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Scanning Behaviour and Spatial Niche

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Introduction

Searching patterns of birds are largely a function of their morphological and perceptual traits. The habitat features which most affect searching and prey-attacking behaviour in forest birds are vegetation structure and the characteristics of the available prey (ROBINSON & HOLMES 1982, CODY 1985, HOLMES & ROBINSON 1988). Vegetation structure influences the way in which birds move through the habitat in order to capture prey. At the evolutionary time scale, habitat and prey features act as selective forces which shape a species' foraging style. Such foraging styles or syndromes are the combination of various morphological and behavioural traits that maximize the foraging efficiency of each species in its environment as has been elucidated already in some groups of birds (ROBINSON & HOLMES 1982).

Vigilance during feeding has been associated with antipredator defense and/or the acquisition of information from other birds when in aggregations. In small passerine species, the vigilance rate related to predation risk varies with aggregation size, temperature, food handling costs, distance to cover, and exposure to predators (BERNARD 1983, BEVERIDGE & DEAG 1986, GLÜCK 1987, HOGSTAD 1988, LIMA & DILL 1990, PIPER 1990). Nevertheless, although vegetation cover has been recognized as a determinant of predation risk, scanning rate, and flocking behaviour, little effort has been devoted to the study of interspecific variation of vigilance behaviour in relation to the spatial niche of individual species.

Here we compare the vigilance behaviour of three small tree-gleaning birds in relation to their spatial niche. Birds engaged in surveillance activity could change either the rate at which they scan their environment or the average duration of individual scans (MCVEAN & HADDLESEY 1980, HART & LENDREM 1984, CARRASCAL et al. 1990a, DESPORTES et al. 1990). Foraging in foliage (e. g. hidden among twigs and needles of pines) might imply a lower exposure to predation risk (but see LIMA et al. 1987), shorter escape distance and less space for scanning. If there is a "foraging syndrome", relating vigilance to spatial niche, it would be expected that the mean duration of individual scans would be shorter in species using tree substrates with higher foliage density than in those using more exposed tree parts (e. g. trunk and/or thick branches with low foliage cover), because of the larger space the latter species must scan in order to forage safely.

Study area and Methods

The study area was in the Sierra de Guadarrama (Madrid, Central Spain), a mountain range covered by extensive pine forests of *Pinus sylvestris*. On 10 days from November 1983 to

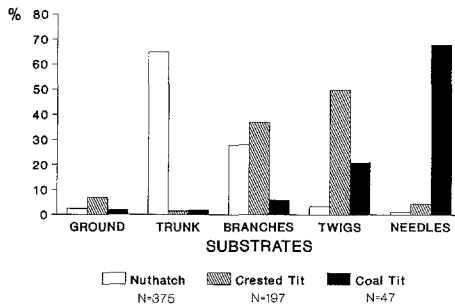


Fig. 1. Percentage use of foraging substrates by Coal Tit, Crested Tit and Nuthatch.

February 1984, we sampled the use of the space (five substrates) by the bird species belonging to the tree-gleaning guild of a forest (Siete Picos) located at 1700 m a. s. l. Point samples were taken at 30-s intervals with no more than six records for each individual bird, a maximum of three records for the same tree. This sampling procedure provided statistically independent records (CARRASCAL 1983).

During autumn-winter 1989/90 we surveyed the vigilance behaviour of the members of this foraging guild at feeders located at the Estación Biogeológica de El Ventorrillo (a mixed forest of *Pinus sylvestris*; 1500 m a. s. l., Sierra de Guadarrama). The feeders were specially designed boxes, 20 x 11 cm in size, made of wood except for one side which was covered by a 4.8 mm mesh plastic net allowing birds access to food (peanuts). They were hung from the middle of an "average pine branch" (equivalent to Branches in Figure 1). Only the Coal Tit (*Parus ater*), Crested Tit (*P. cristatus*) and Nuthatch (*Sitta europaea*) used the feeders. Seven Coal Tits, 7 Crested Tits and 8 Nuthatches were captured and colour-banded. Mean number of records per individual per day was 0.32.

The number of scans and scan duration while feeding on boxes were recorded while individuals were foraging alone (to avoid flock size effects). Only records from visits to the feeders lasting more than 30 seconds were used in analyses. We considered that birds were scanning when they raised the tip of the beak to eye level or higher (see HOGSTAD 1988 for a similar methodological approach). Data were log- or square root arcsin-transformed prior to the use of ANOVAs (SOKAL & ROHLF 1981).

Results and Discussion

All three species used the ground very seldomly but differed significantly in the use of tree substrates $\chi^2 = 527$, 6 d. f., $p < 0.001$; Fig. 1). In a gradient of exposure to predation risk the position of the three species was (from lower to higher) Coal Tit < Crested Tit << Nuthatch.

While feeding on boxes, vigilance rate (seconds spent vigilant per minute feeding) did not differ among the species studied ($F_{2,79} = 0.89$, $p = 0.4$, Tab.). Nevertheless, mean scan duration was significantly higher in the Nuthatch than in Crested and Coal Tits ($F_{2,79} = 12.82$, $p < 0.001$). Mean scan duration and scan frequency (number of scans per minute feeding) covaried significantly (ANCOVA: $F_{1,77} = 22.35$, $p < 0.001$); scan frequency did not differ between the three species when the effect of scan duration was excluded ($F_{2,77} = 1.69$, $p > 0.1$). The percentages of short scans (<1 s) and long scans (>3 s) differed significantly between the three species, the proportion of short scans being higher in the Coal Tit than in Crested Tit and Nuthatch (Fig. 2, $F_{2,79} = 10.67$, $p < 0.001$), whereas Nuthatches showed a higher proportion of long scans than Crested and Coal Tits ($F_{2,79} = 6.96$, $p = 0.002$).

