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EXPLOITATION COMPETITION INFLUENCES THE USE OF FORAGING SITES BY TITS: EXPERIMENTAL EVIDENCE[1]

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Abstract. In coniferous forests of central Sweden, tits (Paridae) and the Goldcrest, *Regulus regulus,* exploit nonrenewable resources in their group territories during winter. The smaller and socially subordinate species, the Goldcrest and the Coal Tit, *Parus ater,* forage on the outermost tree parts, while the larger and dominant Willow Tit, *Parus montanus,* and Crested Tit, *Parus cristatus,* forage on the inner tree parts. We removed Coal Tits and Goldcrests in three flocks in early winter to see if their absence would cause changes in the foraging patterns of the two dominant species. In late winter, Crested Tits foraged farther outward on branches of spruce in experimental flocks than they did in the control flocks. In spruce, Willow Tits foraged nearer the trunk than Crested Tits, and they did not respond to the experiment. In pine, Willow Tits, however, did move from branches to twigs in the absence of Coal Tits and Goldcrests. The experiment indicates that exploitation competition directly based on food depletion, without any interference, may influence the use of foraging sites by tits in coniferous forests.

Key words: coniferous forest; exploitation competition; field experiment; interference; niche shift; Parus; Regulus.

INTRODUCTION

Numerous field experiments have demonstrated the presence of interspecific competition in animals and plants (Connell 1983, Schoener 1983). Frequently the competitive effects are asymmetric, with one of the interacting species being more affected than the other (Connell 1983, Schoener 1983, Persson 1985). Animals from different trophic levels, taxonomic groups, and environments interact in different ways. Therefore, we must not expect too much generality in the mechanisms and importance of interspecific competition. Detailed analyses of the nature of interspecific competition among different types of animals and plants are needed to understand the effects of interspecific competition beyond the mere establishment of its presence or absence.

While there have been many observational studies of the use of foraging sites by birds, experimental studies are missing (Williams and Batzli 1979 is an exception). Interspecific competition in other contexts has been shown experimentally to affect reproductive success (Högstedt 1980, Minot 1981, Gustafsson, 1987), population size (Dhondt and Eyckerman 1980), and territory or habitat selection (Davis 1973, Reed 1982, Garcia 1983, Loyn et al. 1983).

This study is part of a project that aims to reveal the possible effects of interspecific competition on the use of foraging sites in coniferous forest tits (Paridae) during winter. Coniferous forest tits and the Goldcrest, *Regulus regulus,* have largely overlapping diets consisting of spiders and other arthropods; the diet of tits also includes seeds (Palmgren 1932, Haftorn 1956, Jansson 1982). They separate in their use of foraging sites in trees (Haftorn 1956, Alerstam et al. 1974, Ulfstrand 1977, Hogstad 1978, Alatalo 1982). There is already extensive nonexperimental evidence that the foraging-site selection of tit species is restricted in the presence of other tit species (see Alatalo et al. 1986 for review). Also, Alatalo et al. (1985) experimentally reduced the number of Willow Tits, *Parus montanus* (body mass 11.4 g), and Crested Tits, *Parus cristatus* (11.5 g), in winter flocks in coniferous forests of central Sweden. The Coal Tits, *Parus ater* (9.5 g), and the Goldcrest (5.3 g) then responded by increasing their use of the foraging sites of the species that were removed.

What is the actual mechanism that restricts the foraging patterns of coexisting species of tits and Goldcrests? Is it based on hostile interactions with socially dominant species affecting the socially subordinate species, and not vice versa (contest competition sensu Nicholson 1954, interference competition sensu Park 1962, encounter competition sensu Schoener 1983)? Or is it caused directly by the birds reacting to food depletion (scramble competition sensu Nicholson 1954, exploitation competition sensu Park 1962 and Pianka 1978, consumptive competition sensu Schoener 1983)? In tits, interspecific hostility usually occurs in the form of supplanting attacks, and the larger species are socially dominant over the smaller ones (Hinde 1952, Gibb 1954, Ulfstrand 1962, Morse 1970, 1978, Ogasawara 1975, Hogstad 1978). In a previous experiment, Alatalo et al. (1985) removed the socially dominant

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TABLE 1. Habitat characteristics of the areas occupied by each flock.

