

Proximal costs and benefits of heterospecific social foraging in the Great Tit, *Parus major*

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The feeding and vigilance schedules of Great Tits (*Parus major*) at artificial feeders were studied in winter. We compared the behaviour of birds that foraged in pairs (mono- or hetero-specific) and solitarily. The percentage of time spent foraging was higher when a Great Tit was with an individual belonging to a subordinate species rather than with another Great Tit or a member of the dominant species. When a bird was solitary, time spent foraging was less than when it was with an individual belonging to a subordinate species, and greater than when it was with one belonging to the dominant species. The proportion of time spent vigilant did not differ between Great Tits that foraged with an individual from a dominant species or a subordinate species or with a conspecific, but was higher for solitary birds. Vigilance time of solitary Great Tits, Nuthatches, and three other *Parus* species was not negatively correlated with interspecific dominance status. In these small passerines, vigilance does not seem to be directed towards the detection of a competitor species. Surveillance for predators and detection of competitor species may be synchronous, nonexclusive tasks. Scanning rate (number of scans per minute of feeding) was the same for Great Tits that fed either solitarily or in pairs, but mean scan duration was significantly shorter for individuals in groups than when solitary. Individual Great Tits benefited from the presence of Coal, Blue, and Crested tits (subordinate *Parus* species), by a lengthening of the time spent at feeding patches and by conversion of vigilance time into feeding time.

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L'horaire des périodes d'alimentation et de surveillance de Mésanges charbonnières a été étudié à des mangeoires artificielles durant l'hiver. Nous avons comparé le comportement des oiseaux qui se nourrissaient par paires (mono ou hétéroséparées) à celui d'oiseaux solitaires. Le pourcentage de temps consacré à la quête de nourriture s'est avéré plus important lorsqu'une mésange était en présence d'un individu d'une espèce subordonnée qu'en présence d'une autre Mésange charbonnière ou d'un individu d'une espèce dominante. Les mésanges solitaires consacraient moins de temps à la quête de nourriture que les oiseaux en présence d'un individu d'une espèce subordonnée, et plus de temps que les oiseaux en présence d'un individu d'une espèce dominante. Le pourcentage de temps consacré à la surveillance ne différait pas chez les mésanges qui s'alimentaient avec un individu d'une espèce dominante, d'une espèce subordonnée ou avec une autre mésange de la même espèce, mais les mésanges solitaires passaient plus de temps à surveiller. Le temps consacré à la surveillance n'était pas inversement proportionnel au statut de dominance interspécifique chez les individus solitaires de la Mésange charbonnière, chez les sittelles ou chez trois autres espèces de *Parus*. La surveillance chez ces petits passereaux ne semble pas destinée à détecter la présence d'espèces compétitrices. La détection des prédateurs et la détection des espèces compétitrices peuvent être des tâches synchrones, pas nécessairement exclusives. Le taux des « tours d'horizon » (nombre par minute d'alimentation) était le même chez les Mésanges charbonnières qui se nourrissaient par paires ou seules, mais la durée moyenne des tours d'horizon était significativement plus courte chez les groupes que chez les individus solitaires. Les Mésanges charbonnières bénéficiaient de la présence de Mésanges noires, de Mésanges bleues et de Mésanges huppées (espèces subordonnées de *Parus*) en prolongeant leurs visites aux sources de nourriture et en convertissant leurs périodes de surveillance en périodes d'alimentation.

[Traduit par la rédaction]

Introduction

The efficient use of time in winter (feeding versus vigilance) is of high survival value for small passerines (McNamara and Houston 1987), mortality from starvation or predation being the main risks. Small birds are subjected to predation risk and have to devote a great proportion of their time budget to scanning (e.g., Moreno and Carrascal 1991). Living in flocks (mono- or hetero-specific) could enhance survival through the reduction of predation risk, conversion of vigilance time into feeding time, and copying or social learning of foraging skills. There are, however, other costs associated with social foraging, such as hostile interactions and rapid patch depletion (Barnard 1983; Clark and Mangel 1984; Pulliam and Caraco 1984; Hake and Ekman 1988; Waite and Grubb 1988). Individuals differing in dominance status likely experience different benefits and costs associated with flock membership.

