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# THE INFLUENCE OF THE FORAGING NICHE ON THE BEHAVIOURAL RESPONSE TO INCREASED PREDATION RISK IN TREE-GLEANING BIRDS

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SUMMARY.—*The influence of the foraging niche on the behavioural response to increased predation risk in tree-gleaning birds.* The vigilance behaviour of two small tree gleaning birds differing in their spatial niches was studied in relation to variation in predation risk associated with distance to vegetation cover of the foraging patch. The Nuthatch (*Sitta europaea*; searcher on trunk and thick branches) and the Coal Tit (*Parus ater*; foliage gleaner) were used as focal species. The species studied adopted two different strategies while foraging at greater distances from cover: (1) the Nuthatch increased vigilance proportion (time spent vigilant per minute foraging), keeping the time spent at feeders constant, while (2) the Coal Tit decreased time spent at feeders, but showed no significant increase in vigilance proportion. The two components of vigilance (scanning rate and duration of individual scans) changed in different ways in the two species: the Nuthatch, which usually forages in open substrates, scanned more often, while the Coal Tit, which forages in substrates with denser vegetation cover, increased the length of scans (by reducing the proportion of short scans). These differences between vigilance patterns of both species are discussed in the light of differences related to the spatial configuration of the feeding niche (obstruction of visual space by vegetation), and the protection offered by the surroundings.

*Key words: Parus ater*, predation risk, scanning behaviour, spatial niche, *Sitta europaea*.

RESUMEN.—*La influencia del nicho espacial sobre la respuesta al incremento del riesgo de depredación en un gremio de aves arbóreas.* Se analiza el comportamiento de vigilancia de dos especies de pájaros rebuscadores de los árboles en relación con la variación en el riesgo de depredación asociado con la distancia a la vegetación del lugar de alimentación. Se eligieron el Trepador Azul (*Sitta europaea*; rebuscador de troncos y ramas gruesas) y el Carbonero Garrapinos (*Parus ater*; rebuscador de follaje) como especies de estudio. Las dos especies adoptaron estrategias diferentes mientras se alimentaban lejos de la vegetación: (1) el Trepador Azul aumentó la tasa de vigilancia (segundos vigilando por minuto comiendo) manteniendo constante el tiempo de estancia en el parche; (2) el Carbonero Garrapinos acortó el tiempo de estancia en el parche de alimentación, y no mostró un cambio significativo en la tasa de vigilancia (aunque mostró una tendencia a incrementarse). Las dos componentes de la vigilancia (frecuencia de vigilancia y duración de las vigilancias individuales) cambiaron de modo distinto en ambas especies con el aumento de la distancia a la vegetación: el Trepador Azul, que habitualmente busca el alimento en sustratos abiertos, vigiló más frecuentemente, mientras que el Carbonero Garrapinos, que restringe mayoritariamente la búsqueda del alimento a sustratos con una densa cobertura vegetal, incrementó la duración de las vigilancias individuales (disminuyendo el número de vigilancias de corta duración). Estas diferencias entre ambas especies en los patrones de vigilancia son discutidos en relación con diferencias en la configuración del nicho espacial, determinante de la obstrucción del espacio visual que las aves tienen que explorar.

*Palabras clave:* comportamiento de vigilancia, nicho espacial, *Parus ater*, riesgo de depredación, *Sitta europaea*.

## INTRODUCTION

Vigilance behaviour serves both to prevent predator attacks and to acquire information from other individuals (Desportes *et al.*, 1991). Many studies have shown that vigilance rate varies with the distance to the nearest refuge, presence of other individuals, food handling costs, ambient temperature, light intensity and exposure to predators (Lazarus,

