

Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities?

Mikko Mönkkönen¹, Pekka Helle², and Kimmo Soppela¹

¹ Department of Zoology, University of Oulu, Linnanmaa, SF-90570 Oulu, Finland

² Meltaus Game Research Station, Finnish Game and Fisheries Research Institute, SF-97340 Meltaus, Finland

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Summary. We studied experimentally interspecific competition among foliage-gleaning passerine birds by manipulating the density of resident tits. In 1988 tit density was experimentally increased on three small islands in a central Finnish lake, and decreased on three other islands by tit removal. In order to avoid the effects of between-island differences in habitat quality, the role of the islands was reversed when the experiment was repeated in the following year. Censuses and observations on foraging and feeding behaviour were conducted to assess the numerical and behavioural responses of migrant congeners (mainly chaffinches and willow warblers) with respect to the manipulated abundance of the tits. We also measured whether variation in food consumption of tits affected the frequency with which the migrants found food by calculating average intervals between successful prey captures, time lags to prey-capture and giving-up times. Our results indicate that interspecific competition is of minor importance in structuring breeding bird assemblages and species feeding ecologies on the study islands. No consistent difference in foraging or feeding niches of chaffinches and willow warblers was found between low and high tit density conditions. Niche overlap analysis showed no avoidance by chaffinches and willow warblers of the microhabitats which tits used. Tit abundance had no significant effect on feeding success or behaviour. Experimentally increased abundance of resident birds was associated with increased abundance of breeding migrants, however. This pattern was found not only in the foliage gleaning guild but also with all passerine birds, indicating that food was not an important contributor to this pattern. We elaborate a hypothesis suggesting heterospecific attraction in northern breeding bird assemblages. Habitat generalist migrants may use the presence of residents as an indicator of safe and/or productive breeding sites in northern unpredictable circumstances.

Key words: Interspecific competition – Passerine birds – Community structure – Niche shifts – Boreal forest

Offprint requests to: P. Helle

Debate in community ecology in the late 1970s and early 1980s concentrated on the role of interspecific competition. Certain authors argued for the importance of competition in structuring communities and shaping species' ecologies and evolution (e.g. Diamond 1978; Giller 1984), whereas others emphasized the role of predation, parasitism, and chance in community organization (e.g. Connell 1975; Wiens 1977; Strong et al. 1983). The dichotomy between contemporary views was rather marked (e.g. Strong et al. 1984). More recent works have emphasized that interspecific competition should be considered as only one of a number of alternative processes (Martin 1986; Wiens 1989b). The role of competition varies according to conditions, and we need to evaluate the types of situation and taxa where it is (or is not) important. Here, experimental work can bring forth important results (Schoener 1983; Connell 1983; Wiens 1984; Diamond 1986), but only a few bird community studies have been reported to date (see Brawn et al. 1987).

Experimental studies have shown that interspecific competition during the breeding season can affect reproductive success (Högstedt 1980; Minot 1981; Gustafsson 1987), and territory occupation in birds (Reed 1982; Garcia 1983; Sæther 1983; Sherry and Holmes 1988). Shifts in feeding niche and population density as consequences of competition have been experimentally demonstrated only in wintering assemblages of birds (Williams and Batzli 1979; Dhondt and Eyckerman 1980; Alatalo et al. 1985, 1987). Field experiments have demonstrated that competitive effects are frequently asymmetric, with the effects of competition being stronger on one of the interacting species (Persson 1985). Resident birds are commonly held to be superior competitors over migrant members of the same guild in breeding assemblages (Herrera 1978a; O'Connor 1981; but see Ulfstrand 1977). Morse (1989) concluded that in general "migrants fit in where residents have not exploited resources" (p. 130). It is suggested that the decreasing proportion of migrants in avian breeding communities towards the south both in Europe (Herrera 1978b) and eastern North America (Morse 1989) is due to parallel

intensification of interspecific competition by resident birds. Interspecific competition most likely manifests itself as interference competition within a habitat, however (Connor and Bowers 1987).

