calculated grouping all records for each individual bird in each experimental situation, and was expressed in seconds vigilant per minute on feeders. Therefore, our sampling approach avoids pseudo-replication because the sample unit was the individual bird.

Data analysis

A principal components analysis (PCA; StatSoft 2001) was performed with variables describing the characteristics of feeder locations during the first winter (the two study periods on January 1998). Five principal components were obtained after Varimax rotation, accounting for 86.9% of the original variance (Table 1). The first component (PC1) defined a gradient from the most illuminated areas within deciduous forest patches towards dark locations of high tree density dominated by pines. The second component (PC2) was positively related to distance above ground and to the lower edge of the canopy.

The third component (PC3) defined an horizontal tree axis, placing the locations nearest tree trunk in its positive extreme. The fourth component (PC4) located feeders near cover and high within the canopy (mainly in open areas). The last component (PC5) defined the innerness of feeders related to forest border (forest interior feeders on the positive extreme).

The 50 feeders sampled in the third period (December 1998) were positioned on the previously obtained principal components (Table 1). The new factor scores were calculated using the variables describing feeder locations and the standardized regression coefficients of each component (variable scores).

To control the possible effect of the spatial autocorrelation on the degree of feeder use by birds, data analyses have been carried out considering geographical position of feeders using the procedure proposed by Legendre (1993). The values of the X and Y coordinates, as well as the interaction (XY) and the square terms (X^2 and Y^2) were entered in all the analyses as independent nuisance variables.

An ANCOVA model was used to determine the effect of the components that characterize feeder locations on their use by birds in the first two periods with different climatic conditions. Weight loss of each feeder was the dependent variable, sampling period was introduced as a factor, and principal components and position coordinates (X, X^2 , Y, Y^2 and XY) were included as covariates. The regression model for covariates was used to predict the expected weight loss in the third period. The relationship between observed and predicted food consumption rate in the third period was checked by means of simple regression.

Associations between habitat characteristics and position of feeders and time spent by each bird species on them were analyzed by means of partial least squares regression. This is an extension of the multiple linear regression analysis where the effects of several predictors on several dependent (response) variables can be ana-

Table 1. Results of the principal component analysis (PCA), after a 'Varimax normalized' rotation, carried out to characterise the location of the feeders. The PCA was performed with the values of nine variables which define the habitat structure of surroundings of each feeder (see text for more details). Significant correlation coefficients ($p < 0.01$; $n = 104$, in bold) between the original variables and the five principal components (PC), as well as eigenvalues and percentages of total variance explained by these components, are shown. The range column presents the minimum and maximum values of each row variables.

| Variables: | PC1 | PC2 | PC3 | PC4 | PC5 | Range |
|--|--------------|-------------|--------------|--------------|-------------|-----------|
| Type of tree (deciduous: 0; coniferous: 1) | 0.93 | 0.01 | -0.03 | 0.05 | -0.02 | 0–1 |
| Distance to the tree trunk (m) | -0.02 | -0.02 | -0.97 | 0.07 | -0.08 | 0.0–8.5 |
| Distance above ground (m) | 0.01 | 0.97 | -0.01 | 0.06 | 0.01 | 0.2–8.6 |
| Distance to the foliage cover (m) | -0.09 | -0.02 | 0.11 | -0.94 | 0.09 | 0.0–8.5 |
| Distance to the lower edge of tree canopy (m) | -0.13 | 0.60 | 0.10 | 0.69 | -0.06 | -10.0–6.3 |
| Density of tree trunks (no. ha ⁻¹) | 0.53 | 0.03 | 0.31 | -0.41 | 0.26 | 46–2500 |
| Distance to edge within forest (m) | 0.11 | -0.00 | 0.09 | -0.12 | 0.97 | 0.0–45.0 |
| Luminosity (relative index) | -0.87 | 0.18 | -0.07 | -0.08 | -0.21 | 0.01–1.0 |
| Proportion of deciduous trees (%) | -0.91 | -0.07 | 0.02 | 0.07 | -0.00 | 0–100 |
| Eigenvalues | 2.76 | 1.34 | 1.08 | 1.56 | 1.08 | |
| Expl. var. (%) | 30.70 | 14.85 | 12.00 | 17.29 | 12.02 | |

lyzed. In partial least squares regression, associations are established with factors extracted from predictor variables that maximize the explained variance in the dependent variables. These factors are defined as a lineal combination of original variables, so the original multidimensionality is reduced to a lower number of factors to detect structure in the relationships between predictor variables, and between these factors and the response variables. The extracted factors are orthogonal (i.e. independent of each other) and they account for the successive lower proportions of original variance. For more details on this statistical exploratory technique see StatSoft (2001).

Vigilance rates by the four *Parus* species and distance to protective cover was analyzed by means of a two-way ANOVA, considering species and distance as fixed factors. The sampling unit was the individual bird of each species. Because not all individuals were sampled in each experimental trial, ANOVAs for repeated measures were not possible, so two-way ANOVAs were used considering species (four species) and predation risk (FAR vs NEAR) as factors. This statistical approach is a conservative one because the significance of differences between species and risk sessions are computed including differences among individuals within species and treatments in the error term.

