Ann. Zool. Fennici 18: 103-114. 1981

Habitat selection of forest birds in the seasonal environment of Finland

Rauno V. Alatalo

Alatalo, R. V. 1981: Habitat selection of forest birds in the seasonal environment of Finland. — Ann. Zool. Fennici 18: 103—114.

The study is based on the yearround bird censuses of Soveri in southern Finland during 1934—36 and of the author in northern Finland during 1975—78. Congeneric passerines had smaller habitat overlaps and breadths than passerines which are not congeneric with other species in the forest. The habitat breadth of foliage-gleaners decreased with the increasing number of coexisting foliage-gleaning species in the same habitats. Both results suggest that interspecific competition modifies the habitat selection of forest birds. Intraspecific competition may partly be responsible for the clear positive correlation between abundance and habitat breadth of foliage-gleaners. Habitat breadths in general were smallest during the breeding season. This appears to be a consequence of special habitat requirements at that time, such as suitable nest-site and shelter against predation. This postulation is supported by the fact that the annual variation in habitat selection during the breeding season was smaller than in other seasons. Intense interspecific competition during breeding can be rejected as an alternative hypothesis, since the reduction in habitat breadths was particularly pronounced for species which were not congeneric with other species in the forest. All species changed their habitat seasonally to some degree, but for some migrants these changes were relatively slight. Overlaps in the habitats of gallinaceous birds were small in winter, and large overlaps in summer might reflect the absence of interspecific competition during the period of maximum food availability. In contrast, habitat overlaps among foliage-gleaners were smallest during the breeding season, which may be due to the restricted habitat selection, irrespective of competition, at that time.

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1. Introduction

Birds appear to choose habitats to which they are well adapted in terms of resource exploitation (see Hildén 1965, Partridge 1978). Intraspecific competition leads to the occupation of less suitable habitats, increasing the variety of habitats inhabited by each species, whereas interspecific competition has the opposite effect. This idea was suggested by Svärdson (1949), and later works have provided more or less convincing evidence in favour of the hypothesis (see Hildén 1965, Fretwell 1972, Partridge 1978). In addition to food availability, habitat preferences may be affected by differences in the degree of shelter provided by each habitat against predators or adverse weather.

I have studied the habitat distribution of forest birds in northern Finland during all seasons, and Soveri (1940) has published similar information from southern Finland. The present paper investigates the ultimate factors affecting these habitat distributions. Is there any evidence for the role of competition, interspecific and intraspecific, in determining the position or shape of the habitat distributions? Nests and young birds are very susceptible to predation and adverse weather; does this restrict the habitat selection of birds during breeding? In summer, food is more plentiful than in winter, but migrants arrive to share the new resources; how do habitat selection, breadth and overlap vary seasonally?

2. Material and methods

2.1. Bird censuses

Field data from Oulu, northern Finland (64°57′N, 25°48′E) were collected from March 1975 to February 1976 and again from January to March 1978 using the conventional line transect technique (Merikallio 1946, Järvinen & Väisänen 1973), since it is applicable in all seasons. Two transects (lengths 7810 m and 7130 m) were used in 1975 and 1976, and each of them was skied or walked once a week. Two extra transects (5920 m and 5700 m) were used in 1978. The rate of travel was 1.5—2 km/h. Density estimates and habitat distribution were based on individuals observed within 25 m of either side of the fixed transects. Since bird populations are low in winter, I also used observations outside the main belt for the assessment of habitat selection, but not for density estimation, in 1978.

Line transects give underestimations of bird densities (Palmgren 1930, Enemar 1959, Emlen 1971, 1977, Järvinen et al. 1978). In this study absolute densities are of minor importance, but some bias in the results arises through the different conspicuousness of birds in different habitats. However, the bias is slight as I mainly consider only birds within 25 m of the transect, and most of my records of passerines were based on initial voice cues.