According to the original formulation of the Hutchinsonian niche theory (Svärdson 1949; Hutchinson 1957; MacArthur 1972), intensified competition should foster niche narrowing and thence reduced overlap in critical niche dimensions. More recent theoretical and empirical work has shown that this pattern is associated with competition only in certain conditions, such as equal equilibrium densities, difference in resource preference between putative competitors, and identical resource densities. Under other circumstances, competition might result, for example, in increased overlap with broadened niches (Abbot et al. 1977; Abrams 1986; Holt 1987).

In this experiment we manipulated breeding numbers of resident tits (*Parus* spp.) on islands and monitored the effects of this manipulation on migrant birds belonging to the same foraging guild. We intended to determine whether interspecific competition affects avian community structure and feeding ecology of birds on these islands.

Material and methods

Study area and manipulations

The study was carried out in Konnevesi, central Finland (62° 40' N, 26° 30' E). Populations of the willow tit (*Parus montanus*) and great tit (*P. major*) were manipulated on six islands (range 3–8 ha, Table 1). All islands were dominated by pine (*Pinus sylvestris*). Spruce (*Picea abies*) and deciduous trees (mainly birch, *Betula* spp., also aspen, *Populus tremula*, and willows, e.g. *Salix caprea*) together made up at most one-third of the timber volume of trees. On two islands (islands II and VI), there were small (approx. 0.5 ha) clear-cut areas about 5 years old dominated by 2-m high birch, willow, and planted pine saplings. The islands were at least 400 m from each other, and separated from the mainland by at least 300 m of open water. These islands normally support 0–1 breeding tit pairs (P. Helle, unpublished work).

In 1988, tits were induced to breed on three of the islands in numbers as high as possible by providing food during the preceding winter (between September and February) and nestboxes in

excess (islands I–III in Table 1). Birds were also mist-netted on the mainland and released on islands. Tits were removed from three other islands (IV–VI in Table 1) that year. Tits were captured in mist-nets and removed at least 30 km. All of these manipulations took place in early April, well before the onset of breeding and the arrival of migrant birds. In 1989, the roles of the islands were reversed so that tits were removed from islands I–III and added to islands IV–VI. This was done to control for possible effects of differences in habitat quality between islands. Unused nestboxes were removed in early May after the onset of breeding by tits. Hereafter, we will use abbreviations HT and LT for high and low tit density years or islands, respectively.

Foraging and feeding niches

We distinguish foraging and feeding here. If food consumption by competing species significantly reduces availability, an individual bird may be unable to change its foraging habits, but the effect of this depletion is seen in feeding behaviour, i.e. where it finds food.

We concentrated our behavioural study on tits, chaffinches (*Fringilla coelebs*) and willow warblers (*Phylloscopus trochilus*). These two latter species are the most numerous migrant birds, and they belong to the foliage gleaning guild with the tit species (e.g. Alatalo 1982). Observations of foraging and feeding behaviour were made between 28 May and 21 June in both years. Only individuals which were actively searching for food were sampled.

We observed birds' behaviour on a continuous basis. Once an individual was found, it was followed until it disappeared from sight. During that period, the bird's place and behaviour were dictated on tape by categories. Continuous observing largely circumvents visibility bias often involved in behavioural sampling (Bradley 1985; Wiens 1989a).

Foraging niche was determined on the basis of time spent in different categories of the habitat. Three dimensions were distinguished, categorized as follows:

Searching place: (1) ground, (2) pine, (3) spruce, and (4) deciduous tree.

Searching height: (1) lowest, (2) second, and (3) top third of a tree.

Tree part: (1) trunk and inner third, (2) middle, and (3) outer third of foliage.

Feeding niche was determined according to the frequency of actual prey captures in different categories. Feeding place, feeding height, and tree part dimensions were categorized in the same way as foraging niche dimensions. In addition, five feeding substrates were distinguished:

Feeding substrate: (1) ground, (2) trunk, (3) twig/branch, (4) needle/leaf, and (5) air.

Tree part and feeding substrate dimensions were separated because twigs with leaves and needles are also found in the middle and inner foliage zones, and because of the additional categories, ground and air.