Data were analyzed using StatSoft's Statistica 6.0. Before doing these analyses, homocedasticity and normality of residuals of statistical models were checked. The original values of the variables were transformed to achieve the least deviation from normality. Tree density was transformed logarithmically, while the rest of the continuous variables were normalized according to a Box-Cox transformation. The average values and their variations, which appear in the text, have been quoted as average \pm one standard error.

Results

Use of feeders by the guild of omnivorous tree gleaning passerines

All the feeders were used during the two periods of the first winter. Weight losses ranged between 0.01 and 2.56 g of peanuts per hour of diurnal time. A large amount of variability in feeder use (66.8%) was explained by a model including the spatial localization of feeders, the sampling period and the habitat characteristics of the surroundings where the feeders were erected ($F_{11,92} = 16.81$, $p < 0.001$; Table 2).

The position of feeders within the sampling plot were included in the model to account for any confounding spatial effect but did not explain a large component of original variance in among-feeders variability in food consumed (7.5% resulting from the addition of the five localization components, Table 2). The weight loss of feeders was higher during the harshness period dominated by snowstorms (0.96 g h^{-1} of peanuts consumed in the colder period vs 0.42 g h^{-1} in the milder one; $p < 0.001$, 11.4% of original variance explained, Table 2). The amount of food removed from feeders per unit of time was significantly affected to a large extent (47.5%) by habitat structure of surroundings; except the third structural component (PC3), all the remaining components significantly affected feeder use. The second and fourth components were the main ones responsible for food consumption; the higher above ground level and over the lower branches of tree canopy (PC2), and the lower distance to a potential refuge (foliage or thick bunches of twigs) and the higher in the tree canopy (PC4), the greater food consumed per unit of time. Feeder use also increased from dark locations of high tree density dominated by pines, to brighter places with deciduous trees (PC1). Finally, food consumption increased with the proximity to clearing borders and

Table 2. Result of a general linear model for feeders use during the first winter testing for the effects of weather conditions and habitat characteristics around the feeders (principal components PC1 to PC5; Table 1), and controlling for spatial autocorrelation (polynomial terms of latitude and longitude; Methods). F value, statistical significance (P), and the percentage of explained variance by each effect and by the model, as well as the regression coefficients are shown. Degrees of freedom are 11,92 for the model, and 1,92 for each main effect.

| | F | P | Variance explained | Coefficients |
|--|-------|--------|--------------------|--------------|
| Model | 16.81 | <0.001 | 66.77 | |
| Main effects: | | | | 0.90 |
| Weather conditions (0: harsh; 1: mild) | 31.52 | <0.001 | 11.38 | -0.10 |
| PC1 (bright in deciduous [-] vs dark in pine [+] locat.) | 8.41 | 0.005 | 3.04 | -0.04 |
| PC2 (height above ground and upper in tree canopy) | 63.17 | <0.001 | 22.81 | 0.09 |
| PC3 (proximity to trunk) | 3.37 | 0.069 | 1.22 | 0.02 |
| PC4 (proximity to cover and upper in tree canopy) | 48.38 | <0.001 | 17.47 | 0.08 |
| PC5 (distance to edge within forest) | 8.12 | 0.005 | 2.93 | -0.04 |
| Latitude | 1.45 | 0.231 | 0.52 | -0.05 |
| Longitude | 0.24 | 0.627 | 0.09 | -0.03 |
| Latitude ² | 6.72 | 0.011 | 2.43 | -0.19 |
| Longitude ² | 5.34 | 0.023 | 1.93 | -0.58 |
| Latitude \times longitude | 7.04 | 0.009 | 2.54 | 0.52 |

decreased towards the interior of the forest (PC5). Position in the horizontal axis of the tree (i.e. distance to trunk; PC3) had no effect on the use intensity of feeders.

The model obtained in January 1998 was used to predict food consumption the following winter (December 1998) in a different arrangement of feeders within the same sampling plot (i.e. employing the regression coefficients in Table 2). Predicted and observed values of food consumption per unit of time were significantly correlated ($r=0.64$, $n=50$, $p<0.001$; Fig. 1).

In summary, food consumption in identical artificial feeders that control for food quality/availability and handling costs, changed spatially depending on the habitat characteristics of locations where they were erected. The effect of these structural characteristics is prominent, explaining a large amount of the observed variability in food consumption. The habitat structure patterns determining food consumption remain invariable across years and weather conditions. Small tree gleaners avoided feeding on dark places distant from protective cover, outside the tree canopy and near the ground; they preferred deciduous, relatively clear forest plots.

Common patterns in the use of feeders by the guild members.

Table 3 shows the approximate population size of the different bird species of the tree gleaner guild and their overall use of artificial feeders during the second winter. The most common species were the coal, great and blue tits, whereas the crested and long-tailed tits and nuthatch were less abundant. This abundance pattern of the gleaner guild approximately mirrors the interspecific pattern of feeder use, although the coal tit probably used

the feeders in a higher proportion than that expected by its abundance, being the converse for the great tit. The four *Parus* species and the long-tailed tit accounted for more than 95% of the time the feeders were used by the tree gleaner guild. Hereafter, statistical analyses are restricted to this group of five species, excluding the nuthatch due to its low sample size (i.e. the reduced time the species was observed preclude the observation of reliable patterns of feeder use).

