

## **Patch residence time and vigilance in birds foraging at feeders. Implications of bill shape**

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During winter small passerines foraging solitarily at feeders showed two different types of vigilance: the vigilance before initiating feeding that is the time needed to assess the potential risks at the patch (waiting time), and the vigilance related to the continuous scanning of the surroundings while foraging (vigilance rate). The waiting time differed significantly among the species, but vigilance rate did not. Patch residence time also differed among the species, being directly related to the waiting time, because the longer the residence time of the forager, the higher the possibility for ambush predators or competitors to reach it. Patch residence time was inversely related to bill length. This probably results from the different quantity of food per foraging time reached by different bill-sized species. Neither waiting time nor patch residence time when solitary were related to social dominance, hoarding behaviour, or species-specific traits associated with the habit of hanging upside down.

KEY WORDS: vigilance, patch residence time, bill morphology, passerines.

### INTRODUCTION

In studies intended to distinguish energy maximizers from time minimizers, as well as in those modelling patch residence time for feeding, it is very important to consider foraging constraints (meal size, handling time, etc.; STEPHENS & KREBS 1986, HIXON & CARPENTER 1988). In birds, bill morphology has been shown to constrain food access and meal size (e.g. LEDERER 1984; GOSLER 1987a, 1987b; BENKMAN 1988a). Time spent feeding usually interacts with vigilance rate, as determined by the social context in which the forager is included and the distance to a refuge (CARACO & PULLIAM 1984, KREBS & DAVIES 1987). This aspect has been studied in several bird species from a variety of viewpoints (e.g. ELGAR et al. 1984, HOGSTAD 1988, LIMA 1988). Nevertheless, relationships between bill size and shape, patch residence time and vigilance have been studied only rarely (LENDREM 1983; BENKMAN 1988a, 1988b), and never before has vigilance been linked to morphological foraging constraints.

The present study shows the existence of two different types of vigilance with different functional responses: the time needed to assess the potential risks at the

patch before initiating feeding, and the continuous scanning of the surroundings while feeding. We also address the possibility that species with longer patch residence time are more vigilant before initiating feeding, because the longer the residence time of the forager, the higher the possibility for ambush predators to reach it. Finally, we test if patch residence time may be determined by bill shape through constraints on food access.

## MATERIAL AND METHODS

Field work was carried out from October 1989 to January 1990 in El Ventorrillo at 1500 m a.s.l. (Madrid, Sierra de Guadarrama, Spain). The study site was a 6 ha mixed forest of *Pinus sylvestris*, *Castanea sativa*, *Acer* sp. and *Populus* sp.

Within the area five feeding points were established at least 50 m from each other. Each consisted of two feeders of 20 × 11 cm in size filled with peanuts, hanging from a pine branch 30-60 cm below the canopy. We used specially designed boxes made of wood except for one side which was covered by a 4.8 mm mesh plastic net allowing birds access to food.

Coal Tit (*Parus ater*), Blue Tit (*P. caeruleus*), Crested Tit (*P. cristatus*), Great Tit (*P. major*) and Nuthatch (*Sitta europaea*) used feeders frequently. Within the study area 46 different birds which utilized the feeders were captured, colour-banded, weighed and measured (bill length, bill width, and tarsometatarsus length): 7 Coal Tits, 5 Blue Tits, 7 Crested Tits, 20 Great Tits and 7 Nuthatches. Minimum number of individuals for each species estimated by the capture-recapture method for small samples (TELLERIA 1986), were 8 Coal Tits, 6 Blue Tits, 10 Crested Tits, 26 Great Tits, and 10 Nuthatches. Samples were obtained by two people during 11 days. As most of birds were colour-banded we were able to identify most of them avoiding the repeated sample of the same bird on the same feeding point each day. Mean number of records per individual and day ranged between 0.4 (Great Tit) and 1.3 (Nuthatch). This sample procedure did not completely avoid pseudoreplication (HURLBERT 1984), but the mean number of records per individual was very low, considering the amplitude of the survey period (11 days in 4 winter months) and the extent of variability in time of the day and weather.

Although birds were seen as they approached to the feeding points, sampling began only when they came within a radius of 1.5 m around the feeders; this was the distance at which birds actively responded to them and began to eat. The period for which a bird was in that area was named the «patch residence time» and most of that time was devoted to feeding (more than 85% in the five species); although this is an unusual definition of patch residence time, we want to denote with it the duration of the foraging stay in the feeding patch. The vigilance time while feeding on boxes, the time spent vigilant before coming on to the feeders (previous vigilance time), and whether birds left the feeders with a piece of peanut for food caching were also recorded. To avoid competitive effects on feeding time and vigilance only records of solitary birds (no other birds on the same tree) were used for statistical analyses, though hostile interactions when foraging with heterospecifics were also noted in order to establish the interspecific hierarchy.