Transects were planned to represent all forest types in proportion to their distribution in the forest. The habitat of each individual bird was determined in terms of tree species, tree height and soil within 25 m of the observation site. Habitats with tall trees (over 5 m high) were classified according to the tree species present, a given species being included if it made up at least 20 % of all trees. Two types of low tree habitats were distinguished: wooded swamps (soil swampy, most swamps recently drained) and young forests (soil not swampy). Habitats and their proportions in the two main transects were:

Pine forest	P	22.0 %
Spruce forest	S	6.5 %
Mixed coniferous forest	PS	9.6 %
Spruce-deciduous forest	SD	12.8 %
Mixed forest	PSD	17.0 %
Wooded swamp	W	15.2 %
Young forest	Y	16.9 %

The forest was very patchy with respect to these habitat types, since the habitat changed on average at 67 m intervals along the transects.

The weekly bird counts were grouped into four ornithological seasons in 1975—76, and winter 1978 was the fifth study period:

1) Winter 1975—76 (Mar-Apr 1975 and Nov 1975 — Feb 1976; the period with snow cover, 187.1 km of transect).
2) Early summer 1975 (May-Jun 1975; breeding season, 66.9 km).
3) Late summer 1975 (Jul-Aug 1975; post-breeding season, 67.6 km).
4) Autumn 1975 (Sep-Oct 1975; 66.9 km).
5) Winter 1978 (Jan-Mar 1978; 132.1 km).

For bird community structure and energetics in these forests see Alatalo (1978) and Alatalo & Alatalo (1980).

Soveri (1940) carried out extensive censuses of birds in different habitats at Lammi, southern Finland (61°05′N, 25°01′E) in 1934—36. He studied pure plots of each habitat during four periods (22 km^2 in each season):

1) Winter (10 Dec — 20 Jan).
2) Spring (1 Apr — 25 Apr).
3) Early summer (20 May — 20 Jun).
4) Late summer (1 Aug — 25 Aug).

Using the proportions of habitat types in the forests of Lammi as given by Soveri (1940) and the bird densities in each habitat, I estimated for each bird species the proportions of all individuals found in each habitat, producing data comparable to that from Oulu. I grouped the 11 habitats defined by Soveri into five classes determined in terms of tree species:

Pine forest	8.3 %
Mixed coniferous forest	18.6 %
Spruce forest	26.9 %
Mixed forest	28.0 %
Deciduous forest	18.5 %

2.2. Statistical methods

I measured habitat overlap (C_{xy}) between species x and y by the simple measurement of overlap recommended by Alatalo & Alatalo (1979), in which minimum values of the relative frequencies p_{xi} (proportion of individuals of species x in habitat i) and p_{yi} are summed over r habitats (e.g. Colwell & Futuyma 1971 Eq. 3, Hurlbert 1978 Eq. 1):

$$C_{xy} = \sum_{i=1}^{r} \min\,(p_{xi},\, p_{yi})$$

I estimated the within-habitat component of diversity for the whole bird community as described by Alatalo & Alatalo (1977), which measures average habitat overlap between species each species being weighted by its abundance in the average. As a diversity index I used the antilogarithmic Shannon's entropy (Exp H').

To measure habitat breadth (B_k) I used a formula which attains its maximum value (1) when species k uses all habitats exactly in proportion to their presence in the forest (constant density in the whole forest). Strictly speaking I measured how widely a species used the whole area of the forest. The approach is suitable when comparing seasonal changes in the width of habitat use, and, most importantly, avoids much of the difficulty in determining the distinctness of each habitat type (cf. Colwell & Futuyma 1971). This would be important for measuring actual habitat tolerance, i.e. how many kinds of habitat are used (habitat amplitude sensu Haila et al. 1980). The formula is based on Colwell & Futuyma (1971) with the exception that each habitat is weighted by its proportional area instead of distinctness, and the formula thus becomes:

$$B_k = \frac{\mathrm{Exp}\left[-\sum_{i=1}^{r} d_i K\ (p^*_{ki}\ \ln p^*_{ki})\right]}{K}$$

where

d_i = the relative proportion of habitat i in the forest
r = number of habitats
K = number of new categories (each habitat is divided into identical subcategories, and their number is related to the proportional area of the habitat). K is such that $d_i K > 1.0$ in all cases in order to avoid positive logarithms.