Artificial feeders were used, on average, 7.5% of the observation time in the second winter (range: 0.01–14.5 min of use by any bird species per one hour of observation). This time devoted to feeder exploitation was associated to a consumption rate of 0.59 g of peanuts per hour of diurnal time (range: 0.05–1.83 g h^{-1}). Thus, the average use of feeders in the second winter was between the consumption rates observed in the two study periods of the first studied winter. Time that the bird community spent using each feeder was significantly correlated with the consumption rate ($r=0.92$, $n=50$, $p<0.001$; $g\ h^{-1}=0.162+0.094\cdot\min\ h^{-1}$). Therefore, intensity use of feeders estimated by weight loss per unit of time tightly resembles time exploitation by the bird community of omnivorous tree gleaners.

A partial least squares regression analysis, exploring the variation in the intensity use of the 50 feeders by five species, produced two significant components accounting for 47.1% of the variance (Table 4). The first component explained 39.8% of the variability in feeder use by the five species ($p<0.0001$) considering 13.0% of the information in the predictor variables. This component defines a common pattern of visit frequency by the four *Parus* species related to the height above ground level (PC2; $p<0.0001$), the shorter distance to a potential refuge (foliage or thick bunches of twigs; PC4, $p=0.0005$), and the height over the lower branches of tree canopy (common presence of this variable in both PC's; Table 1, Fig. 2). The geographic position of the feeders and the other PC's defining the habitat characteristics of their surroundings had no effect on food consumption. This component accounts for 36–55% of within-species variance in the use of feeding locations of the four *Parus* species.

A second component (Table 4) accounted for 7.4% of original variance in response variables (i.e. time spent by the five tit species at feeders; $p<0.0001$) considering 35.7% of information in predictor variables. This component mainly identifies the use of feeders by the long-tailed tit (28% of variance in this species), and opposes it to the use made by the crested tit. It considers the spatial arrangement of feeders (i.e. different preferential places in the sampling area) and the habitat structure factor PC1 ($p<0.0001$): crested tit preferred dark foraging locations with high tree density dominated by pines

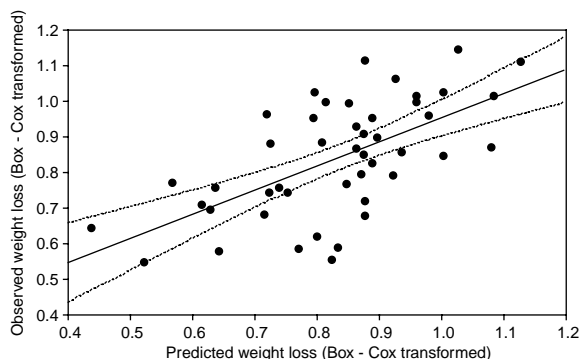


Fig. 1. Relationship between observed and predicted values of feeders weight loss for the second winter. The continuous line represents regression line and the dashed lines denotes its 95% confidence interval.

Table 3. Global use of feeders by the tree gleaning birds during the second winter. The approximate population size was obtained by capture–recapture method after this sampling period (*for long-tailed tit and nuthatch values estimated are shown). The percentages of interspecific interactions won by each species foraging on feeders are also shown (in brackets, the number of interspecific interactions).

| | Body mass | Visited feeders | Time use (accumulated min.) | Percentage use | Number of birds | % interac. won |
|-----------------|-----------|-----------------|-----------------------------|----------------|-----------------|----------------|
| Coal tit | 9.3 | 48 | 680.0 | 42.9 | 28 | 8.3 (148) |
| Great tit | 18.6 | 34 | 322.1 | 20.3 | 32 | 71.8 (202) |
| Blue tit | 11.2 | 32 | 310.1 | 19.6 | 27 | 43.0 (116) |
| Crested tit | 11.6 | 39 | 154.4 | 9.7 | 10 | 35.6 (115) |
| Long-tailed tit | 7.1 | 24 | 81.8 | 5.2 | 10* | 8.1 (37) |
| Nuthatch | 21.5 | 17 | 36.3 | 2.3 | 8* | 100.0 (116) |
| TOTAL | | 50 | 1584.7 | | 115 | |

(PC1), while long-tailed tits favoured brighter places with deciduous trees.

In summary, there is a common pattern of selection of foraging locations by the four *Parus* species, and a different one for the long-tailed tit that segregates this species from the crested tit. The sharing of feeding places by the *Parus* species reaches a relatively high proportion of within-species variability in habitat use (35–55%), identifying that distance to protective cover (negatively), and height above ground and over the lowest branches of the tree canopy (positively) markedly determines the use of feeding places.