Vigilance in aggregations may be directed towards both predators and dominant competitors (Waite 1987a), so net gain in vigilance could differ between species in heterospecific flocks according to their dominance status (Popp 1988a). Subordinate species may be more vigilant than dominants, as they must keep higher ranking individuals under surveillance to avoid aggressive interactions, while remaining vigilant for predators (see Waite 1987a and 1987b for an experimental approach at the intraspecific level).

The present study focuses on a defined guild of small foliage gleaners feeding on a discrete resource (at artificial feeders). Comparisons are made between the winter feeding and vigilance schedules of Great Tits (*Parus major*) foraging in pairs (mono- or hetero-specific) and solitarily. The same foraging traits are compared between Great Tits in mono-specific and in heterospecific pairs. We test the prediction that

subordinate species will spend more time vigilant than dominants, and address the following questions:

1. Do the components of vigilance (scan duration and scanning rate; McVean and Haddlesley 1980) differ between solitary birds and pair members when foraging?
2. Are vigilance and foraging times at the feeding patch affected similarly by the presence of heterospecifics and conspecifics? In the heterospecific context, do these traits differ according to the dominance status of the focal individual?
3. Does heterospecific flocking impose a cost on subordinate species? If so, are the costs of interactions between Great Tits and the other species asymmetrical (Schoener 1983) in relation to interspecific dominance status?

Materials and methods

Study site and food supply

The study was performed from October 1990 to January 1991 in a 6-ha mixed forest of *Pinus sylvestris*, *Castanea sativa*, *Acer* sp., and *Populus* sp. (El Ventorrillo, 1500 m asl, Sierra de Guadarrama, Madrid).

Five feeding points were spaced 75–100 m from one another, each consisting of two feeders (18 × 12 cm) filled with husked peanuts, suspended 1 m apart from pine branches ca. 50 cm below the canopy. The feeders were wooden boxes with one side covered by a 4.8 mm mesh plastic net, allowing birds access to the food. The birds were allowed 3 weeks to familiarize themselves with the feeders prior to sampling. We assume, therefore, that all birds had had experience with the feeders.

Species involved

Coal Tits (*Parus ater*), Blue Tits (*P. caeruleus*), Crested Tits (*P. cristatus*), Great Tits, and Nuthatches (*Sitta europaea*) used the feeders as common feeding places. Forty-six individuals were captured using mist nets near the feeding points and were colour banded: 7 Coal Tits, 5 Blue Tits, 7 Crested Tits, 20 Great Tits, and 7 Nuthatches. The mean numbers of individuals belonging to the different species in the food-supplemented section of the study area (ca. 4 ha), estimated by the capture–recapture method for small samples (Tellería 1986), were 8 Coal Tits, 6 Blue Tits, 10 Crested Tits, 26 Great Tits, and 10 Nuthatches.

The Great Tit was chosen as the focal species because of its high population density and its intermediate social status. In the study area the Nuthatch was dominant to the Great Tit, whereas Blue, Coal, and Crested tits were subordinate to the Great Tit. Dominance relationships among species were determined prior to the study by recording hostile interactions between species at feeding points during forty 1-h periods. A bird won when it supplanted another bird or chased it from the feeders. All 65 interactions between Nuthatches and Great Tits were won by Nuthatches, 12.5% of 64 interactions between Crested Tits and Great Tits were won by Crested Tits, and none of the interactions between Blue Tits ($n = 24$) or Coal Tits ($n = 20$) and Great Tits were won by the Blue Tits and Coal Tits. The dominance status of each of the five species was calculated as the percentage of hostile interactions won by each species when aggressively interacting at feeding points with each of the other four species.

Within the study area Sparrowhawks (*Accipiter nisus*), Tawny Owls (*Strix aluco*), and Great Grey Shrikes (*Lanius excubitor*) are common predators on small passerines. During ringing we observed a Great Grey Shrike capturing a Great Tit, and Sparrowhawks and Owls were observed flying over the study area, just a few metres from the feeders. Great Tits and the other members of the guild responded to the presence of these predators by flying towards the canopy enclosure, and by alarm calling.

Procedures

Observations were made from two nearby houses or from behind bushes to minimize disturbance. Behaviour at feeders was recorded at each feeding point for sampling periods of 40 min.