Niche breadths were calculated by the antilogarithm of the Shannon index of diversity ($\exp H'$) standardized to be proportional to unity in each dimension. Multidimensional foraging (3-D) and feeding (4-D) niche breadths were determined by summation of original dimensions (see Hanski 1978).

Pairwise niche overlaps were calculated using Renkonen's (1938) percentage similarity index

$$PS = \sum \min(p_{xi}, p_{yi}),$$

where p_{xi} is the proportion of time spent (foraging), or the proportion of feeding maneuvers observed (feeding) in the i th category by species x , and, respectively, p_{yi} for species y . Multidimensional foraging niche overlaps were measured using the original data matrix including 28 categories (three tree species * three height categories * three horizontal categories + ground; so-called full multidimensional measurement, May 1975; Hanski 1978; Alatalo 1982). Full multidimensional overlap of feeding niche was calculated simi-

Table 1. Habitat characteristics of the study islands. Mean values (total row) for stand age and tree species composition are calculated by weighting area. Decid. = deciduous trees

No.	Island	Area (ha)	Stand age (yr)	Percentage timber volume of		
				Pine	Spruce	Decid.
I	Honkanen	6.1	105	70	10	20
II	Huutsaari	7.9	110	80	0	20
III	Mustasaari	3.9	90	90	5	5
IV	Järvisalo	6.2	95	80	5	15
V	Savolaissaari	4.7	80	65	30	5
VI	Siikasaari	3.2	80	70	10	20
Total		32.0	96	76	9	15

larly over three dimensions (feeding place, height, and tree part), but the fourth dimension, feeding substrate, was included by calculating the average of 3-D overlap and feeding substrate. Including the fourth dimension in the full multidimensional overlap would have split the data into too small samples per category. This would have led to underestimation of true overlap (Feinsinger 1976). Averaging was employed because feeding substrate was not independent of other dimensions; for example, a χ^2 -test for independence showed a significant dependence between feeding substrate and tree part ($\chi^2 = 10.8$, $P < 0.05$).

Here, niche breadths and overlaps are used only as descriptive indices. Statistical significance of possible emerging niche shifts are determined by the frequency of particular shifts in replicates (=islands). Statistical testing of mere indices would be difficult due to the nature of indices and to the partial dependence of observations (see Virkkala 1988).

Continuous dictation of actual prey captures on tape enables different kinds of time analysis. These are used to infer food depletion. Time interval between successive prey captures (INT) should become longer as the food availability decreases. The same should be true for time lag (from the beginning of the observation to the first prey capture, LAG). Giving-up times (interval between the last prey capture and the end of observation, when the bird was lost, GUT) are dependent on, in addition to food availability, on patchiness of resources (e.g. McNair 1982). Given the same scale of patchiness of resources, GUT should shorten as resource level decreases.

Breeding numbers

The number of occupied territories of birds on islands was determined during behavioural study, and by bird censuses. Each island was visited many times during the study period (at least five times), and each time a rough estimate was made of the number of singing males.

Breeding birds were also formally censused once in both summers by the study plot method (Palmgren 1930), which involved walking through the island along parallel lines 50 m apart from each other. Special attention was paid to simultaneous observations, as recommended in the territory mapping method (Anon. 1970). Each observation was drawn on a map. These results together are assumed to yield an almost accurate picture on the number of permanent territories.

Results

Numerical response

Addition of tits (HT) resulted in from two to three breeding pairs per island. No tits bred on islands where tits were removed (LT). However, one great tit female avoided removal on Island I and recruited an immigrant male in late May. Island II retained a single willow tit male (Table 2).