Table 4. Result of a partial least square model (PLS) carried out with the values of intensity use of feeders by five tit species (response variables) and variables which characterise the location of the feeders (predictor variables). Correlation coefficients and significance level (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****: $p < 0.0001$) between the original variables and the two components are shown. The percentage of explained variability in feeder use by each species are given for the two components PLS.

| | Comp. 1 | Comp. 2 |
|---|----------|-----------|
| Response variables (intensity use of feeders) | | |
| Coal tit | 0.48*** | 0.03 |
| Great tit | 0.52*** | 0.14 |
| Blue tit | 0.52**** | 0.15 |
| Crested tit | 0.42** | -0.45*** |
| Long-tailed tit | 0.21 | 0.87**** |
| Predictor variables | | |
| PC1 (bright in deciduous [-] vs dark in pine [+] locations) | -0.10 | -0.63**** |
| PC2 (height above ground and upper in tree canopy) | 0.84**** | -0.04 |
| PC3 (proximity to trunk) | -0.05 | -0.12 |
| PC4 (proximity to cover and upper in tree canopy) | 0.47*** | 0.17 |
| PC5 (distance to edge within forest) | -0.13 | 0.11 |
| Latitude | 0.03 | 0.16 |
| Longitude | -0.18 | -0.21 |
| Latitude ² | 0.02 | -0.44** |
| Longitude ² | 0.09 | -0.32* |
| Latitude × longitude | 0.03 | -0.42** |
| Explained variance (%) | | |
| Coal tit | 46.1 | 0.0 |
| Great tit | 52.9 | 0.7 |
| Blue tit | 54.8 | 0.8 |
| Crested tit | 35.9 | 7.5 |
| Long-tailed tit | 9.1 | 27.9 |

Interspecific hierarchy and use of exposed and safe feeding locations

Overall, birds suffered 8.2 aggressive displacements per hour of foraging on feeders. Nuthatches won all interspecific interactions they were involved in (Table 3). Great tits dominated over the remaining tit species, although some individuals lost against blue tits (4% of the 52 interactions with this species) and crested tits (14% of 42 interactions) on some occasions. Crested tits won nearly all interactions with coal tits (97% of 32 interactions), but there was not a clear winner species in the hostile interactions with blue tits (43% out of 7 interactions between both species won by crested tits). Blue tits won all interactions with long-tailed tits, and nearly all with coal tits (93% out of 30 interactions). Finally, coal tits dominated on many occasions over long-tailed tits (75% of 12 interactions). Thus, the dominance status of these six species was established as nuthatch > great tit > crested tit \approx blue tit > coal tit > long-tailed tit.

Feeders nearer to ground and more distant to protective cover and below the lower branches of tree canopy were used in a very low proportion by all species, although long-tailed tits proportionally used them more

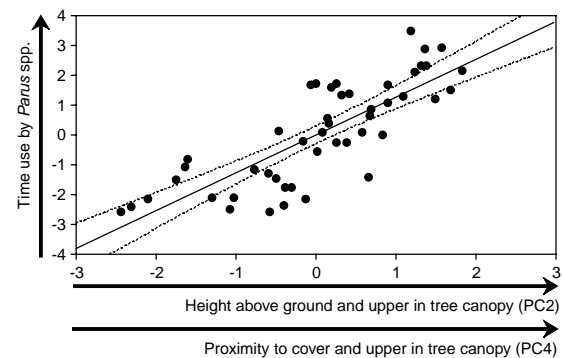


Fig. 2. Relationship between time spent using feeders by *Parus* spp. and the habitat structure variables that determined the observed pattern of time use. Tits presented a common pattern of feeder use, which was positively correlated with the values of PC2 and PC4 (Table 1 and 4). The continuous line represents regression line and the dashed lines denotes its 95% confidence interval.

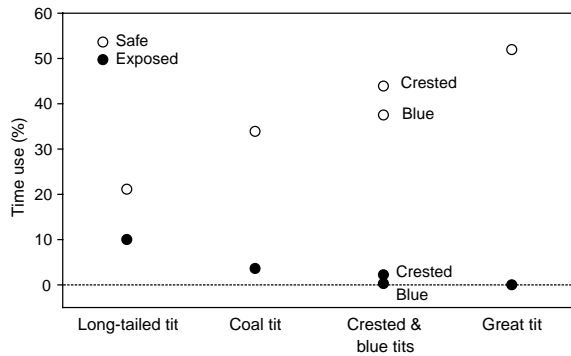


Fig. 3. Relationship between time use of exposed (filled symbols) and safe feeders (open symbols) and interspecific dominance hierarchy. The use of feeders is represented by the percentage of use of each position by each species. Dominance rank was established according to agonistic interactions (usually simple supplantations) observed while birds using feeders.

frequently, followed, at a distance, by coal and crested tits (Fig. 3). Conversely, the feeders located farther above ground, higher over the lower branches of the tree canopy and nearer to protective cover of vegetation (i.e. the safest ones) were used in a high proportion by all species, although there was a clear order among them. The interspecific dominance hierarchy of these five species was significantly correlated with the percentage use of these feeders, positively with the safest ones ($r_s = 0.97$, $p = 0.005$) and negatively with the most exposed ($r_s = -0.97$, $p = 0.005$).

Vigilance rates and distance to cover.