Although birds were observed as they approached the feeding points, sampling only began when the focal individual came within a radius of 1.5 m around the feeders, the distance at which birds actively responded to the feeders and began to eat. The selected focal individual was the first Great Tit to enter the feeding point. Activity was recorded until the focal bird abandoned the feeding point (only one Great Tit was sampled each time; continuous recording method for sequences of behaviour (Martin and Bateson 1986)). Only records longer than 15 s were included in the analysis (mean record length 76.5 s, range 15–297 s). Only two behaviours occurred at the feeders: foraging and scanning. The following variables were recorded: time spent at feeding points (period of time in which a bird was within a radius of 1.5 m around the feeders), time spent on the feeders, and number and duration of scans while foraging at the feeders. Birds were considered to be vigilant when the tip of the beak was raised to eye level or higher (see Lendrem (1983) and Hogstad (1988) for a similar methodological approach with the Blue Tit and the Willow Tit, *Parus montanus*). Time spent at feeding points, time spent on feeders, and number and duration of scans were also recorded for the other *Parus* species and the Nuthatch (records were obtained in the same way as when sampling Great Tits).

During a pilot study, pecking rate was recorded. Although pecking rate is not an accurate measure of food intake (e.g., weight of peanuts ingested), under the controlled circumstances provided by the specially designed feeding boxes, it was assumed that an increase in number of pecks produced an increase in food consumption. Number of pecks was positively correlated with time spent at feeding boxes ($r = 0.87$, $n = 46$, $p < 0.001$), so we assumed that the longer the time spent at feeding boxes, the higher the food intake per foraging bout.

Two hundred recordings (observations estimating the relative time spent at different activities) were made for Great Tits by the two authors. Most of the birds were colour banded, allowing us to avoid repeatedly sampling the same bird each day. Only one time bout per individual was recorded in each feeding context (see below) each day. This sampling procedure did not completely eliminate pseudoreplication (Hurlbert 1984), but the mean number of records per individual was very small (less than 0.5 samples/bird each day in all cases) in each feeding context, considering the length of the survey period (4 winter months) and the variability in time of day and weather conditions.

In the mixed forests of the Sierra de Guadarrama, Great Tits usually join loose heterospecific flocks with other *Parus* species (mainly Blue Tits and Coal Tits) containing 5–20 birds (personal observation) as at other European sites (e.g., Morse 1978; Herrera 1979). The aggregation frequency of species at feeders was recorded at each feeding point for sampling periods of 40 min (concurrent with focal-bird sampling). Both the species and the number of individuals per species at feeding sites were recorded at 2-min intervals by means of an audio beeper (instantaneous sampling method; Martin and Bateson 1986). This sampling procedure estimated the frequency of appearance of the tit species and the Nuthatches, as well as their coincidence with Great Tits, at the 20 time points of the 40-min sampling periods. The total of 40-min sampling periods at different times of day at the five feeding points was 25.

The average flock size outside the feeding points was small and aggregations were loose social units, probably as a result of food supplementation in the study area (see also Berner and Grubb 1985; Grubb 1987). A pair of individuals (including the focal Great Tit) was the modal size of bird groups at feeding points (conspecific context: $\bar{x} = 2.14$, $SD = 0.35$, $n = 42$; with subordinate species: $\bar{x} = 2.13$, $SD = 0.34$, $n = 62$; with dominant species: $\bar{x} = 2.04$, $SD = 0.20$, $n = 47$). On some occasions the remainder of each flock was in the vicinity of the feeding point, and the presence of other group members may have influenced the behaviour of the focal individual. To alleviate this problem, we have considered only those records in which only one other bird was with the focal Great Tit in the same tree containing feeders. Our analysis focused on the effect of one other individual in the vicinity of the Great Tits (within 2 m or less),

TABLE 1. Frequencies of appearance of Great Tits, Nuthatches, and other *Parus* spp. (Blue, Coal, and Crested tits) at feeding points, and frequencies of coincidence of an individual Great Tit with either a Great Tit or a member of a subordinate (other *Parus*) or the dominant species (Nuthatch)

	Observed			Observed - expected		
	<i>n</i>	\bar{x}	SD	\bar{x}	SD	<i>t</i> -test
Frequency of appearance at feeding points						
Great Tit	25	0.507	0.149			
Other <i>Parus</i> spp.	25	0.288	0.211			
Nuthatch	25	0.101	0.121			
Frequency of coincidence of an individual Great Tit:						
with another Great Tit	25	0.103	0.107	-0.175	0.133	***
with other <i>Parus</i> spp.	25	0.117	0.122	-0.033	0.054	**
with a Nuthatch	25	0.082	0.073	-0.007	0.050	ns

NOTE: The *t*-tests refer to the difference of the "observed minus expected" values from 0. **, $p < 0.01$; ***, $p < 0.001$; ns, not significant; *n*, sample size.