During LT, 18 chaffinch and 35 willow warbler territories were permanently occupied on the islands, whereas these numbers were 22 and 39 in HT, respectively (Table 2). LT was associated with a lower number of chaffinch and willow warbler territories than HT on five islands, and not a single island showed the opposite change. This result is statistically significant (Wilcoxon's test, $T=0$, $P < 0.025$). The same was true for the chaffinch alone ($T=0$, $P=0.05$), but not for the willow warbler ($T=2.5$, $P < 0.1$); the trend for the latter species was the same. Furthermore, other birds, including spe-

Table 2. Number of adult tits and occupied territories of other birds present on islands in low (LT) and high density years of tits (HT). Numbers in parentheses depict the great tit. All other *Parus* spp. are willow tits

Species	Treat-ment	Island						Total
		I	II	III	IV	V	VI	
<i>Parus</i> spp	LT	2(2)	1	0	0	0	0	3(2)
	HT	6	6	4(2)	4	4(2)	4(2)	28(6)
<i>Fri coe</i>	LT	3	3	3	4	2	3	18
	HT	4	4	4	4	3	3	22
<i>Phy tro</i>	LT	8	7	3	8	5	4	35
	HT	9	7	4	9	4	6	39
Others	LT	11	7	3	6	5	10	42
	HT	7	8	6	8	12	12	53

Fri coe = *Fringilla coelebs*, *Phy tro* = *Phylloscopus trochilus*

cies not belonging to the foliage gleaning guild, were present with higher numbers during HT than LT (Table 2; $T=3$, $P=0.05$). In summary, experimental increase of tit density on islands was associated with a concurrent increase in other birds' breeding numbers, regardless of their feeding ecology.

Foraging niches

Fig. 1 depicts relative time spent by tits (willow tit and great tit data combined), chaffinches, and willow warblers in different categories of foraging height and tree part (islands pooled). Tits and willow warblers preferred the two uppermost parts of trees as their foraging places. Willow warblers also clearly preferred the middle and outer zone of foliage in foraging. Chaffinches preferred middle parts of branches in the second third of trees. During HT chaffinches seemed to select ground as their foraging place more frequently than during LT, but this shift was not statistically significant ($T=0$, $n=3$, n.s.). Among the tree species, tits and chaffinches preferred spruces and deciduous trees, and willow warblers deciduous trees, when compared to their availability (Table 3). Quantitatively, similarity between LT and HT of relative utilization of different foraging niche dimensions by the willow warbler varied from 90 to 96%, and by the chaffinch from 70 to 96%. Multidimensional niche similarity between LT and HT was 83% for willow warblers and 58% for chaffinches.

Chaffinches and willow warblers showed practically no difference in niche breadths between LT and HT (Table 4; multidimensionally, for both species, $T=7$, $n=6$, n.s.). Total foraging niche overlap between tits and chaffinches did not change significantly between LT and HT ($T=7$, $n=6$, n.s.), although the general trend seemed to be decreasing (Table 4). Willow warblers' overlap with tits remained more or less constant in every individual dimension, as well as the multidimensional overlap (Table 4).

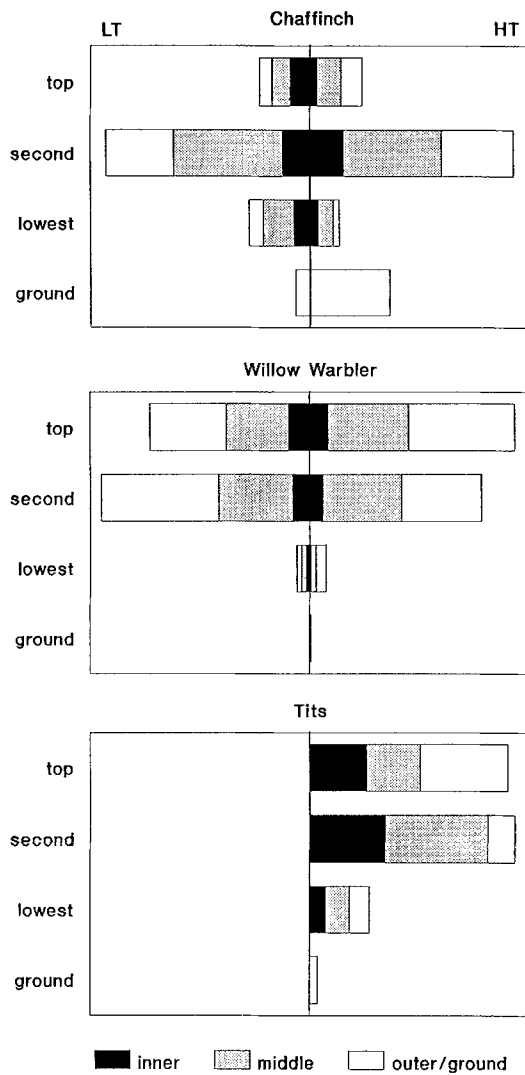


Fig. 1. Foraging of the species on the ground and in trees depicted by relative time spent in different height and tree part categories. *Left hand bars* denote low (LT) and *right hand bars* high tit density conditions (HT, islands pooled). Sample sizes are given in Table 4