There were significant differences between species in vigilance rate (two-way ANOVA: $F_{3,174} = 18.19$, $p < 0.001$; Fig. 4), mainly due to a lower vigilance rate in the blue tit ($p < 0.001$ in the four 'a posteriori' comparisons between the blue tit with the remaining species; Tukey tests for unequal sample sizes). There was also a significant difference between the vigilance rate at safe

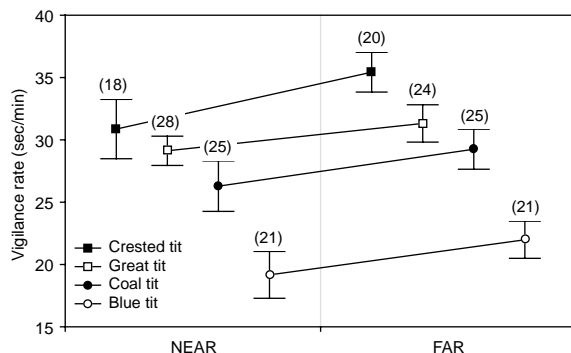


Fig. 4. Vigilance rate of *Parus* spp. at safe (NEAR) and exposed (FAR) feeders. Bars denote means \pm SE. Numbers above bars are sample size.

feeders near protective cover (pine foliage 3–4 m above ground) and at exposed feeders (2 m below the lowest branches of the tree canopy; $F_{1,174} = 6.70$, $p = 0.010$); the vigilance proportion was significantly higher when birds were feeding far from protective cover than near pine foliage in the four *Parus* species. This pattern was common for the four studied species, as the interaction term species \times distance was not significant ($F_{3,174} = 0.16$, $p = 0.922$).

Discussion

Foraging constraints which reflect selective pressures during evolutionary history, might determine where birds search for and capture food (Robinson and Holmes 1982). The selection of feeding places by species of forest birds is related to inter and intraspecific competence, food availability, ecomorphological constraints and the risk of predation (Norberg 1979, Ekman and Askenmo 1984, Alatalo et al. 1985, Hogstad 1988b, Carrascal et al. 1990, Suhonen et al. 1992, Suhonen 1993a, Krams 1996, Forstmeier et al. 2001). It is very difficult in the wild to separate the effect of food abundance from exploitation ability or predation risk at different locations. The use of feeders allows to control the effect of natural variations on food availability and quality, and morphological limitations while foraging, on the habitat use patterns of different species. If food distribution or species morphology were the only factors that determine the use of space within the habitat, we would expect all of the feeders to be used equally. However, this paper shows striking differences in feeder use depending on their position within the habitat. The most used feeders were those close to vegetation cover, and located higher above ground and higher in the tree canopy. This pattern did not vary under different weather conditions, was predictable and repeatable throughout time, and was also identical for four species of the genus *Parus*. These results are clearly interpretable considering the perceived predation risk of the studied species, being higher in those feeding patches more distant from vegetation cover providing refuge against predators. Accordingly, the four tit species spent more time vigilant far from vegetation cover.

For small passerines, places that are safe against predators vary according to the species of trees or the type of predator (Ekman 1987, Suhonen 1993a, Krams 1996, Kullberg 1998). Parids benefit from foraging in sites that afford good antipredator vigilance (Krams 2001). The choice of upper and inner parts in the tree canopy has been shown in several species of tits (Ekman and Askenmo 1984, Ekman 1986, 1987, Hogstad 1988a, Suhonen 1993a, 1993b, Krams 1996). This pattern is the result of predator-avoidance behaviour, because these locations provide shelter against predation by owls (e.g.

little owl, *Glaucidium passerinum* L.) and sparrowhawks. Besides, species that forage at high locations on tree canopy represent a small fraction of the sparrowhawk's diet (Götmark and Post 1996). Moreover, birds perceive a high risk of predation while feeding away from protective cover, since the risk of being captured by the sparrowhawk increases with the distance from cover (Hinsley et al. 1995). While foraging away from cover, safe refuges are farther, and, therefore, birds should decrease patch exploitation and/or increase vigilance to enhance predator detection (Lima and Dill 1990; Fig. 4).

It is surprising that the distance from the trunk had no consistent effect on feeder use, considering that some authors have pointed out that inner tree parts are preferred by small passerine birds (mainly willow tit, *Parus montanus* and crested tit) because they probably have a lower predation risk (Ekman and Askenmo 1984, Ekman 1986, Hogstad 1988b, Suhonen 1993a). The absence of such a relationship in our work indicates that the influence found by other authors may be explained by differences in food distribution and/or the ability of the species to exploit different substrata (thick branches and trunks in inner parts vs twigs and foliage in outer parts). The exploitation of slender and pliable substrata found in outer tree parts requires hanging postures and special leg and bill morphological designs, together with light body mass (Norberg 1979, Carrascal et al. 1990). These foraging and morphological characteristics are present in species like coal tit, blue tit and goldcrest, whose habitat use is mainly restricted to the outer tree parts (Alatalo 1982, Carrascal and Telleria 1985).