TABLE 2. Time spent at feeding points by Great Tits when solitary, with an individual belonging to a subordinate species (Blue Tit, Coal Tit, or Crested Tit), with a conspecific, or with an individual belonging to a dominant species (Nuthatch)

	Time spent at feeding points (s)		
	<i>n</i>	\bar{x}	SD
1. Solitary	44	96.0	89.9
2. With subordinate spp.	20	134.0	96.5
3. With conspecific	23	61.2	92.3
4. With dominant spp.	24	92.3	115.7

ANOVA (2 vs. 3 vs. 4): $F_{[2,64]} = 4.40$, $p = 0.016$

t-tests

1 vs. 2 $t = 1.54$, $p = 0.128$

1 vs. 3 $t = 2.02$, $p = 0.047$

1 vs. 4 $t = 0.88$, $p = 0.381$

NOTE: Statistical tests were performed on log-transformed data.

so that we could understand the proximal costs and benefits of flock formation. Three social contexts were considered: a Great Tit foraging (i) with a conspecific individual, (ii) with an individual of a subordinate species, and (iii) with an individual of the dominant species. In the fourth "feeding context" a Great Tit foraged solitary.

Statistical analyses performed were one-way ANOVAS, *t*-tests (both with log-transformed data; two-tailed tests in all cases), and χ^2 tests (Sokal and Rohlf 1983).

Results

Foraging behaviour at feeding points

The relative frequency of coincidence of an individual Great Tit with another Great Tit was significantly lower than that expected by chance (squared frequency of appearance of Great Tit; Table 1). Similarly, the relative frequency of coincidence of an individual Great Tit with an individual of another *Parus* species was significantly lower than that expected by chance (product of their frequencies; Table 1). When Nuthatches were present at feeding points, the frequency of coincidence did not differ significantly from that expected by chance ($p = 0.485$ in the *t*-test).

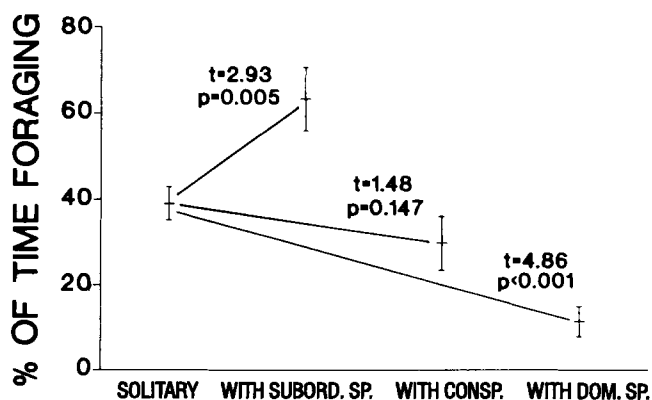


FIG. 1. Percentage of time spent foraging at feeders (mean \pm standard error) by Great Tit feeding solitary, and by a Great Tit with an individual of a subordinate species (subord. sp.) or the dominant species (dom. sp.) or another Great Tit (consp.), with the results of *t*-tests comparing the solitary Great Tit with the Great Tit in the three social contexts mentioned. For sample sizes see Table 2.

Time spent at feeding points (Table 2) was significantly different among the three social contexts. It was shorter when a Great Tit shared the feeding site with another Great Tit than when it fed with an individual of a subordinate species (Coal Tit, Blue Tit, or Crested Tit); time spent at feeding points with an individual of the dominant species (Nuthatch) was intermediate.