Feeding niches

Feeding and foraging niches of the species studied were very similar (cf. Figs. 1 and 2). Their similarity varied from 78 to 97% in different dimensions. Also tree species

Table 4. Foraging niche metrics of the chaffinch (*Fri coe*) and the willow warbler (*Phy tro*) on the study islands (pooled data) during LT and HT (see Table 2). Number of observations (*n*) and total sampling times in seconds (Sec.) are also given. Total column denotes multidimensional niche. None of the differences in niche breadths or overlaps between LT and HT is statistically significant

	Treat	Niche breadths			Total	Sample size <i>n</i> (Sec.)
		Foraging place	Foraging height	Tree part		
<i>Fri coe</i>	LT	0.79	0.81	0.93	0.84	54 (2996)
	HT	0.92	0.73	0.93	0.87	57 (3569)
<i>Phy tro</i>	LT	0.59	0.75	0.86	0.72	76 (4856)
	HT	0.63	0.77	0.84	0.74	81 (5025)

Niche overlaps with *Parus* spp.

	Treat		Niche overlaps with <i>Parus</i> spp.		<i>Parus</i>	
<i>Fri coe</i>	LT	0.89	0.73	0.88	0.61	<i>Parus</i> 52 (2468)
	HT	0.59	0.73	0.85	0.47	
<i>Phy tro</i>	LT	0.75	0.90	0.77	0.57	
	HT	0.79	0.91	0.76	0.58	

preferences were nearly identical in feeding and foraging (Table 3). Tits preferred branches and twigs, chaffinches and willow warblers needles and leaves, as feeding substrate (Table 5). Chaffinches also frequently picked food items from the air.

The feeding niche of the chaffinch was slightly broader during HT than LT (pooled data, Table 6). This trend, which was not common to every dimension, however, cannot be tested statistically with the island-specific data, because sample sizes were only large enough on two islands ($n \geq 10$ in both treatments); these two islands show opposite trends to the pooled data.

In willow warblers, changes in feeding niche breadth seemed to be minor (Table 6). This was corroborated with individual island data: on five islands where sample sizes were sufficient, no statistical changes took place between LT and HT in multi- ($T=6.5$, n.s.) or one-dimensional niche breadths ($T=4-7$, n.s.).

Feeding niche overlap between tits and both migrant species seemed to be smaller during HT than LT (Table 6). These trends remained untested due to small sam-

Table 3. Relative proportion of tree species use by birds during LT and HT (for abbreviations see Table 2). Numbers in parentheses denote preference of given tree species calculated by dividing availability (Table 1) by relative utilization

	Treat	Tree species					
		Pine		Spruce		Deciduous trees	
		Foraging	Feeding	Foraging	Feeding	Foraging	Feeding
<i>Parus</i> spp.	HT	56 (0.7)	60 (0.8)	23 (2.5)	23 (2.5)	22 (1.5)	18 (1.2)
<i>Fri coe</i>	LT	51 (0.7)	38 (0.5)	18 (2.0)	8 (0.9)	32 (2.1)	54 (3.6)
	HT	27 (0.4)	18 (0.2)	19 (2.1)	14 (1.6)	55 (3.6)	68 (4.5)
<i>Phy tro</i>	LT	49 (0.6)	39 (0.5)	5 (0.5)	2 (0.2)	47 (3.1)	59 (3.5)
	HT	50 (0.6)	42 (0.5)	7 (0.8)	6 (0.7)	43 (2.9)	53 (3.5)