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1979; Caraco *et al.*, 1980; Barnard,1980; Lendrem, 1983; Beveridge & Deag, 1986; Lima & Dill, 1990; Cassini,1991). Although it is usually assumed that the probability of detecting an approaching predator increases as time spent in vigilance increases, few studies have considered whether this probability depends on the scanning patterns of birds (scanning rate and average scan duration; Hart & Lendrem, 1984), and that those patterns may be related to habitat structure (Metcalfe, 1984; Díaz & Asensio, 1991; Lima, 1992; Suhonen, 1993). In a previous study dealing with the scanning behaviour of small tree-gleaning passerines (Carrascal & Moreno, 1992), the existence of a foraging syndrome relating the vigilance pattern to the spatial niche was suggested. Birds foraging within thick vegetation cover showed shorter and more frequent scans than those foraging in the open. Such a pattern probably results from the interaction between scan frequency and scan duration in relation to the space a bird must survey for predators and the protection offered by the surroundings. Foraging constraints (*e.g.* morphology related to locomotion or prey handling) which reflect selective pressures during evolutionary history, might determine where birds search for and capture food (Robinson & Holmes, 1982, Holmes & Robinson, 1988), and within this limited range of conditions (realized niche) some patterns of vigilance-use of space would emerge (Carrascal & Moreno, 1992).

Here we investigate the way in which birds modify their vigilance behaviour and patch residence time when predation risk is increased due to a decrease in the vegetation cover of the foraging patch. Several authors have demonstrated that birds perceive a high risk of predation while feeding away from cover, and thus prefer to feed as close to dense vegetation as possible (see Lima & Dill, 1990 and references therein). While foraging away from cover, birds have a longer distance of escape to a safe refuge, and, therefore, they should increase the proportion of time spent vigilant to enhance predator detection. It may also be expected that the patch residence time should decrease when far from cover, as the shorter the stay the lower the probability of being caught by a predator. This is because the potential prey may abandon the patch before the predator can reach it. Birds could either change the rate at which they scan the surroundings of the feeding patch, or the average duration of individual scans, the two processes not being mutually exclusive (McVean & Haddlesey, 1980; Hart & Lendrem, 1984). Foraging in an open patch with less visual obstruction and a greater exposure to predation should determine different changes in vigilance behaviour in species differing in their spatial niches, if there is a foraging syndrome relating spatial niche and scanning behaviour. These differences would be related to habituation (in both evolutionary and ecological time) to the physical structure of usual foraging areas that could determine different perception abilities. This syndrome suggests that species display a vigilance pattern related to the vegetation structure of the foraging areas they occupy (Carrascal & Moreno, 1992; see Robinson & Holmes, 1982). Bird species that usually forage hidden among foliage (*e.g.* foliage gleaners) should increase average scan duration to evaluate the potential risks in a more open space. Conversely, species with spatial niches with less visual obstruction (*e.g.* trunk searchers), should not change average scan duration because they usually scan large open spaces, but should increase scanning rate to a higher degree to have sufficient time to identify and escape from an initiated predator attack when foraging in a more open space. To test these predictions we compare the vigilance behaviour while foraging during winter of two small tree-gleaning birds of the pine forests of Central Spain differing in their spatial niches (Nuthatch, *Sitta europaea* and Coal Tit, *Parus ater*; Carrascal, 1984).

## Material and Methods

Field work was carried out from November 1992 to January 1993, and from November 1993 to January 1994, in a 6 ha mixed forest of *Pinus sylvestris, Castanea sativa, Acer* sp., and *Populus* sp. (El Ventorrillo, 1500 m a.s.l., Sierra de Guadarrama, Madrid).

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 pi-

ne branches. The feeders were wooden boxes (20 × 11 cm) with one side covered by a 4.8 mm mesh plastic net, allowing birds access to food. Each year the birds were allowed three weeks to familiarize themselves with feeders prior to sampling. We assume therefore that all birds had experience with the feeders. Two experimental situations were designed to simulate low and high risk sessions. The low risk session (NEAR hereafter) consisted of one feeder suspended 0.5 m below the canopy, whereas the high risk session (FAR hereafter) consisted of one feeder suspended 2 m below the canopy (in both sessions feeders were at least 2 m above the ground).