Use of the antilogarithmic Shannon's entropy ensures that the value of K has no effect on the result. It would have an effect if the logarithmic Shannon's entropy were used, this being the property of the original Golwell-Futuyma method which was criticised by Sabath & Jones (1973).

$$p^*_{ki} = \frac{n_{ki}/(d_i K)}{n_{k.}}$$

where

p^*_{ki} = the relative proportion of the use of the new subdivided habitat category i, of which we have $d_i K$ examples, by species k

n_{ki} = the number of observations of species k in habitat i

$n_{k.}$ = the number of observations of species k in the whole forest.

Any measurement of niche (or habitat) breadth might be ambiguous as the method of categorization and the availability of resources affect the result (see Petraitis 1979). In the present case, however, the actual proportions in which each habitat is used by birds are known. Besides, the proportional areas of the habitats are available, and we can make a valid estimate of habitat breadth in the sense of to what degree each species uses the area of the whole forest. The weighting of habitats by their proportional areas is important, as illustrated by the following example. We have two habitats making up 4/5 and 1/5 of the forest each. Species A has the same density in both habitats, but species B is four times more abundant in the small than in the large habitat. Without weighting, B would reach a maximum habitat breadth value and A a lower value. According to the present procedure, however, species A will score a maximum habitat breadth value and B a lower value, which seems to be appropriate.

Seasonal or variation from year to year in habitat selection (V %) was measured in parallel with components of diversity (Alatalo & Alatalo 1977) as components of habitat breadth, the between-season component being the proportion by which the average seasonal habitat breadth was lower than the breadth of the pooled annual habitat distribution.

3. Results

3.1. Habitat distribution of all birds

At Oulu, birds were most evenly distributed over the forest in late summer and least evenly in winter (Table 1). In general, bird density was highest in mixed forests, particularly those in which deciduous trees were present. Pure pine forests and forests with low trees had the lowest densities. During winter, foliage-gleaners favoured pine forests over spruce forests, which was most likely due to the abundance of the eggs of Lachnidae on pine needles (see Alatalo 1980). In winter 1978 such eggs were common in wooded swamps, too, and bird density was high, although birds otherwise visited habitats with low trees less often in winter than in summer.

At Lammi, bird density in summer was highest in deciduous forests and in mixed forests and clearly lowest in pine forests (Soveri 1940). In winter, the relative use of deciduous forests was drastically reduced. Habitats were used most widely by all birds in late summer ($B_k = 0.93$) and spring (0.91) and least widely in early summer (0.84) and winter (0.83).

3.2. Seasonal changes in habitat selection

At Oulu seasonal variation in habitat use was most prominent in *Emberiza rustica,* which preferred wooded swamps as its breeding habitat, but spread to all habitats in late summer (Table 2, Appendix). It is to be noted that the values of V are only relative, and permit a comparison of species: their absolute values are of little interest. At Lammi seasonal habitat shifts were not as prominent as at Oulu (Table 3), perhaps because there were fewer important distinctive habitat types, the great majority of birds staying in two or three habitats only. Seasonal habitat shifts were greatest in species with different diets in summer and winter: *Dendrocopos major, Tetrao urogallus, Pyrrhula pyrrhula.* Both residents and summer visitors seem to change their habitats to some degree while staying in the forest, but for some summer visitors these changes were comparatively slight.

Table 1. Habitat selection of all birds at Oulu. Selectivity is measured by bird density in each habitat divided by the average density in the whole forest.