	Area (ha)	Tree age (yr)	Tree volume (m^3/ha)	Tree composition (biomass %)		Tree height (m)	
				Pine	Spruce	Pine	Spruce
Experiment							
Flock 1	16	90	213	37	63	24	23
Flock 2	10	90	213	37	63	24	23
Flock 3	14	89	142	63	37	18	17
Average	13.3	89.7	189	45.7	54.3	22.0	21.2
Control							
Flock 1	14	87	185	46	54	20	19
Flock 2	13	85	224	36	64	21	22
Flock 3	17	100	183	52	45	22	21
Average	14.7	90.7	197	44.7	54.3	21.0	20.8
Tests among treatments							
t	0.63	0.21	0.29	0.10	0.00	0.56	0.18
(df = 4)	$P > .5$	$P > .5$	$P > .5$	$P > .5$	$P > .5$	$P > .5$	$P > .5$

species, and the smaller species were found to respond to their absence. In that case, the shift in foraging sites of the smaller species could be due to interference competition, exploitation competition, or both. Observational studies (Alatalo 1981, Alatalo et al. 1986) suggest that even the larger species may expand their use of foraging sites in the natural absence of the smaller species, as a result of release from exploitation competition.

Schoener's (1983) review includes only one experimental demonstration of exploitation competition as the true cause of changes in foraging patterns without any interference effects, namely the moose–hare interaction studied by Belovsky (1984). In the present study, to see if exploitation competition operates among tit species, we removed the smaller species, i.e., the Coal Tit and the Goldcrest. If the larger species, the Willow and Crested Tits, were to change their respective use of foraging sites, that would justify the conclusion that exploitation competition without any interference can influence the use of foraging sites in the "tit guild."

METHODS

In general, removal experiments in birds are difficult because enclosures cannot be used. Tits and Goldcrests hold group territories in winter and the immigration of new birds usually stops by December (Ekman 1979, Ekman et al. 1981, Hogstad 1984), but in the experiment of Alatalo et al. (1985) immigration was still considerable. To try to eliminate immigration, we chose for the present study areas isolated by clearcuts.

The study was conducted at the Grimsö Wildlife Research Area in central Sweden (59°40′ N, 15°25′ E). The area is mainly covered by spruce, *Picea abies,* and pine, *Pinus silvestris,* forest. The forest has been subject to commercial logging, which has created patches of old forest intermingled with clearcuts and patches with various stages of young forest. We chose for the study four areas with old forest surrounded by clearcuts in order to eliminate as far as possible any immigration of birds. Two areas were larger and contained two separate flock territories each, while the two smaller ones supported only one flock each.

To ensure sufficient replication (see Hurlbert 1984, Alatalo et al. 1985) we used three flocks for experimentation (experimental flocks 1 and 2 in a large area and 3 in a small area) and retained three flocks as controls (control flocks 1 and 2 in a large area and 3 in a small area). Table 1 summarizes the major habitat characteristics, derived from the forest manual of the forest owner, for the areas occupied by each flock. There are no significant differences between the areas occupied by the experimental and control flocks in any of the environmental variables.

We removed the Coal Tits and Goldcrests in the experimental flocks during early winter by shooting and mistnetting using song and call playback attraction. Most birds were removed between 16 November and 13 December (16 individuals). Between 5 and 8 January, five additional individuals that had immigrated to the experimental areas were removed. We did not succeed in removing one Coal Tit in flock 1, and that bird stayed in the flock throughout the experiment. In February no immigration occurred, but in March one Goldcrest had joined flock 3. Thus, the removal procedure was generally successful with only one Coal Tit in the experimental flocks as compared with five Coal Tits in the control flocks, and one Goldcrest arriving late in winter in the experimental flocks against eight Goldcrests in the control flocks (Table 2).