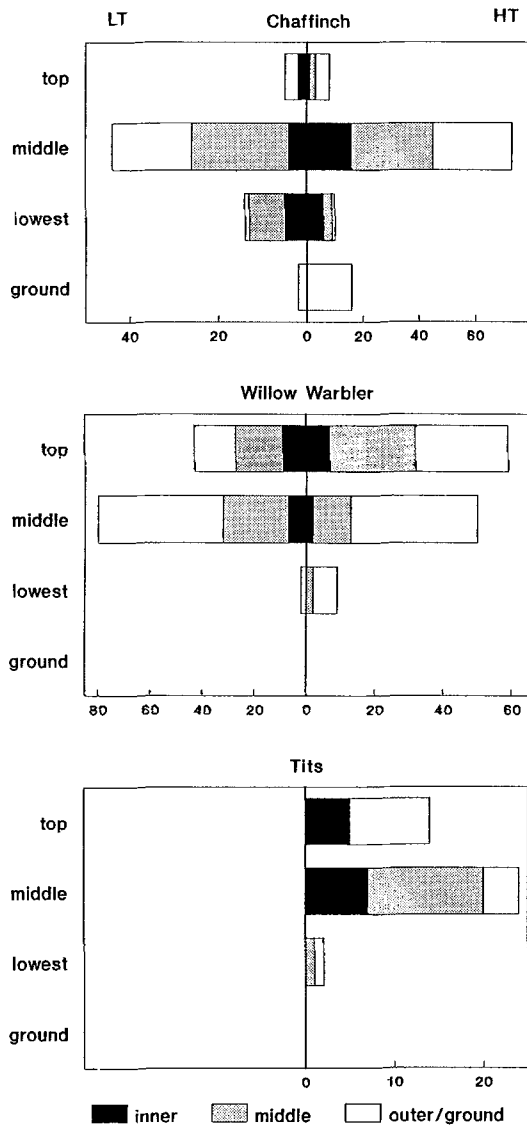


Fig. 2. Feeding of the species on the ground and in trees depicted by the number of actual prey captures in different height and tree part categories. *Left hand side bars* denote low (*LT*) and *right hand side bars* high tit density conditions (*HT*, islands pooled). *X-axis values* refer to the number of observations. Sample sizes are given in Table 5

Table 5. Percentage distribution of feeding observations into five feeding substrate category for the chaffinch (*Fri coe*), the willow warbler (*Phy tro*) and tits (*Parus*) during *LT* and *HT* (see Table 2). *n* = the number of observations

Feeding substrate	<i>Fri coe</i>		<i>Phy tro</i>		<i>Parus</i>
	<i>LT</i>	<i>HT</i>	<i>LT</i>	<i>HT</i>	<i>HT</i>
Air	23	31	18	16	15
Needle/Leaf	48	32	62	64	20
Branch/Twig	20	22	19	20	48
Trunk	9	3	2	0	18
Ground	0	12	0	0	0
<i>n</i>	65	107	125	118	40

Table 6. Feeding niche metrics of the chaffinch (*Fri coe*) and the willow warbler (*Phy tro*) on the study islands (pooled data) during *LT* and *HT* (see Table 2). Total column depicts multidimensional feeding niche. For sample sizes see Table 5

	Treatment	Niche breadths				
		Feeding place	Feeding height	Tree part	Feeding substrate	Total
<i>Fri coe</i>	<i>LT</i>	0.69	0.73	0.93	0.69	0.72
	<i>HT</i>	0.78	0.63	0.99	0.83	0.80
<i>Phy tro</i>	<i>LT</i>	0.53	0.68	0.88	0.53	0.59
	<i>HT</i>	0.60	0.82	0.79	0.50	0.61

		Niche overlaps				
<i>Fri coe</i>	<i>LT</i>	0.62	0.73	0.87	0.64	0.50
	<i>HT</i>	0.45	0.74	0.95	0.60	0.43
<i>Phy tro</i>	<i>LT</i>	0.58	0.96	0.82	0.56	0.47
	<i>HT</i>	0.65	0.82	0.75	0.55	0.43