In woodland bird species, there is a positive relationship between perceived predation risk and distance to forest edge in clearings or outside woodlands (Koivula et al. 1994, Hinsley et al. 1995, Desrochers et al. 2002). Rodriguez et al. (2001) show that there is a lower use of forest edges and adjacent areas outside woodlands when predation risk increases (Desrochers et al. 2002). This paper also shows that woodland edges have higher habitat use than interior patches, although this subtle effect explains only a low proportion of bird distribution (Table 2). Our results are consistent with some observations of higher densities near forest edges than in inner parts (Hansson 1983, McCollin 1998), which is usually attributed to a higher food availability in woodland borders (Hansson 1983, 1994, Brotons and Herrando 2003). Nevertheless, we found the same results after controlling for food availability. Thus, there should be other factors determining larger bird abundances towards forest edges, such as higher visibility (more light and less visual obstruction, Metcalfe 1984) or better thermal properties (more radiation) outside forest tracts.

The overall use of feeders was greater in more illuminated areas dominated by deciduous trees, and smaller in dark locations with high pine densities. More

illuminated forest patches have better visibility, which may enhance detection of predators, increasing the likelihood of an effective escape (Krause and Godin 1995, Kaby and Lind 2003). A low level of illumination, such as that found in very dense areas dominated by coniferous trees, has a negative effect on foraging efficiency (Kacelnik 1979) and increases the time dedicated to vigilance (Lima 1988), as the vision of diurnal passerines is not well adapted to conditions of poor illumination (Martin 1994). Thus, birds avoid foraging under low light conditions when risk of predation is high (Lahti et al. 1997, Krams 2000). A second possible explanation is that the more open areas receive greater solar radiation, improving the thermic qualities of these locations during the cold winter days. The costs of thermoregulation of small passerines during winter time are very high (Walsberg 1993), so one way of improving the energy balance would consist of choosing microhabitats with better thermic conditions as has been demonstrated in small passerines (Morton 1967, Wolf and Walsberg 1996, Carrascal et al. 2001).

When starvation risk increases, due to both higher metabolic demands or diminished food availability, animals face higher risks (McNamara and Houston 1986, Houston et al. 1993). For example, Yasué et al. (2003) found that as weather becomes more severe, redshanks (*Tringa totanus*) choose riskier, but more profitable, feeding habitats with higher food intake rates and lower thermoregulatory costs. On the other hand, Walther and Gosler (2001) found that tits searched for seeds closer to protective cover during a year of super-abundant beechmast. In contrast, our results show that the use of supplementary food sources was 2.3 times greater during the cold spell, although the selection of feeding places remained unchanged. These discrepancies could be explained considering that the harsh conditions observed in our study area are not severe enough to promote straightforward changes in foraging behaviour. Consistently, the feeders were unused 86.9% of the time, they were never emptied (on average, 31.4% of the available peanut mass was consumed) and ambient temperature was relatively high (2°C at midday) in the 'harsh' study period when compared to other studied ecological situations at northern latitudes (usually < -10°C). Wintering populations of mediterranean woodland birds seem not to be heavily limited by food, as bird densities do not track spatial variations in food availability (Herrera 1998, Carrascal et al. 2001) or populations only marginally rely on supplemented food (Carrascal et al. 1998; less than 4% of the winter time budget).

Tit species usually move together in plurispecific flocks during winter (Morse 1978, Herrera 1979). In this plurispecific social context where the five species have similar preferences in habitat use (Carrascal and Telleria 1985, Carrascal et al. 1987 for the Iberian

peninsula), the effect of interspecific competition should be expected, specially if tit densities are high (178 birds per 10 ha for the five species pooled in the study area). Accordingly, we observed a large frequency of hostile interactions among birds (8.2 aggressions per hour foraging on feeders). Under these circumstances, the dominant species could force subordinate ones to use the less profitable patches (i.e. subordinate species should be displaced from safer to riskier place). In natural conditions, it has been demonstrated that the subordinate species are forced to use suboptimal feeding places and/or those with a greater predation risk (Alatalo 1981, Ekman 1987, Hogstad 1988a, 1988b, Suhonen 1993b, Koivula et al. 1994, Krams 1996). Our results support this prediction, as the within-species relative use of riskiest feeders decreased with increasing interspecific dominance hierarchy, being the converse for the safest feeders (Fig. 3). This discrepancy among species in the use of artificial feeders is the main explanation of observed interspecific differences in habitat exploitation.

In summary, the results of this paper demonstrate that habitat use by small woodland passerines is very similar after controlling for spatial differences related to food identity and availability, and for interspecific differences related to foraging capabilities based upon morphofunctional associations. Selection of feeding locations within habitat follows a pattern minimizing predation risk. Interspecific dominance hierarchies can lead to the exploitation of unfavourable risky patches by subordinate species.

Acknowledgements – We thank Claire Jasinski for improving the English of the text. José Martín, Will Cresswell and Indrikis Krams contributed with valuable suggestions to the first version of the manuscript. This paper is a contribution to the project BOS2000-0993 funded by the Spanish Ministerio de Ciencia y Tecnología. C. L. Alonso benefited from a FPI grant of the Spanish Ministerio de Educación y Ciencia. We thank Luisa Amo and Jorge for helping with the field-work.