Mean (\bar{x}) and standard error (se) of vigilance rate (s vigilant per min feeding), and mean scan duration (s) for tree-gleaning species.

	vigilance rate		scan duration		n
	\bar{x}	se	\bar{x}	se	
Coal tit	16.7	1.73	1.20	0.17	27
Crested Tit	20.6	2.38	1.28	0.18	27
Nuthatch	20.9	0.26	2.42	0.26	28
$F_{2,79}$	0.89		12.82		
p	0.415		<<0.001		

The similar vigilance rates provide evidence that the three bird species experienced the same level of predation risk in experimental trials; however, each species attained vigilance rate in a different way. Nuthatches which foraged in the most open parts of the tree, scanned less often but with longer individual scans whereas Coal Tits, which used substrates with higher vegetation cover, showed shorter, more frequent scans. Crested Tits foraged in substrates with intermediate vegetation cover, and showed intermediate levels for the two surveillance variables. It appears, therefore, that at the interspecific level, mean scan duration and scan frequency were intimately related to the amount of protective cover provided by pine foliage in each foraging substrate.

The inverse relationship between vegetation cover and mean scan duration could be related to the smaller surrounding area in which to search for predators from the foraging site. In open substrates, such as the trunk, the space from which an attack may come is larger than when foraging among pine foliage. Predator detection in larger surrounding area should require a longer time for a correct evaluation of the risk, and therefore, longer individual scans. Visual obstructions can also affect the vigilance patterns of bird species (METCALFE 1984, LIMA 1987). Although obstructions provided by foliage reduce the space a bird must search, they also allow predators to initiate attacks closer to a potential victim. So birds foraging in foliage should increase vigilance frequency to continuously asses changes in predation risk due to an approaching ambush predator.

These results suggest that each species displays a vigilance pattern related to the spatial niche it occupies. Such pattern might emerge from the interaction between scan frequency and scan duration, in relation to the space a bird must survey and the protection offered by the surroundings. This "vigilance-spatial niche" syndrome adds to those niche-morphology and niche-prey

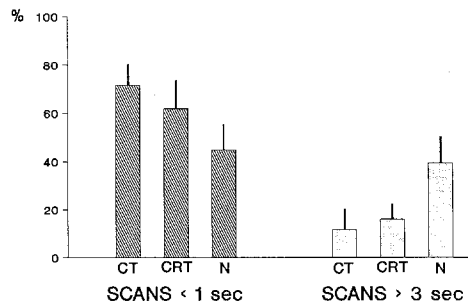


Fig. 2. Mean ($\pm 95\%$ confidence intervals) percentage of short (<1 s) and long (>3 s) individual scans in the Coal Tit (CT), Crested Tit (CRT) and Nuthatch (N).

characteristic interactions already demonstrated (MILES & RICKLEFS 1984, WINKLER & LEISLER 1985, HOLMES & ROBINSON 1988, CARRASCAL et al 1990b, SHERRY 1990). Foraging constraints (e. g. morphology related to locomotion or prey handling) which reflect selective pressure during evolutionary history, 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" emerge.

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Summary

The scanning behaviour of three small tree-gleaning passerines (Nuthatch, Coal Tit and Crested Tit) was investigated in relation to their spatial niche by observing vigilance while feeding on artificial feeders under controlled conditions. Coal Tits which forage in substrates with denser vegetation cover, showed shorter, more frequent scans than Nuthatches, which usually forage in open substrates. Our results suggest the existence of a foraging syndrome relating the vigilance pattern to the spatial niche of a species, which 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.

Zusammenfassung

An drei kleinen, Bäume nach Nahrung absuchenden Singvögeln (Kleiber, Tannenmeise, Haubenmeise) wurde das Suchverhalten in Beziehung zur räumlichen Nische untersucht. An künstlichen Futtergeräten wurde unter normierten Bedingungen die Aufmerksamkeit registriert, die die nahrungssuchenden Vögel der Umgebung schenkten. Bei Tannenmeisen, die in dichter Vegetation nach Nahrung suchen als Kleiber, sind die Phasen der Nahrungssuche kürzer und häufiger. Dies deutet auf ein Syndrom des Verhaltens, das ein Zeitmuster der Kontrolle der Umgebung mit der räumlichen Nische einer Art in Beziehung bringt. Dieses Muster entsteht vermutlich aus dem Zusammenwirken von Häufigkeit und Dauer der Phasen der Nahrungssuche auf dem Substrat mit der Größe des Raumes, den ein Vogel nach Feinden zu kontrollieren hat, sowie der Deckung, die von der Umgebung angeboten wird.

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The Position of the Hybrid Zone Between the House Sparrow *Passer domesticus domesticus* and the Italian Sparrow *P. d. italiae* in the Alpes Martimes

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Introduction

The breeding ranges of the House Sparrow (*Passer domesticus domesticus*) and the Italian Sparrow (*P. d. italiae*) currently come into contact in an arc which broadly follows the line of the Italian Alps, from the coast of the Mediterranean Sea in the west to that of the Adriatic in the east. Hybrids between the two occur, and several studies have mapped the occurrence of the two phenotypes and their intermediates in various Alpine regions (e. g. RIS 1957, NIETHAMMER 1958, V. WETTSTEIN 1959, SCHWEIGER 1959, SCHOLL 1959, SCHOLL 1960, NIETHAMMER & BAUER 1960, SCHIFFERLI & SCHIFFERLI 1980).