The Coal Tit (*Parus ater*) and Nuthatch (*Sitta europaea*) were chosen as focal species because of their differences in the use of foraging substrates and their abundances in autumn-winter in the study area (Carrascal, 1984). Because birds had been netted and colour-ringed, we were able to identify them when they used the feeders. Eight male and eight female Nuthatches were colour-ringed. We were unable to sex Coal Tits with certainty due to its difficulty outside the breeding season (Svensson, 1992), but the large number of birds captured and colour-ringed (31) reduces the probability of biassing the results towards a sex-ratio significantly different to that obtained for the Nuthatch. Records obtained per individual were averaged prior to statistical analyses, so sample sizes refer to the number of individuals.

The behaviour 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 programmed as an event recorder using The Observer (Noldus Information Technology, Wageningen, The Netherlands). Sampling began when one individual came into the feeders 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 while foraging at the feeders. 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 the tip of the beak was raised to eye level or higher (see Lendrem, 1983 and Hogstad, 1988 for a similar methodological approach). Sparrowhawks (*Accipiter nisus*) and Tawny Owls (*Strix aluco*) are common predators on small passerines within the study area. Sparrowhawks and Tawny Owls were observed flying over the study area, just a few metres from the feeders. The two species responded to the presence of these predators by flying towards the canopy enclosure, and by alarm calling.

Because not all individuals were sampled in each experimental trial, ANOVAs for repeated mesures were not possible, so two-way ANOVAs were used considering species (Coal Tit vs Nuthatch) 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. Because we were mainly interested in testing differences between FAR and NEAR within species, and not in global differences between FAR and NEAR, we used planned comparisons after defining specific contrast coefficients. Interspecific differences in patterns of change of vigilance between FAR and NEAR were tested using the interaction term (species * risk session). Response variables used in ANOVAs were time spent at feeders, vigilance proportion (seconds vigilant per minute on feeders), scanning rate (number of scans per minute on feeders) and proportion of short scans (scans shorter than 1 second). All variables were log- or arcsin-transformed prior to statistical analyses, carried out using the STATISTICA of StatSoft™ statistical package.

## Results

Time spent at feeders and proportion of time spent vigilant did not differ significantly between the two species ($P = 0.702$ and $P = 0.141$ respectively; Table 1), but changed significantly with distance to cover ($P = 0.017$ and $P < 0.001$ respectively). Time spent at feeders was significantly lower in the risky patch (FAR) in the Coal Tit (planned comparison: $F_{1,72} = 25.93$, $P \ll 0.001$; Fig.1a), but did not change in the Nuthatch ($F_{1,72} = 0.67$, $P = 0.41$), the difference between both patterns of change being highly significant ($P$