References

Alatalo, R. V. 1981. Interspecific competition in tits *Parus* spp. and the goldcrest *Regulus regulus*: foraging shifts in multi-specific flocks. – *Oikos* 37: 335–344.
 Alatalo, R. V. 1982. Multidimensional foraging niche organization of foliage-gleaning birds in northern Finland. – *Ornis Scand.* 13: 56–71.
 Alatalo, R. V., Gustafsson, L., Lindén, M. et al. 1985. Interspecific competition and niche shifts in tits and the goldcrest: an experiment. – *J. Anim. Ecol.* 54: 977–984.
 Brotons, L. and Herrando, S. 2003. Effect of increased food abundance near forest edges on flocking patterns of coal tit *Parus ater* winter groups in mountain coniferous forests. – *Bird Study* 50: 106–111.
 Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. – *Behav. Ecol. Sociobiol.* 22: 37–47.
 Caraco, T., Martindale, S. and Pulliam, H. R. 1980. Avian time budgets and distance to cover. – *Auk* 97: 872–875.

Carrascal, L. M. and Tellería, J. L. 1985. Estudio multidimensional del uso del espacio en un grupo de aves insectívoras forestales durante el invierno. – *Ardeola* 32: 95–113.
 Carrascal, L. M., Potti, J. and Sánchez-Aguado, F. J. 1987. Spatio-temporal organization of the bird communities in two Mediterranean montane forests. – *Holarct. Ecol.* 10: 185–192.
 Carrascal, L. M., Moreno, E. and Tellería, J. L. 1990. Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. – *Holarct. Ecol.* 13: 105–111.
 Carrascal, L. M., Senar, J. C., Mozetich, I. et al. 1998. Interaction between environmental stress, body condition, nutritional status and dominance in mediterranean great tits (*Parus major*) during winter. – *Auk* 115: 727–738.
 Carrascal, L. M., Díaz, J. A., Huertas, D. et al. 2001. Behavioral thermoregulation by treecreepers: a tradeoff between energy saving and reduced crypsis. – *Ecology* 82: 1642–1654.
 Desrochers, A., Be Lisle, M. and Bourque, J. 2002. Do mobbing calls affect the perception of predation risk by forest birds? – *Anim. Behav.* 64: 709–714.
 Ekman, J. 1986. Tree use and predator vulnerability of wintering passerines. – *Ornis Scand.* 17: 261–267.
 Ekman, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. – *Anim. Behav.* 35: 445–452.
 Ekman, J. and Askenmo, C. 1984. Social rank and habitat use in willow tit groups. – *Anim. Behav.* 32: 508–514.
 Forstmeier, W., Bourski, O. V. and Leisler, B. 2001. Habitat choice in *Phylloscopus* warblers: the role of morphology, phylogeny and competition. – *Oecologia* 128: 566–576.
 Götmark, F. and Post, P. 1996. Prey selection by sparrowhawks, *Accipiter nisus*: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. – *Philos. Trans. R. Soc. B* 351: 1559–1577.
 Grubb, T. C. Jr. and Greenwald, L. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. – *Anim. Behav.* 30: 637–640.
 Hansson, L. 1983. Bird numbers across edges between mature conifer forest and clearcuts in central Sweden. – *Ornis Scand.* 14: 97–103.
 Hansson, L. 1994. Vertebrate distributions relative to clear-cut edges in a boreal forest. – *Landscape Ecol.* 9: 105–115.
 Herrera, C. M. 1979. Ecological aspects of heterospecific flock formation in a Mediterranean passerine bird community. – *Oikos* 33: 85–96.
 Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. – *Ecol. Monogr.* 68: 511–538.
 Hinsley, S. A., Bellamy, P. E. and Moss, D. 1995. Sparrowhawk *Accipiter nisus* predation and feeding site selection by tits. – *Ibis* 137: 418–420.
 Hogstad, O. 1988a. Social rank and antipredator behaviour of willows tits *Parus montanus* in winter flocks. – *Ibis* 130: 45–56.
 Hogstad, O. 1988b. Rank-related resource access in winter flocks of willow tit *Parus montanus*. – *Ornis Scand.* 19: 169–174.
 Houston, A. I., McNamara, J. M. and Hutchinson, J. M. C. 1993. General results concerning the tradeoff between gaining energy and avoiding predation. – *Philos. Trans. R. Soc. B* 341: 375–397.
 Kaby, U. and Lind, J. 2003. What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? – *Behav. Ecol. Sociobiol.* 54: 534–538.
 Kacelnik, A. 1979. The foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. – *Anim. Behav.* 27: 237–241.
 Koivula, K., Lahti, K., Rytönen, S. et al. 1994. Do subordinates expose themselves to predation? field experiments on feeding site selection by willow tits. – *J. Avian Biol.* 25: 178–183.