The percentage of time devoted to foraging at feeders (discounting vigilance time while at feeders) was significantly different among the three social contexts (Fig. 1; $F_{[2,64]} = 18.54$, $p < 0.001$). Great Tits spent a greater proportion of their time foraging when accompanied by an individual of a subordinate species than when accompanied by an individual of the dominant species. The percentage of time devoted to foraging by a solitary Great Tit was lower than when it was feeding with a member of a subordinate species, and higher than when it was feeding with a Nuthatch (Fig. 1). There was no significant difference between solitary Great Tits and those foraging with a conspecific (Fig. 1). Nevertheless, the absolute time spent at feeding points was longer for solitary Great Tits than for those feeding with a conspecific (Table 2).

TABLE 3. Foraging behaviour of different species when feeding solitarily and in the presence of one Great Tit

	<i>n</i>	Time spent at feeding points (s)		% time feeding	
		\bar{x}	SD	\bar{x}	SD
Coal Tit					
Solitary	38	93.0	85.1	56.4	21.1
With Great Tit	11	34.6	31.8	19.6	26.4
		$t = 2.39$	$p = 0.013$	$t = 5.01$	$p < 0.001$
Blue Tit					
Solitary	29	131.1	111.1	54.1	21.4
With Great Tit	10	14.1	23.4	39.2	70.2
		$t = 4.89$	$p < 0.001$	$t = 5.07$	$p < 0.001$
Crested Tit					
Solitary	44	66.1	53.6	44.2	26.7
With Great Tit	39	44.9	43.7	28.3	25.0
		$t = 2.53$	$p = 0.014$	$t = 2.74$	$p = 0.008$
Nuthatch					
Solitary	48	41.2	27.9	66.1	20.1
With Great Tit	25	82.4	76.3	74.7	21.4
		$t = 2.58$	$p = 0.012$	$t = 1.49$	$p = 0.141$

TABLE 4. Proportion of time spent vigilant (number of seconds vigilant per minute on feeders) of solitary individuals belonging to five passerine species, and the interspecific dominance hierarchy measured as the percentage of hostile interactions won by each species against individuals of all other species

	Vigilance time			Interspecific interactions won	
	<i>n</i>	\bar{x}	SD	%	<i>n</i>
Blue Tits	14	19.1	11.8	8.3	48
Coal Tits	27	19.0	10.4	3.8	53
Crested Tits	26	22.3	13.6	17.6	119
Great Tits	44	21.9	14.5	59.5	173
Nuthatches	28	19.2	11.3	100.0	133

In spite of the marked decrease in the percentage of time spent foraging when a Great Tit was at feeding points with a Nuthatch (Fig. 1), the time spent at feeding points was not significantly different from that spent by solitary Great Tits (Table 2). On many occasions, a Great Tit waited near the feeders until a Nuthatch left. On these occasions the Great Tit later used the same foraging location at the feeders as the Nuthatch ("copying" frequency = 93.1% ($n = 29$) vs. 12.5%; a foraging location was one of eight rectangular sectors measuring 9×6 cm in the two feeders at each feeding point; $p < 0.001$ in the χ^2 goodness-of-fit test).

Subordinate *Parus* species spent less time at feeding points in the presence of the dominant Great Tit than when they were foraging solitarily. Moreover, the percentage of time devoted to foraging (see above) was reduced when Great Tits were present (Table 3). Conversely, when a Nuthatch foraged in the presence of a Great Tit (the subordinate species in this case), the time spent at feeding points lengthened.

Scanning behaviour

The proportion of time spent vigilant (number of seconds vigilant per minute on feeders) by solitary individuals was similar among species ($F_{[4,134]} = 0.29$, $p = 0.9$; Table 4).

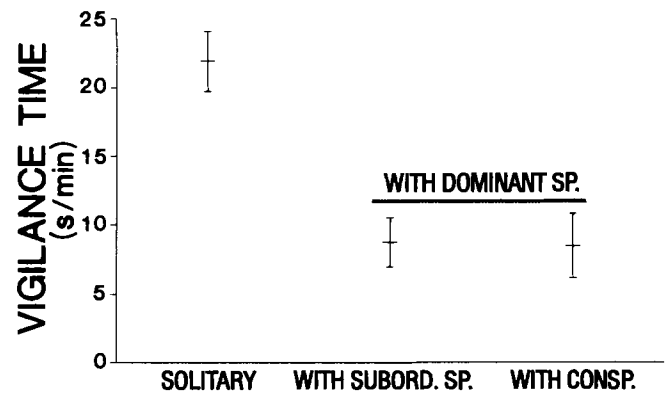


FIG. 2. Proportion of time spent vigilant at feeders (number of seconds vigilant per minute on feeders; mean \pm 1 standard error) by solitary Great Tits, and a Great Tit with an individual of a subordinate species (subord. sp.) or a conspecific (consp.). The horizontal hatched line shows the average value for a Great Tit feeding with a Nuthatch (dominant species; $n = 3$). For sample sizes see Table 3.