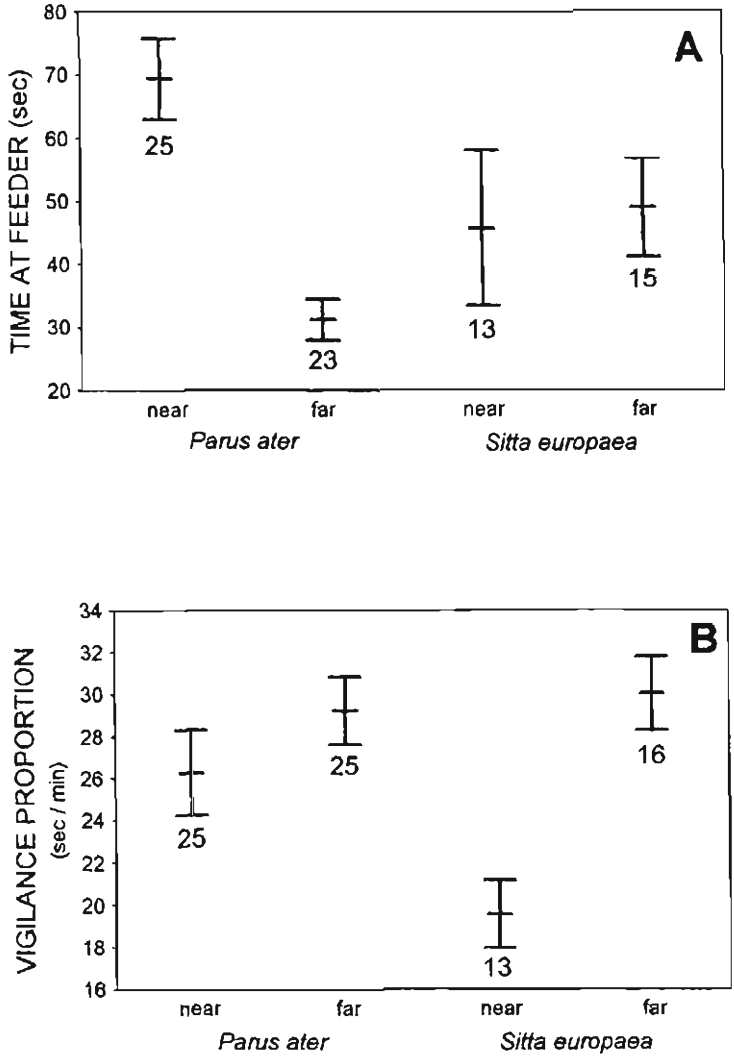


FIG 1.—Variation (mean ± SE) in time at feeders (A; seconds) and vigilance proportion (B; seconds spent vigilant per minute at feeders) as a function of distance to cover (NEAR: 0.5 m apart; FAR: 2 m apart). Sample size (number of individuals) are shown below bars.
*[Variación (media ± SE) del tiempo de estancia en los comederos (A; segundos) y proporción de tiempo vigilando (B; segundos vigilando por minuto comiendo) en función de la distancia a la cobertura (NEAR: 0,5 m de distancia; FAR: 2 m de distancia). Los tamaños muestrales se muestran bajo las barras de error estandard.]*

$<0.001$; see the interaction term in Table 1). In contrast, proportion of time spent vigilant (seconds spent vigilant per minute at feeders) increased significantly when feeders were farther from branches (high-risk foraging bouts) in the Nuthatch (planned comparison: $F_{1,75} = 13.47$, $P = 0.0005$), but did not significantly change in the Coal Tit, although it showed a similar increasing trend ($F_{1,75} = 2.75$, $P = 0.10$; Fig. 1b). The interaction term (species * risk treatment) was significant ($P = 0.05$), showing that the increase in