Table 7. Different time aspects of feeding depicted by species for *LT* and *HT* separately (pooled data). *LAG* = mean time lag (in sec) measured from the beginning of observation to the first prey capture. *INT* = average interval (in sec) between succeeding prey captures. *GUT* = giving-up time (in sec), i.e. time between the last prey capture and the end of observation. *P* values denote significance level between *LT* and *HT* calculated by Mann-Whitney *U* test in pooled data

	<i>Fri coe</i>			<i>Phy tro</i>		
	<i>LT</i>	<i>HT</i>	<i>P</i>	<i>LT</i>	<i>HT</i>	<i>P</i>
<i>LAG</i>	29.6 (22)	26.6 (26)	0.47	18.7 (35)	18.5 (35)	0.85
<i>INT</i>	18.2 (49)	18.9 (79)	0.06	16.0 (91)	16.9 (82)	0.54
<i>GUT</i>	29.7 (22)	21.9 (26)	0.33	34.0 (34)	29.5 (35)	0.94

ples for feeding tits (total $n=40$). Niche shifts in willow warblers were minor as a consequence of manipulation: the similarity index between *LT* and *HT* varied from 78% (tree part dimension) to 97% (feeding substrate), and was 81% overall. In chaffinches, shifts were somewhat larger, varying from 78% to 90%, 69% overall.

Time analysis

LAG did not differ between *LT* and *HT* in either species. Similarly, there were no differences in *INT* (Table 7, pooled data). In willow warblers, data were sufficient to allow testing islands as replicates. No significant differences emerged (*LAG*, $T=6$, $n=5$, n.s.; *INT*, $T=7$, $n=5$, n.s.).

GUTs were shorter in both species during *HT* than *LT*. Neither species showed significant differences in pooled data, however (Table 7). This also holds true for

willow warblers in the island-specific data ($T=5$, $n=5$, n.s.).

Discussion

Connell (1983) explicitly defined as experimental evidence for competition the situation where manipulation of the abundance of a potential competitor was followed by the species being studied responding in the opposite direction. Contrary to this competition prediction, other species responded in the same direction to the experimental change in abundance of tits. This pattern extended outside the foliage gleaning guild, suggesting that factors other than food are important.

Manipulation and niche shifts

Manipulation experiments have demonstrated that interspecific competition can affect bird community structure (Hogstad 1975; Garcia 1983; Sæther 1983; Sherry and Holmes 1988), but other studies have provided little support for competition (Enemar and Sjöstrand 1972; Brawn et al. 1987). This seeming contradiction does not appear to reflect different methodology or the way in which competition is investigated (Haila 1982). For example Enemar and Sjöstrand (1972), Hogstad (1975), and Brawn et al. (1987) did very similar experiments. They increased the abundance of hole nesting birds by providing nest-boxes in excess, but their results are not concurrent. It is a commonplace to say that competition is not an all-or-nothing process, rather its importance and intensity vary according to conditions (Martin 1986). Reed (1982) explicitly showed how competition can manifest itself under certain circumstances but not in others. On Scottish islands, chaffinches and great tits inhabited non-overlapping territories. Following removal of chaffinches, great tits expanded to vacated areas. On mainland habitats, in contrast, their territories were widely overlapping and the two species were not interspecifically aggressive, as they were on islands. Reed (1982) related this pattern to difference in habitat quality: mainland woods are richer and more diverse than those on islands. Moreover, territories of great tits and chaffinches tended to co-occur more than expected on mainland habitats, possibly indicating mutualistic interactions.

Pair densities of tits during HT were higher (30–60 p/km²) than maximal natural densities in pine dominated forests in central Finland (approx. 20 p/km², e.g. Haapanen 1965; Mönkkönen 1984). The relevance of manipulations where abundances are increased has been doubted, since the aim of such studies is to investigate whether or not competition is important over the natural range of densities (e.g. Connell 1983). We agree with Brawn et al. (1987) that such caution is “warranted only if competition is found subsequent to density increases”.