The length of bill segment able to pass through the hole of the net (4.8 mm in side) was estimated for each individual bird, from data on length (up to the skull), and width of the bill. For individuals with bills narrower than 4.8 mm, the whole bill length was considered, while for individuals with bills broader than 4.8 mm a corrected measure of bill length was employed [length';  $\text{tg } \alpha = \text{length}/(\text{width}/2)$ ,  $\text{tg } \alpha = \text{length}'/(4.8/2)$ , and therefore,  $\text{length}' = 4.8 \cdot \text{bill length}/\text{bill width}$ ].

## RESULTS

Patch residence time as well as previous vigilance time differed significantly among the five species ( $F_{4,494} = 30.4$ ,  $P < 0.001$  and  $F_{4,396} = 29.9$ ,  $P < 0.001$

respectively). The means of the species for these two variables were significantly correlated ( $r_s = 1$ ,  $n = 5$ ,  $P = 0.01$ ; see Table 1). This interspecific relationship was also attained when considering the sample records of each species (Coal Tit:  $r = 0.49$ ,  $n = 57$ ,  $P < 0.001$ ; Blue Tit:  $r = 0.48$ ,  $n = 28$ ,  $P < 0.01$ ; Crested Tit:  $r = 0.17$ ,  $n = 85$ ,  $P = 0.12$ ; Great Tit:  $r = 0.35$ ,  $n = 88$ ,  $P < 0.001$ ; Nuthatch:  $r = 0.29$ ,  $n = 109$ ,  $P < 0.01$ ). The patch residence time and previous vigilance time were shortest in the Nuthatch and longest in the Great Tit and Blue Tit. While feeding on the boxes, vigilance rate (seconds spent vigilant per minute feeding) did not differ among the species studied ( $F_{4,155} = 0.95$ ,  $P = 0.44$ , Table 1).

The interspecific dominance hierarchy (see Table 2) was not correlated with patch residence time, or with previous vigilance time ( $r_s = -0.5$ ,  $P = 0.32$  in both cases).

Food caching frequency differed significantly among the five species ( $\chi^2_4 = 97.3$ ,  $P < 0.001$ ; Table 2), the Nuthatch being responsible for this difference ( $\chi^2_3 = 3.95$ ,  $P = 0.27$  for *Parus* spp). Patch residence time and previous vigilance time were not correlated with food caching frequency ( $r_s = -0.3$ ,  $P = 0.55$  in both cases) at interspecific level. Patch residence time in the Nuthatch did not differ significantly between foraging bouts ending or not with a food cache ( $F_{1,138} = 1.216$ ,  $P = 0.272$ ).

Table 1.

Mean ( $\bar{x}$ ), standard error (SE), and sample size (n) of «patch residence time» (PRT; seconds), previous vigilance time (PVT; seconds), and vigilance rate (VR; seconds spent vigilant per minute feeding).

	PRT			PVT			VR		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
<i>P. ater</i>	90.4	8.6	68	8.5	1.3	57	17.7	1.7	31
<i>P. caeruleus</i>	160.0	21.6	44	17.7	4.9	28	18.8	3.2	14
<i>P. cristatus</i>	76.0	5.2	119	7.6	0.9	85	22.8	3.0	29
<i>P. major</i>	104.3	7.7	126	14.0	3.0	88	18.2	2.2	37
<i>S. europaea</i>	44.2	4.0	142	3.0	1.0	109	16.9	1.9	49

Table 2.

Mean ( $\bar{x}$ ), standard error (SE), and sample size (n) of bill length able to pass through the hole net (4.8 mm; BL), food caching frequency (FCF), and percentage of hostile interspecific interactions won (HIW).

	BL			FCF		HIW	
	$\bar{x}$	SE	n	%	n	%	n
<i>P. ater</i>	11.7	0.2	7	2.9	70	3.8	53
<i>P. caeruleus</i>	9.8	0.1	5	9.8	41	8.3	48
<i>P. cristatus</i>	12.2	0.1	7	8.8	113	17.6	119
<i>P. major</i>	11.4	0.2	20	4.8	125	59.5	173
<i>S. europaea</i>	17.4	0.5	7	42.9	140	100.0	133

The length of bill able to pass through the feeder-net was longer in the Nuthatch and shorter in the Great Tit and Blue Tit ( $F_{4,41} = 83.6$ ,  $P < 0.001$ ; Table 2), and was inversely correlated with the patch residence time ( $r_s = -1$ ,  $n = 5$  species,  $P = 0.01$ ).