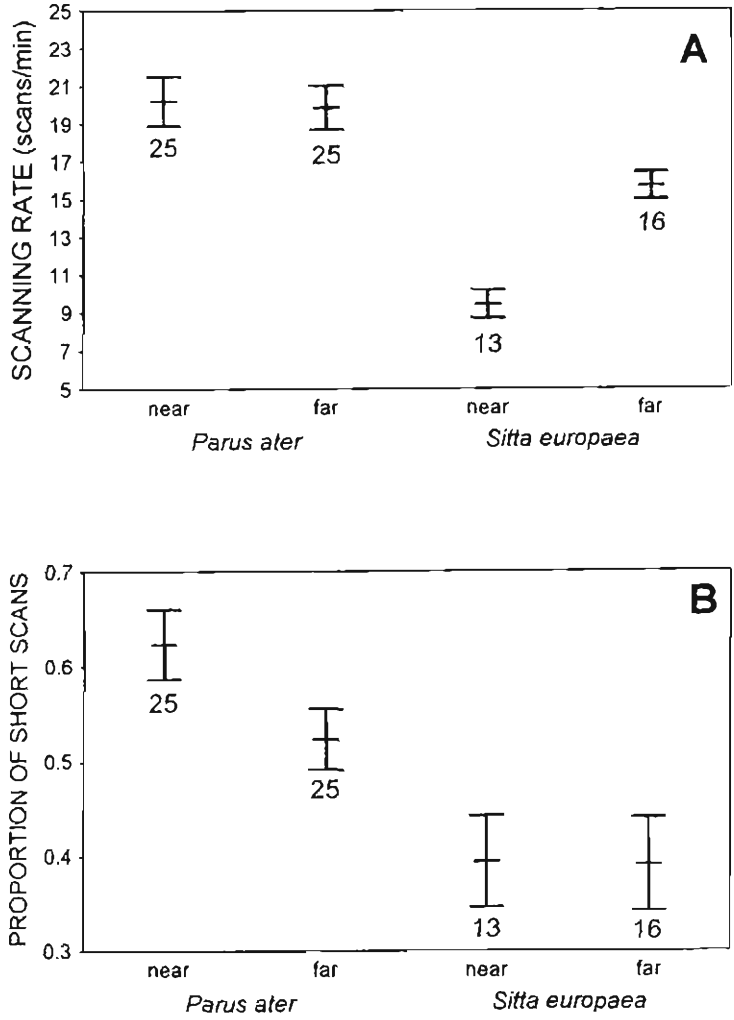


FIG 2.—Variation (mean ± SE) in scanning rate (A; number of scans per minute at feeders) and percentage of scans shorter than 1 second (B) as a function of distance to cover (NEAR: 0.5 m apart; FAR: 2 m apart). Sample sizes (number of individuals) are shown below bars.
*[Variación (media ± SE) de la frecuencia de vigilancia (A; número de vigilancias individuales por minuto) y proporción de vigilancias menores de 1 segundo de duración del total de vigilancias efectuadas (B) en función de la distancia a la cobertura (NEAR: 0,5 m de distancia; FAR: 2 m de distancia). Los tamaños muestrales se muestran bajo las barras de error estandard.]*

vigilance proportion in the patch with lower vegetation cover and longer escape distance (FAR) was more pronounced in the Nuthatch than in the Coal Tit.

The scanning rate (number of scans per minute at feeders) differed significantly between the species and the predation risk treatments ($P < 0.001$ for both terms; Table 1). The scanning rate was higher in the FAR treatment for the Nuthatch (planned comparison: $F_{1,75} = 18.93$, $P \ll 0.001$; Fig. 2a), while it was statistically indistinguishable in the

TABLE 1

Two-way ANOVAs of vigilance variables.
*[ANOVAs bifactoriales con las variables de vigilancia.]*

| | d.f. | *F* | *P* |
|---|---|---|---|
| *Time spent at feeders* | | | |
| Species | 1,72 | 0.147 | 0.702 |
| Distance to vegetation cover | 1,72 | 5.927 | 0.017 |
| Interaction | 1,72 | 13.992 | 0.0003 |
| *Vigilance proportion* | | | |
| Species | 1,75 | 2.206 | 0.141 |
| Distance to vegetation cover | 1,75 | 15.411 | 0.0002 |
| Interaction | 1,75 | 3.970 | 0.050 |
| *Scanning rate* | | | |
| Species | 1,75 | 39.036 | <0.0001 |
| Distance to vegetation cover | 1,75 | 12.217 | 0.0008 |
| Interaction | 1,75 | 11.845 | 0.0009 |
| *Proportion of short scans* | | | |
| Species | 1,75 | 18.665 | <0.0001 |
| Distance to vegetation cover | 1,75 | 1.931 | 0.169 |
| Interaction | 1,75 | 0.931 | 0.338 |

Coal Tit ($F_{1,75}=0.002$, $P=0.965$). The pattern of change in scanning rate with increasing predation risk differed significantly between the two species (interaction term: $P=0.0009$; Table 1). The proportion of scans that were shorter than 1 s differed significantly between species ($P<0.0001$; Table 1), but did not globally change with distance to cover ($P=0.169$). It decreased ($F_{1,75}=3.97$, $P=0.05$; Fig. 2b) in the Coal Tit when vegetation cover was lower (FAR). In the Nuthatch the difference in the proportion of short scans between NEAR and FAR was not statistically significant ($F_{1,75}=0.07$, $P=0.79$). The lack of significance in the interaction term ($P=0.338$; Table 1) shows that the two species did not differ in the pattern of change in percentage of short scans (*i.e.*, scan duration) with the increase in escape distance and decrease of vegetation cover.