- Kotler, B. P. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. – *Oikos* 78: 274–282.
- Krams, I. 1996. Predation risk and shifts of foraging sites in mixed willow and crested tit flocks. – *J. Avian Biol.* 27: 153–156.
- Krams, I. 2000. Length of feeding day and body weight of great tits in a single- and two-predator environment. – *Behav. Ecol. Sociobiol.* 48: 147–153.
- Krams, I. 2001. Seeing without being seen: a removal experiment with mixed flocks of willow and crested tits *Parus montanus* and *cristatus*. – *Ibis* 143: 476–481.
- Krause, J. and Godin, J. G. J. 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. – *Anim. Behav.* 50: 465–473.
- Kullberg, C. 1998. Spatial niche dynamics under predation risk in the willow tit *Parus montanus*. – *J. Avian Biol.* 29: 235–240.
- Lahti, K., Koivula, K. and Orell, M. 1997. Dominance, daily activity and winter survival in willow tits: detrimental cost of long working hours. – *Behaviour* 134: 921–939.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? – *Ecology* 74: 1659–1673.
- Lima, S. L. 1988. Vigilance during the initiation of daily feeding in dark-eyed juncos. – *Oikos* 53: 12–16.
- Lima, S. L. 1990. Protective cover and the use of space: different strategies in finches. – *Oikos* 58: 151–158.
- Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack. – *Wilson Bull.* 105: 1–47.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. – *Adv. Study Behav.* 27: 215–290.
- Lima, S. L. and Dill, L. M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Lima, S. L. and Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. – *Am. Nat.* 153: 649–659.
- Martin, G. R. 1994. Form and function in the optical structure of bird eyes. – In: Davies, M. N. O. and Green, P. R. (eds), *Perception and motor control in birds: an ecological approach*. Springer-Verlag, pp. 5–34.
- Martin, J. and López, P. 1995. Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*. – *Can. J. Zool.* 73: 129–132.
- McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. – *Ecography* 21: 247–260.
- McNamara, J. M. and Houston, A. I. 1986. The common currency for behavioral decisions. – *Am. Nat.* 127: 358–378.
- Metcalf, N. B. 1984. The effect of habitat on the vigilance of shorebirds: is visibility important? – *Anim. Behav.* 32: 981–985.
- Morse, D. H. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during winter. – *Ibis* 120: 298–312.
- Morton, M. L. 1967. The effects of insulation on the diurnal feeding pattern of the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). – *Ecology* 48: 690–694.
- Naguib, M., Mundrya, R., Ostreiherb, R. et al. 1999. Cooperatively breeding Arabian babblers call differently when mobbing in different predator-induced situations. – *Behav. Ecol.* 10: 636–640.
- Norberg, U. M. 1979. Morphology of the wings, legs and tail of three coniferous tits, the goldcrest, and the treecreeper in relation to locomotor patterns and feeding station selection. – *Philos. Trans. R. Soc. B* 287: 131–165.
- Perrins, C. M. 1998. The complete birds of the western Palearctic on CD-ROM, version 1.0. – Oxford Univ. Press.
- Pulliam, H. R. and Mills, G. S. 1977. The use of space by wintering sparrows. – *Ecology* 58: 1393–1399.
- Repasky, R. R. 1996. Using vigilance behavior to test whether predation promotes habitat partitioning. – *Ecology* 77: 1880–1887.
- Robinson, S. K. and Holmes, R. T. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. – *Ecology* 63: 1918–1931.
- Rodríguez, A., Andrén, H. and Jansson, G. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. – *Oikos* 95: 383–396.
- Senar, J. C., Domenech, J., Carrascal, L. M. et al. 1997. A funnel trap for the capture of tits. – *Bull. Grup Catala Anellament* 14: 17–24.
- StatSoft, I. 2001. Statistica (data analysis software system). – StatSoft.
- Suhonen, J. 1993a. Predation risk influences the use of foraging sites by tits. – *Ecology* 74: 1197–1203.
- Suhonen, J. 1993b. Risk of predation and foraging site of individuals in mixed-species tit flocks. – *Anim. Behav.* 45: 1193–1198.
- Suhonen, J., Alatalo, R. V., Carlson, A. et al. 1992. Food resource distribution and the organization of the *Parus* guild in a spruce forest. – *Ornis Scand.* 23: 467–474.
- Thorson, J. M., Morgan, R. A., Brown, J. S. et al. 1998. Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. – *Behav. Ecol.* 9: 151–157.
- Walsberg, G. E. 1993. Thermal consequences of diurnal microhabitat selection in a small bird. – *Ornis Scand.* 24: 174–182.
- Walther, B. A. and Gosler, A. G. 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (*Aves: Parus*). – *Oecologia* 129: 312–320.
- Watts, B. D. 1991. Effects of predation risk on distribution within and between habitats in savannah sparrows. – *Ecology* 72: 1515–1519.
- Wiens, J. A. 1989. The ecology of bird communities. Vol 1, foundations and patterns. – Cambridge Univ. Press.
- Wolf, B. O. and Walsberg, G. E. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. – *Ecology* 77: 2228–2236.
- Yasué, M., Quinn, J. L. and Cresswell, W. 2003. Multiple effects of weather on the starvation and predation risk tradeoff in choice of feeding location in Redshanks. – *Funct. Ecol.* 17: 727–736.

Subject Editor: Jan Lindström