Although we did not completely succeed in removing all the tits from islands during LT, manipulation yielded clearly differing abundances of tits between LT and HT

(Table 2). If fledglings (approx. 6/pair) are also taken into account, it can be estimated that food consumption by tits was at least 12 times larger during HT than LT. Foraging observations of tits were more or less evenly distributed on islands. Therefore, it is highly improbable that the migrant birds could avoid spatial overlap with tits on these islands.

Despite large differences between LT and HT in food consumption by tits, no niche shifts were obvious either in the chaffinch or in the willow warbler. Traditionally, if the community were resource limited, intensified interspecific competition should have led to niche specialization and reduced overlap between competitors (e.g. MacArthur and Pianka 1966). According to a survey by Wiens (1989b; see also Schoener 1982) niche overlap generally decreases in periods of relative resource scarcity. Abrams (1986) asserted that almost anything can accompany interspecific competition depending on species' resource utilization preferences, population growth parameters, magnitude of intraspecific limiting factor etc. For example, “... competition can alter resource utilization without increasing the difference between species (equal parallel displacement), or can decrease the difference between species (convergent displacement)” (Abrams 1986, p. 148; see also Nilsson and Ebenman 1981; Holt 1987). But even in these cases, some patterned alterations of niche parameters should be evident, were the competition an important factor (see Abrams 1986, p. 119), because the basic conditions and the species being studied are the same. Therefore, we conclude that in the present study interspecific competition is not structuring species' feeding ecologies.

To summarize, we conclude that competition via resource limitation was not an important factor structuring communities and shaping species' feeding ecologies, as measured by present niche parameters. It is important here to distinguish between the intensity and importance of competition, however (Welden and Slauson 1986). Because we did not measure resource levels directly, we can say little about the intensity of competition. Our time analysis lent inferential support to our conclusion, and it also suggests that interspecific competition between the species studied here was weak in intensity as well.

Heterospecific attraction?

High tit density was associated with high densities of other birds in this study. This result suggests that there was a heterospecific attraction between species; because tit abundance was experimentally manipulated this pattern cannot be due to parallel responses to habitat characteristic by tits and migrants. Heterospecific attraction was also suggested by Mönkkönen (1990) with respect to territories of willow warblers and chaffinches in relation to willow and great tits' nests in Finland.

The idea that conspecifics attract other individuals to settle down in adjacent territories and form aggregated distribution patterns can be traced back many decades (Lack 1948; Svårdson 1949; Kalela 1952). Heter-

ospecific aggregation has been described only for waterfowl or passerines searching for protection against nest predators in colonies of other birds (Lack 1968; Slagsvold 1980). In a recent paper Stamps (1988) reviewed hypotheses to account for conspecific attraction. With respect to heterospecific attraction, only two hypotheses may apply. Firstly, aggregated distribution may provide protection against predators by means of co-operative defence or information delivered by neighbours. Secondly, territorial clustering may benefit an individual if settled neighbours reflect the quality of habitat. It is highly improbable that heterospecific individuals might attract more females or, by means of providing social stimulus, accelerate or improve breeding performance of another species. It is also doubtful that heterospecific individuals would aggregate in order to improve their ability to defend against intruders or competitors.

Migrant birds surviving the winter tend to return to their previous year's breeding territory in spring (Hildén 1965); it is suggested that males of many species select their territories only once in life. Given the common between-year variation in conditions, it is not evident that breeding sites retain their relative quality from year to year. Directly assessing the quality of available habitats accurately is very difficult and time-consuming, if possible at all. Tropical migrants are especially time constrained in breeding (O'Connor 1981; Mönkkönen and Helle 1987; Morse 1989). Therefore, especially for a first-time migrant bird searching for a place to settle down, it would be profitable to use resident birds as cues to safe or otherwise productive breeding sites, because residents are supposedly more familiar with and more accurately reflect the current quality of sites than conspecifics, which have selected their territories in previous years. This would only apply to habitat generalists. Were the resources not actually limiting, it would still be beneficial to select a safe place with an even higher level of resources. Based on this logic we conclude that the competition idea of Herrera (1978b) does not apply to this level of resolution at least in northern, often unpredictable conditions. This hypothesis can be experimentally tested.

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