The use of foraging sites by tits was observed in mid-March, that is, after the experimental areas had been nearly devoid of Goldcrests and Coal Tits for 3 mo. Because the food resources of tits and Goldcrests (spiders and other arthropods and conifer seeds) are not renewed during the winter period, the reduced consumption of those food sources in the experimental areas should have led to a better food situation for the

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TABLE 2. Species composition in the study flocks in March and the numbers of birds removed between 16 November and 8 January.

	Number of individuals in March							Removed individuals	
	Crested Tit	Willow Tit	Coal Tit	Gold-crest	Great Tit	Tree-creeper	Nut-hatch	Coal Tit	Gold-crest
Experiment									
Flock 1	3	3	1	...	2	3	1	2	4
Flock 2	2	2	...	...	...	1	...	1	4
Flock 3	3	3	...	1	...	2	...	3	7
Control									
Flock 1	3	3	2	3	...	2	...		
Flock 2	3	3	2	3	...	2	1		
Flock 3	3	3	1	2	1	3	...		

remaining species toward the end of winter, if exploitation competition were important.

In March, all the flocks consisted of two to three Crested Tits and two to three Willow Tits (Table 2). Great Tits, *Parus major,* and single Nuthatches, *Sitta europaea*, visited some of the flocks occasionally, but the effect of those species on Crested and Willow Tits was probably small. Treecreepers, *Certhia familiaris,* were common, but differed so clearly from tits in their foraging sites, being specialized to feed on tree trunks, that their impact on the food conditions of the other species was probably negligible (Alatalo 1982).

We recorded the foraging sites of the birds in experimental flock 1 and control flock 1 on seven occasions and in all the other flocks on five occasions. The experimental and control flocks were visited during the same days, alternating the order of visits, to eliminate any possible biases caused by the effects of weather on foraging behavior. On each occasion we took, at most, 20 observations of each species in each flock. The moment of recording the site of the bird was determined by a metronome emitting a signal at 15-s intervals. If the bird was resting or handling a food item found in some other place, no record was made. We tried to get at least five observations of birds in each of the two coniferous tree species. Crested Tits preferred spruce, and therefore the number of observations in that tree was higher than in pine (81.0% in experimental flocks, $n = 268$; 78.4% in control flocks, $n = 227$). For Willow Tits the observations were more equally distributed (43.6% for spruce in experimental flocks, $n = 243$; 50.4% in control flocks, $n = 127$). In the control flocks, Coal Tits and Goldcrests almost invariably foraged in spruce. However, earlier in winter, Goldcrests in particular were frequently seen foraging in pines.

In general, species of the tit guild separate out best by their choice of foraging substrate in trees (Alatalo 1982). The type of substrate (or tree part) in this study was divided into four categories (trunk; branch, >1 cm in diameter; twig, <1 cm in diameter; and needled twig, usually <1 cm in diameter), as has been done in many other studies (Alerstam et al. 1974, Alatalo 1982, Alatalo et al. 1985). It was sometimes difficult to see the type of substrate in the inner parts of spruce. Therefore, we also estimated the distance of the bird from the trunk and the distance of the tip of the branch used by the bird from the trunk. Those variables were transformed to relative distance from trunk and divided into five categories for further analysis. In spruce, for 12.4% of the Crested Tit and 4.5% of the Willow Tit observations, only that relative distance could be estimated, and records of the tree part were missing. In pine, almost all observations included foraging substrates (missing in 4.9% of the Crested Tit and 2.5% of the Willow Tit observations). For pine, we will therefore present data on foraging substrate only, and not on relative distance.

For statistical testing of the use of foraging sites of Willow and Crested Tits between experimental and control flocks one-tailed tests were used, because the statistical alternative hypothesis (H_1) was that those species increase the use of the outer tree parts in experimental areas in the absence of Goldcrests and Coal Tits, which were specialized to forage on outer tree parts. The independent observations in the data set were presented by the average parameters for each of the three experimental and control flocks.