The vigilance time of these five species was not negatively correlated with interspecific dominance status ($r_s = 0.60$, $n = 5$, $p = 0.23$).

The proportion of time spent vigilant did not differ significantly between Great Tits foraging with an individual of a subordinate species and Great Tits foraging with a conspecific ($t = 0.61$, $p = 0.549$; Fig. 2). Nevertheless, Great Tits spent more time vigilant when solitary than when an individual of a subordinate species was present ($t = 2.34$, $p = 0.023$), or when a conspecific was present ($t = 3.01$, $p = 0.004$). Due to the high rate of hostile interactions between Nuthatches and Great Tits at feeders (Nuthatches always displaced Great Tits from feeders; see Materials and methods), we obtained only three records of vigilance (foraging bouts longer than 15 s) by Great Tits in the presence of a Nuthatch, with a mean of 11.6 s vigilant per minute of foraging. The vigilance rate of a Great Tit in the presence of a dominant Nuthatch was similar to that obtained when the Great Tit was feeding with a member of a

subordinate species or a conspecific (t -test of deviation from a hypothesized mean: $t = 1.65$, $p = 0.127$, and $t = 1.36$, $p = 0.197$, respectively). It was, however, lower than that obtained for a solitary Great Tit ($t = 4.72$, $p < 0.001$).

The scanning rate (number of scans per minute on feeders) was similar for Great Tits feeding solitarily and in pairs (Table 5). Mean scan duration, however, was significantly less for dyads than for solitary birds (this parameter was marginally different between a Great Tit foraging with a member of a subordinate species and with a conspecific; Table 5).

Discussion

Although multiple selective pressures may have led to the evolution of flock formation in birds, reduction of an individual's predation risk and improvement of its foraging efficiency have been pointed out as the major but not mutually exclusive benefits of group living (Pulliam and Caraco 1984; Lima 1985). The coincidence of an individual Great Tit with another Great Tit at feeding stations was significantly lower than that expected by chance, a result which it is not in agreement with that predicted by the "many eyes" hypothesis of antipredation and foraging efficiency models (Pulliam and Caraco 1984). In single-species flocks the main disadvantage might be associated with competition (a marked decrease in both intake rate and search efficiency), as all flock members exploit the same food resources (Hake and Ekman 1988; but see Gustafsson 1988). Considering the provision of extra food in our study, it would have been more profitable for Great Tits to avoid dominant conspecifics and to forage solitarily or with subordinate species under less competitive pressure. Intraspecific competition for food may, therefore, explain why Great Tits prefer to forage in heterospecific dyads, incurring low competition costs, more often than with conspecifics (compare observed minus expected frequencies in Table 1).

Our results indicate that not all species gain advantages by foraging in heterospecific dyads (see also Millikan *et al.* 1985). Individual Great Tits benefited from the presence of Coal, Blue, and Crested tits, both by a lengthening of the time spent foraging at feeders (a patch of high food availability), and by conversion of vigilance time into feeding time. So flocking may enable foraging Great Tits to maximize food intake through minimizing the time spent vigilant, a strategy of high survival value in winter, when food availability is low and is depressed by birds (Jansson *et al.* 1981; Gunnarsson 1983; Stairs 1985). Dominant Great Tits should seek the presence of subordinate *Parus* species to enhance foraging efficiency under safer conditions (using other species as early warners), the converse being true for subordinate species, i.e., they should avoid dominant Great Tits and terminate social foraging more often (Table 3; see Caraco *et al.* (1989) for an experimental example at intraspecific level). Accordingly, under natural conditions the Great Tit is a flock-positive species, joining groups of other *Parus* species, whereas subordinate *Parus* species form discrete social units with conspecifics (Herrera 1979; review by Ekman 1989). Our results demonstrate a clear asymmetry in competitive contests among the small passerines involved (see review by Schoener 1983; Alatalo and Moreno 1988).