Habitat	1978	1975—1976				
	Winter	Winter	Early summer	Late summer	Autumn	Year
Pine forest	0.84	0.96	0.54	0.65	1.09	0.75
Spruce forest	0.47	0.54	1.28	1.05	0.82	1.00
Mixed coniferous forest	1.09	1.31	0.89	1.28	1.03	1.14
Spruce-deciduous forest	2.18	1.13	1.56	1.10	1.04	1.21
Mixed forest	1.97	1.91	1.34	1.30	1.76	1.45
Wooded swamp	1.21	0.39	1.22	1.05	0.78	0.97
Young forest	0.29	0.60	0.60	0.86	0.40	0.67
Habitat breadth, B_k	0.89	0.89	0.92	0.97	0.92	0.96
Average density, ind./km^2	25	34	251	429	208	170

Table 2. Seasonal habitat breadths (B_k) and the variation in habitat selection during a one-year cycle (V %) at Oulu (* = variation significant, $P < 0.05$, chi-square test for original numbers of observations).

	1978	1975 — 1976					
Species	Winter	Winter	Early summer	Late summer	Autumn	Year	V %
Foliage-gleaners							
Parus montanus Conrad	0.92	0.92	0.93	0.86	0.81	0.90	3.6*
Parus cristatus L.	0.68	0.81	0.60	0.69	0.62	0.78	10.8
Regulus regulus (L.)	0.72	0.63	0.49	0.55	0.75	0.71	11.5*
Phylloscopus trochilus L.	—	—	0.73	0.90	—	0.87	3.7*
Fringilla coelebs L.	—	—	0.77	0.76	—	0.80	4.8*
Ground passerines							
Turdus iliacus L.	—	—	0.76	0.91	0.84	0.98	13.1*
Trudus philomelos Brehm	—	—	0.86	0.86	0.95	0.95	6.4*
Anthus trivialis (L.)	—	—	0.95	0.89	—	0.92	2.0
Erithacus rubecula (L.)	—	—	0.72	0.57	—	0.65	11.4*
Emberiza rustica Pall.	—	—	0.33	0.75	—	0.71	21.2*
Others							
Muscicapa striata (Pall.)	—	—	0.69	0.75	—	0.76	6.6
Carduelis flammea (L.)	0.39	0.33	—	—	0.41	0.43	11.2*

Table 3. Seasonal habitat breadths (B_k) and the variation in habitat selection during the year (V %) at Lammi (for data see Soveri 1940). * = variation statistically significant ($P < 0.05$, chi-square test).

Species	Winter	Spring	Early summer	Late summer	Year	V %
Foliage-gleaners						
Parus major L.	?	0.54	0.42	0.38	0.47	10.1*
Parus caeruleus L.	0.44	0.30	0.18	0.37	0.38	3.7
Parus ater L.	0.59	0.77	0.67	0.65	0.66	3.6*
Parus cristatus L.	0.72	0.68	0.65	0.69	0.73	4.5*
Parus montanus Conrad	0.77	0.87	0.77	0.95	0.84	3.8*
Regulus regulus (L.)	0.74	0.78	0.67	0.72	0.74	1.6*
Fringilla coelebs L.	—	0.76	0.89	0.91	0.90	0.1
Phylloscopus trochilus L.	—	—	0.62	0.55	0.60	0.3*
Sylvia borin (Bodd.)	—	—	0.35	0.30	0.34	0.1*
Treecreepers						
Certhia familiaris L.	0.74	0.83	0.61	0.79	0.75	3.3
Ground passerines						
Trudus pilaris L.	—	0.31	0.42	0.44	0.42	0.3
Turdus iliacus L.	—	0.67	0.63	0.74	0.70	3.9*
Turdus philomelos Brehm	—	0.54	0.70	0.85	0.79	7.2*
Anthus trivialis (L.)	—	0.72	0.63	0.68	0.68	3.4*
Erithacus rubecula (L.)	—	0.86	0.75	0.88	0.83	3.1*
Flycatchers						
Muscicapa striata (Pall.)	—	—	0.66	0.46	0.64	0.5*
Ficedula hypoleuca (Pall.)	—	—	0.47	0.52	0.49	3.0*
Phoenicurus phoenicurus (L.)	—	—	0.51	0.71	0.63	7.6*
Passerine seed-eaters						
Carduelis spinus (L.)	?	0.88	0.80	0.84	0.86	5.8*
Pyrrhula pyrrhula (L.)	0.64	0.72	0.58	0.83	0.76	11.1*
Omnivorous Corvidae						
Corvus corone L.	—	0.79	0.82	0.81	0.82	1.3
Garrulus glandarius (L.)	0.73	0.63	0.62	0.78	0.73	3.9
Gallinaceous birds						
Tetrao urogallus L.	0.70	0.88	0.62	0.95	0.87	12.6*
Lyrurus tetrix (L.)	0.66	0.76	0.57	0.79	0.72	4.0
Tetrastes bonasia (L.)	0.63	0.79	0.57	0.71	0.69	5.5*
Others						
Dendrocopos major (L.)	0.79	0.88	0.44	0.72	0.80	12.7*
Dryocopus martius (L.)	0.77	0.81	0.72	0.82	0.79	2.6
Columba palumbus L.	—	0.68	0.66	0.88	0.74	5.8*
Scolopax rusticola L.	—	—	0.46	0.56	0.50	2.1