Although body weight and relative tarsometatarsus length (length/weight<sup>1/3</sup>; NORBERG 1979) differed significantly among the species studied ( $F_{4,38} = 163.1$ ,  $P < 0.001$ , and  $F_{4,38} = 24.2$ ,  $P < 0.001$  respectively), these variables were not correlated with patch residence time ( $r_s = -0.500$  for body weight, and  $r_s = 0.051$  for tarsometatarsus length;  $n = 5$  and  $P > 0.3$  in both cases). This supports the finding that species-specific traits usually associated with hanging habits are not related with time on feeders in our study (see NORBERG 1979 and CARRASCAL et al. 1990 for relationships between morphology, and foraging methods and substrates).

#### DISCUSSION

These results show the existence of two different types of vigilance. First, vigilance before initiating feeding (our previous vigilance time and the «waiting time» of LIMA 1988), that is the time needed to assess the potential risks at the feeding patch. The risk source would be the foliage around the feeders where predators (Sparrowhawk in our study area) could be in ambush. This is consistent with the fact that birds scan at a higher rate if solitary when arriving in the patch but at a lower rate if other birds are present (WAITE 1987). This previous vigilance time is related to the time birds expect to stay feeding (which could be determined by their internal state and circadian rhythms; LEHIKONEN 1986, HAFTORN 1989); the longer the patch residence time the higher the necessity for correctly identifying the potential predation risks, as predators are more likely to reach a target bird (see also PÖYSÄ 1988).

The second vigilance type is related to the continuous scanning of the surroundings. It is independent of patch residence time, as after feeding is initiated the necessity exists only to identify risk levels instantaneously. Once bird species have assessed initial risk levels, vigilance should be maintained at a similar rate without interspecific differences, due to the similar changing predation pressure under which birds engage in foraging bouts. Nevertheless, this statement can only be assumed if perception of the apparent level of risk is similar considering small species differences in flight speed and escape behaviour.

The relationship between the length of bill able to pass through the feeder-net and patch residence time is likely to result from the different amount of seed reached by different bill-sized species. Nuthatches, with longer bills, are able to obtain more food, and require a shorter time to make a profitable foraging stay and travel cost to reach the feeders. Instead, the thick-billed Great Tit and Blue Tit, have greater difficulty in getting food from the feeders and they need to forage for a longer time. Thus, in studying feeding behaviour in birds under some optimality premises (e.g. STEPHENS & KREBS 1986, HIXON & CARPENTER 1988), it is necessary to consider differences in bill size and shape to understand seasonal, inter- and intraspecific variations in foraging patterns (GOSLER 1987a, 1987b, and MATTHYSEN 1989 have shown interindividual and seasonal differences in bill length related to Great Tit and Nuthatches respectively). Our results also agree with those from GRANT (1986) and

BENKMAN (1987) in indicating that the significance of bill size differences may not be so much in association with different prey and meal sizes (e.g. LEDERER 1984; GOSLER 1987a, 1987b; BENKMAN 1988a), as in the association with different microhabitats and foraging patterns which require different bill-related skills to penetrate (but see GOSLER 1987b).

Although the social system of the five species studied are essentially different in winter (ENOKSSON 1988 and EKMAN 1989), this does not help to explain differences in vigilance and residence at feeders when individuals are feeding solitarily. Dominant species keep subordinate ones away from rich food resources and could obtain advantages from previously handled items (pers. obs.), but vigilance rate while feeding is not significantly correlated with interspecific dominance hierarchy in the group of species studied ( $r_s = -0.3$ ,  $P = 0.549$ ). These results indicate out that the outcome of the social hierarchy is only manifest when contenders are involved in an actual contest (see WAITE 1987 for a similar result).

Although it could be expected that hoarding species should have shorter patch residence time as they leave the feeding point to cache food, our results do not agree with this when considering all the species together. Only the Nuthatch seems to follow this trend as it is the species with the shortest patch residence time and the higher food caching frequency, but patch residence time at artificial feeders is independent of food caching behaviour. However, its shorter foraging stay at feeders can be explained if its longer bill is considered.

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