## DISCUSSION

Our results suggest that there are two strategies by which the species studied altered their antipredator behaviour in response to the perceived predation risk: 1) to increase vigilance proportion at greater distances from cover, keeping the time spent at feeders constant (pattern observed in the Nuthatch), and 2) to decrease time spent at feeders, keeping the proportion of time spent vigilant constant (Coal Tit). Studies dealing with the effect of distance from protective cover on patch departure have shown contrasting results. Newman *et al.* (1988) and Lendrem (1983) found shorter patch residence times in the risky patches. Conversely, Cassini (1991) found that animals stayed for shorter periods in the areas closer to the refuge. Kieffer (1990), however, found no differences in time spent at the food patch across various levels of predation risk. On the other hand, results obtained by most authors on the proportion of time devoted to vigilance (Caraco *et al.*, 1980; Hogstad, 1988; Ekman, 1987; Díaz & Asensio, 1991) and scanning rate (Barnard, 1980; Barnard & Stephen, 1983) in several bird species are congruent, and show an increase with distance to cover (but see Lima, 1987). The different ways of solving the in-

creased perceived predation risk in both studied species seem to reveal a trade-off between time foraging at patch and vigilance time. Shortening the time spent at an exposed patch should diminish the probability of being preyed upon while foraging in the patch. On the other hand, if time at the feeding patch does not vary with increasing predation risk, potential prey should increase the proportion of time spent vigilant for monitoring changes in predation risk in the surroundings of the feeding patch. Thus, the individuals could detect an initiated attack with sufficient time to fly to a distant refuge that requires a long escape time.

The way by which vigilance proportion was attained was markedly different in the two species when considering the change in distance to vegetation cover around feeders. When foraging farther from vegetation cover under higher predation risk, the Nuthatch scanned more often, while the Coal Tit increased the length of scans (*i.e.* reducing the proportion of short scans). These differences between species in vigilance behaviour may reflect differences related to their spatial niches and the way in which they normally behave. Nuthatches usually forage in the most open part of the tree (*e.g.* trunk or thick branches with low foliage cover) and the space they must survey for detecting predator attacks is larger than in those species that forage in denser vegetation cover (*e.g.* the Coal Tit in pine foliage). Detection of predators in a larger surrounding space would require a longer time for a correct evaluation of risk, and therefore longer individual scans. When increasing the perceived predation risk by lengthening the distance between the feeding patch and the nearest refuge, the space the Nuthatch must survey did not increase considerably, probably due to the scant vegetation cover in the substrates where it usually forages. Therefore, the increase in vigilance proportion was attained by increasing the scanning frequency, which would be more effective in reducing the risk of being caught unawares by a predator. In contrast, Coal Tits used substrates with higher vegetation cover, and thus the visual obstruction provided by foliage reduces the space a bird must survey for detecting approaching predators (Elton, 1939). Therefore, while feeding among foliage, shorter, more frecuent scans would be more effective to detect predator attacks. When increasing the distance between the feeding patch and the nearest refuge, the visual space that must be scanned for detecting a predator is larger than when foraging among pine twigs and needles. Therefore, an increase in scan duration should be more effective in increasing the probability of detection of a concealed predator, thus reducing the probability of being preyed upon.

These results suggest that the spatial configuration of the feeding niche may determine different perceptive adaptations and responses to a common selective pressure (predation risk). In view of this complexity, a more detailed analysis of the surveillance variables is required to establish the degree to which perceived predation risk affects foraging behaviour, and which components of vigilance behaviour are modified.

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