For estimating overlap in foraging niche utilization we used the simple index:

$$\text{Overlap} = \Sigma \min(p_{xi}, p_{yi})$$

where p_{xi} and p_{yi} are the proportions of usage of foraging site i by species x and y, respectively, and min indicates minimum (e.g., Hurlbert 1978: Eq. 1).

RESULTS

Because spruce was preferred by foraging tits, we have more comprehensive data from that tree species than from pine. Looking at the overall use of foraging substrates (Fig. 1), the preference for needles by Coal Tits and Goldcrests in control areas is obvious. Crested Tits used needled twigs for about one-third of their foraging time, whereas Willow Tits seldom used that category and mainly foraged on branches.

In the experimental areas, Crested Tits increased their use of needles up to two-thirds of their foraging

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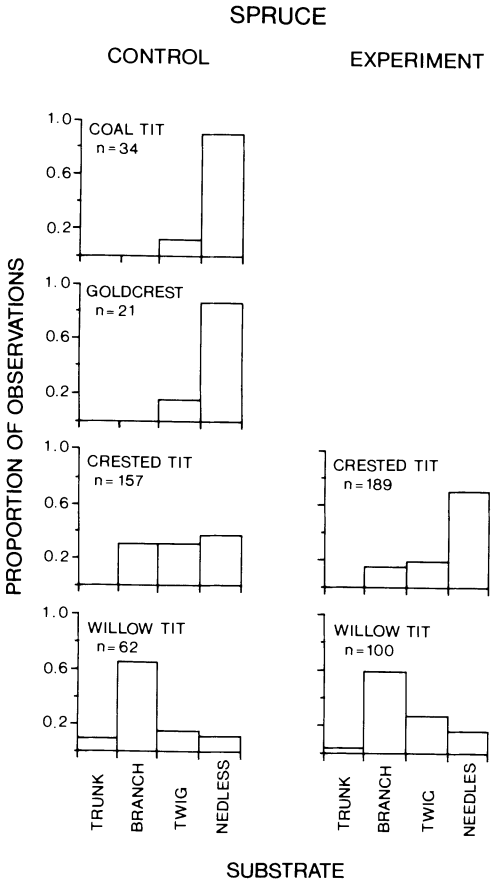

FIG. 1. The foraging substrate distributions in spruce in the control and experimental flocks.

time, and reduced their use of branches and twigs. In the Willow Tit there was no apparent change in the use of foraging substrates. For statistical testing, we calculated the proportion of feeding on needles and thin twigs combined for each of the study flocks (Table 3). In that way we could use each of the flocks as one independent observation. In all three experimental flocks, the Crested Tits used outer tree parts more frequently than was the case in any of the three control flocks; hence the treatment had a significant effect on the Crested Tit. In the Willow Tit, there was no significant difference between experimental and control flocks.

Analysis of the foraging sites in terms of relative distance to trunk led to a similar result (Fig. 2, Table 4). The average relative distance in the Crested Tit increased from 0.42 in control flocks to 0.53 in experimental flocks, while in the Willow Tit there was no change at all. Since the average relative distances were near 0.50, it was legitimate in this case to use parametric statistics (Table 4). We also performed an analysis of variance, based on the average relative distance recorded during each of our visits (five to seven per flock). In the Crested Tit there was no significant variation among flocks within the treatment ($F = 0.39$, $df = 4$, $P > .80$), whereas the difference between treatments was significant ($F = 4.42$, $df = 1$, $P < .05$). In the Willow Tit there was no significant variation at all.

To illustrate the magnitude of niche shifts in the manner proposed by Alatalo (1981) and Alatalo et al. (1986), we estimated the difference in niche overlap associated with the difference in foraging-site distribution between experimental and control areas. With respect to type of substrate, the overlap between the Crested Tit and Coal Tit in control areas was 0.487. If the Crested Tits had foraged in the same way in the control areas as they did in the experimental areas, the overlap would have been 0.801, indicating an overlap reduction of 0.314 units by the Crested Tit in the presence of Coal Tits. In the Willow Tit the corresponding reduction was only 0.027, i.e., from 0.258 on the basis of its behavior in experimental flocks to 0.231 actually recorded in control flocks.