3.3. Habitat breadth

Seasonal variation

In all guilds (groups of ecologically similar species) the average habitat breadth was lower during the breeding season than after breeding in late summer (Table 4). At Lammi, the increase (0.10 on average) in habitat breadths of species from early to late summer was significant, $P < 0.05$ t-test for dependent observations. The increase in habitat breadth after early summer was most prominent in gallinaceous birds, *Phoenicurus phoenicurus, Parus montanus, Parus caeruleus, Certhia familiaris, Pyrrhula pyrrhula* and *Dendrocopos major* at Lammi (Table 3), and *Phylloscopus trochilus* and *Emberiza rustica* at Oulu (Table 2). However, there were exceptions to the general trend (about 25 % of all species); e.g. *Erithacus rubecula* withdrew to low forests almost exclusively in late summer at Oulu (Appendix), but most decreases in estimated habitat breadths in late summer were fairly slight. At Lammi habitat breadths were also significantly higher (average 0.09, $P < 0.05$) in spring than in early summer, with only four exceptions among 23 species.

At Lammi, the specific habitat breadths were significantly higher in winter (average 0.10) than in early summer, but lower (average 0.07) than in late summer (both *t*-tests, $P < 0.05$). The trends were similar for both foliage-gleaners and gallinaceous birds (Table 4). In contrast, at Oulu, foliage-gleaners used habitats most widely in winter.

In only three out of 16 cases was habitat breadth lower in winter than during the breeding season. The average habitat breadth, each species weighted by its abundance, was reduced in winter and in autumn at Oulu because of the presence of a habitat specialist, *Carduelis flammea*, in great numbers.

Table 4. Average habitat breadths (B_k) within each guild. Averages for all residents and/or summer visitors are estimated by weighting each species according to its abundance. Based on Tables 2 and 3, and the values for Oulu during winter refer to 1975—76/1978.

	Winter	Spring	Early summer	Late summer	Autumn
OULU					
Residents					
Foliage-gleaners	0.79/0.77	—	0.67	0.70	0.73
Residents and migrants					
Foliage-gleaners	—	—	0.70	0.75	—
Ground passerines	—	—	0.72	0.80	—
Weighted averages					
Residents	0.71/0.60	—	0.65	0.68	0.62
Summer visitors	—	—	0.71	0.81	0.70
All species	0.70/0.60	—	0.70	0.77	0.65
LAMMI					
Residents					
Foliage-gleaners	0.65	0.68	0.59	0.68	—
Gallinaceous birds	0.66	0.81	0.59	0.82	—
Residents and migrants					
Foliage-gleaners	—	—	0.58	0.61	—
Ground passerines	—	0.62	0.63	0.72	—
Flycatchers	—	—	0.55	0.56	—
Weighted averages					
Residents	0.72	0.78	0.64	0.77	—
Summer visitors	—	0.71	0.71	0.80	—
All species	0.71	0.76	0.69	0.79	—