In the presence of the dominant Nuthatches, Great Tits probably obtained less food per foraging bout at feeders, as they were more vigilant and were aggressively excluded from feeding places. Although the frequency of hostile interactions was markedly lower when Great Tits were in the presence of

TABLE 5. Scanning rate (number of scans per minute on feeders) and mean scan duration in Great Tit when feeding solitarily, with an individual of a subordinate species (Blue Tit, Coal Tit, or Crested Tit), and with a conspecific

	Scan frequency			Scan duration (s)		
	<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}	SD
1. Solitary	44	15.9	12.9	41	1.73	1.01
2. With subordinate spp.	12	10.3	6.8	11	0.84	0.25
3. With conspecific	13	12.5	11.6	11	0.66	0.19
<i>t</i> -test						
1 vs. 2	$t = 0.89$, $p = 0.377$		$t = 2.96$, $p = 0.005$			
1 vs. 3	$t = 1.12$, $p = 0.269$		$t = 3.87$, $p < 0.001$			
2 vs. 3	$t = 0.21$, $p = 0.832$		$t = 1.89$, $p = 0.074$			

NOTE: t -tests were performed with log-transformed data. Sample sizes vary because some individuals did not scan during their foraging bouts.

a conspecific (43.5%, $n = 23$) than when they were with a Nuthatch (75%, $n = 24$; Fisher's exact test, $p = 0.039$), the coincidence of the Great Tit was higher with a Nuthatch than with another Great Tit (see observed minus expected frequencies in Table 1; $t = 5.91$, $p < 0.001$). Great Tits probably counterbalanced the costs of social foraging with Nuthatches by copying foraging locations (Morse 1978; Waite and Grubb 1988).

Looking for predators and detecting conspecifics who might attempt to displace them from their feeding sites have been pointed out as the main reasons for individuals maintaining a high vigilance rate (Knight and Knight 1986; Ekman 1987; Waite 1987a; Popp 1988a). Like those of other studies (Studd *et al.* 1983; Elgar *et al.* 1984; Hogstad 1988; Popp 1988a), our results indicate that the time spent vigilant by Great Tits in groups is shorter than when they are feeding alone. Nevertheless, the proportion of time spent vigilant did not differ among the three social contexts, and the net gain in vigilance was not related to dominance status in this tree foliage-gleaning guild (Fig. 2 and Table 3). Therefore, scanning behaviour in Great Tits seems to be related to predator detection rather than to avoidance of aggressive interactions with dominant species. This result is contrary to the prediction that subordinate species will spend more time vigilant because they have to watch for dominant competitor species that may displace them from food resources (as pointed out by Hegner 1985; Waite 1987a, 1987b; Popp 1988a). Our data suggest that vigilance for predators and detection of competitors may not be mutually exclusive. Surveillance may be used by subordinate species to ascertain the risk from an approaching predator or competitor, but the amounts of time required for these two activities may not necessarily be additive (synchronous tasks; Waite 1987a).

Birds have two options for reducing vigilance time when in larger aggregations: to reduce scanning frequency and (or) to reduce scan duration (McVean and Haddlesley 1980; Lendrem 1984; Metcalfe 1984). Great Tits reduce scan duration but do not change scanning frequency. The shorter scan duration, with no changes in the scanning rate, supports the assumption that the time needed to scan for predators is longer than the time needed to verify if other individuals in the vicinity are vigilant (Studd *et al.* 1983; Pöysä 1985; Carrascal *et al.* 1990). Great Tits in flocks probably need to scan for only a few seconds to assess that other flock members are still there,

and devote proportionately less time to true predator detection (Pulliam *et al.* 1982). Moreover, by lengthening scan duration, Great Tits achieve greater vigilance with fewer changes between vigilant and nonvigilant states, thus not interrupting the search for hidden food that is difficult to capture ("handling time constraint" hypothesis of Lendrem 1983; Popp 1988b). Mean scan duration was slightly shorter when Great Tits were foraging with a conspecific than when they were in the presence of an individual from a subordinate species. This may indicate that Great Tits do not "trust" neighbours, irrespective of their specific identity (Metcalfe 1984). So transfer of information on predators between species may depend on the degree of sharing of behavioural tasks related to predator detection and foraging.

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