The numbers of observations were lower for pine because the Crested Tits preferred to forage in spruce. In the Crested Tit, there was only a tendency ($P = .10$) for greater use of the outer parts of pine trees in experimental flocks (Fig. 3, Table 3). In the Willow Tit, the difference was significant, and it was mainly due to a greater use of twigs without needles. Because Goldcrests and Coal Tits in March foraged almost exclusively on spruce, they are not represented in Fig. 3.

DISCUSSION

In spruce, the Crested Tits clearly increased their use of the outermost tree parts in flocks from which Goldcrests and Coal Tits had been absent for a period of 3 mo. By contrast, the Willow Tits did not change their foraging-site distribution in spruce. This difference between the two tit species may be due to the fact that

TABLE 3. The proportion of foraging observations in which the bird was on needles or thin twigs (<1 cm diameter) for Crested and Willow Tits in each flock.

	Spruce				Pine			
	Crested Tit		Willow Tit		Crested Tit		Willow Tit	
	Prop.	*n*	Prop.	*n*	Prop.	*n*	Prop.	*n*
Experiment								
Flock 1	0.88	81	0.44	64	0.60	5	0.58	84
Flock 2	0.87	52	0.39	13	0.71	7	0.50	4
Flock 3	0.82	56	0.30	23	0.74	38	0.44	45
Average	0.854		0.376		0.684		0.509	
Control								
Flock 1	0.71	66	0.23	13	0.48	25	0.38	8
Flock 2	0.65	34	0.39	13	0.59	17	0.32	25
Flock 3	0.65	57	0.22	36	0.67	3	0.33	27
Average	0.669		0.279		0.578		0.343	
Tests comparing treatments (one-tailed)								
U (df = 4)	0 $P = .05$		1.5 $P > .1$		1 $P = .1$		0 $P = .05$	

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the Willow Tit uses foraging sites that are more distinct from those of the removed species (overlap with Coal Tit in control areas 0.23) than does the Crested Tit (overlap 0.49). The Willow Tit is more likely to undergo competition for foraging sites with the Crested Tit in spruce, than with the Goldcrest and Coal Tit, and therefore the absence of the latter two species may have less impact.

In pine, by contrast, the Willow Tit reacted significantly to the removal of the Goldcrests and Coal Tits. The different result in pine may be explicable by the fact that the Crested Tit rarely used pines, and the foraging-site distribution of the Willow Tit was not as different from that of the Crested Tits in pine as in spruce (overlap between Willow and Crested Tits in control area 0.80 and 0.58, respectively). It is uncertain whether the foraging pattern of the Crested Tits in pine changed at all in response to the experiment.

For the Crested Tit, the shift in spruce between experimental and control flocks was of the same magnitude as that observed between northern Finland, where Coal Tits and Goldcrests are naturally rare, and central Sweden (Alatalo et al. 1986), where Coal Tits and Goldcrests are common. That suggests that geographical niche shifts do not necessarily require morphological or any other evolutionary changes, but that they can result from rapid adjustment of foraging behavior as a response to a change in food availability. That flexibility in the behavior of tits is also indicated by the observational studies of Hogstad (1978), Herrera (1979), and Alatalo (1981) where the use of foraging sites was observed to change between flocks of different structure in a way that could be attributed to interspecific competition.

In only one earlier experiment have foraging-site changes been explained by exploitation competition, without any interference effects (Belovsky 1984). In general, foraging-site (macro- or microhabitat) shifts have been caused by some kind of interference (see Schoener's 1983 review, see also Morse 1974, Persson 1985). Still, that does not necessarily prove exploitation competition to be less important than interference in causing foraging site changes. Overt interference behavior is easier to observe than are behavioral changes caused directly by depletion of food or other resources. It is also to be remembered that appearance of interference competition assumes underlying exploitation competition for commonly used limiting resources (MacArthur 1972, Roughgarden 1979). Therefore, pure interference competition is unlikely to exist, whereas pure exploitation competition is possible.