Foliage-gleaners

I compared habitat breadth with abundance in the large guild of foliage-gleaners at Lammi (Fig. 1). In order to avoid circularity (see McNaughton & Wolf 1970), I measured abundance as the average proportion in the guild made up by each species in the habitats, each habitat being weighted in proportion to its use by the species in question. The question was accordingly: are the dominant species of each habitat also widely distributed in other habitats? In summer the correlation between the within-habitat dominance and the habitat breadth was clearly

Table 5. Average habitat breadths B_k for passerines with no congeneric species and for congeners at Lammi, including all species with at least 15 observations per season (10 pairs in early summer). Asterisks indicate the significance of the difference from noncongeners (t-test: o = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

	Winter			Spring			Early summer			Late summer		
	B_k	S.D.	n	B_k	S.D.	n	B_k	S.D.	n	B_k	S.D.	n
Noncongeners	0.67	0.11	6	0.75	0.10	10	0.57	0.22	16	0.74	0.14	12
Congeners	0.63	0.15	4	0.58*	0.20	8	0.49*	0.19	16	0.56*	0.25	10
Parus	0.63	0.15	4	0.63	0.22	5	0.54	0.24	5	0.61	0.24	5
Sylvia	—			—			0.43	0.18	4	0.27***	0.04	2
Phylloscopus	—			—			0.51	0.13	3	—		
Turdus	—			0.51**	0.18	3	0.49	0.22	4	0.67	0.22	3

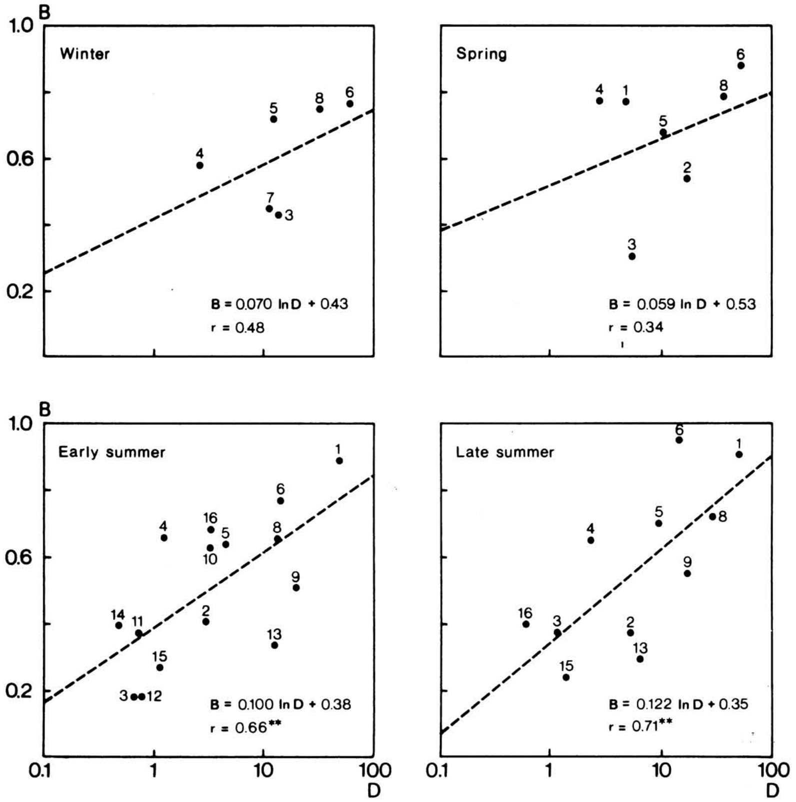

Fig. 1. The relation between habitat breadth B_k and numerical dominance D (%) among foliage-gleaning passerines at Lammi. Dominance is the average throughout habitats, each habitat being weighted in proportion to its use by the species in question. The species are: 1 = *Fringilla coelebs,* 2 = *Parus major,* 3 = *P. caeruleus,* 4 = *P. ater,* 5 = *P. cristatus,* 6 = *P. montanus,* 7 = *Aegithalos caudatus,* 8 = *Regulus regulus,* 9 = *Phylloscopus trochilus,* 10 = *P. collybita,* 11 = *P. sibilatrix,* 12 = *Hippolais icterina,* 13 = *Sylvia borin,* 14, = *S. atricapilla,* 15 = *S. communis,* 16 = *S. curruca.*

positive. In winter and spring the correlation, though positive, was not equally pronounced.