Our experiment shows that exploitation competition alone can cause foraging niche shifts in tits, but we will underline that this does not exclude the possibility that interference competition can be important in situations where smaller species respond to the presence of larger species (e.g., Alatalo et al. 1985). In such cases it will, however, be difficult to estimate the relative influence of interference vs. exploitation competition.

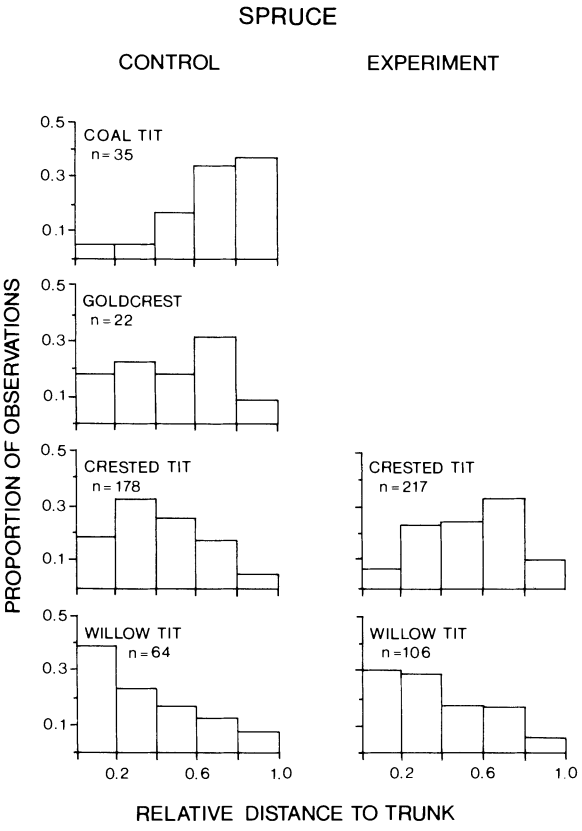

FIG. 2. The relative distances to trunk (0 = trunk, 1 = tip of branch) in spruce in the control and experimental flocks.

TABLE 4. The average relative distances of foraging sites from trunk (0 = trunk, 1 = tip of branch) for Crested and Willow Tits in each flock.

	Spruce			
	Crested Tit		Willow Tit	
	$\bar{X}$	n	$\bar{X}$	n
Experiment				
Flock 1	0.56	90	0.39	66
Flock 2	0.50	68	0.39	15
Flock 3	0.53	59	0.32	25
Average	0.530		0.370	
Control				
Flock 1	0.41	77	0.43	14
Flock 2	0.46	38	0.31	14
Flock 3	0.40	63	0.34	36
Average	0.423		0.361	
Test comparing treatments (one-tailed)				
t (df = 4)	4.38 $P < .01$		0.22 $P > .5$	

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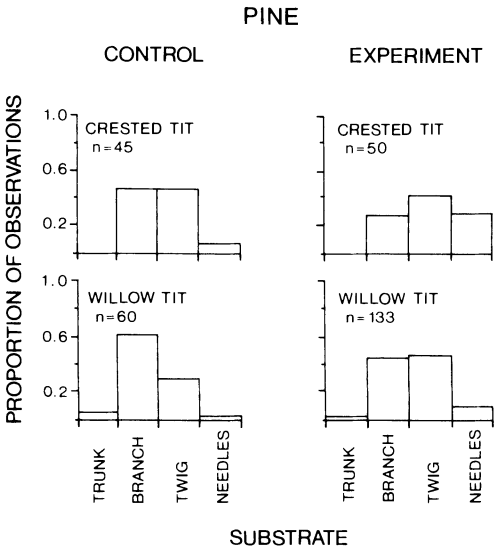

FIG. 3. The foraging substrate distributions in pine in the control and experimental flocks.

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