Secondly I compared habitat breadth with the presence of other species, measured as the average foliage-gleaning species diversity in the habitats used by each species, each habitat again being weighted in proportion to its use (Fig. 2). In winter and spring habitat breadths were lowest for those foliage-gleaners which inhabited habitats with the highest number of other species of the guild. The negative correlation was weaker in summer, but in late summer it was just on the boundary of significance.

Congeneric versus noncongeneric species

Passerines are the most abundant order among forest birds, both in numbers of individuals and of species, including many species which are congeneric to others in the forest, and species which are the only representatives of their genus in the forest. In all seasons, except in winter when only few species are available for comparison, the habitat breadths of passerine species congeneric to some other species in the forest were smaller than those of passerines not coexisting with congeneric species (Table 5). For both groups, habitat breadths were smallest during the breeding season, the difference between that and other seasons being particularly overt in noncongeneric species.

3.4. Habitat overlap

Seasonal variation

The within-habitat component of diversity measures habitat overlap between species for the

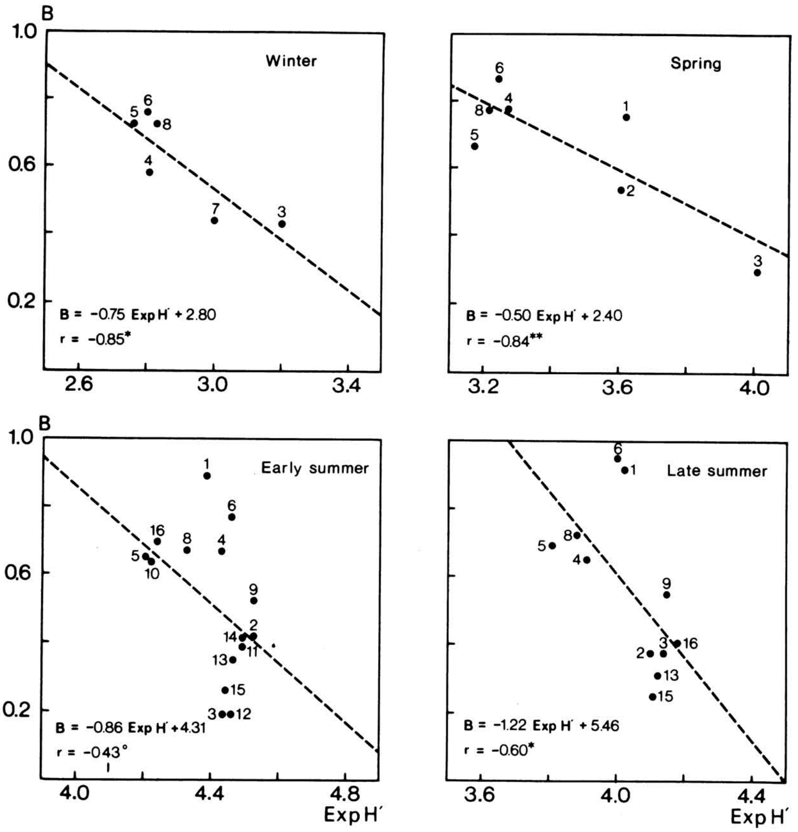

Fig. 2. The relation between habitat breadth B_k and number of concurrently occurring species (species diversity Exp H') among foliage-gleaning passerines at Lammi. The average foliage-gleaning species diversity in the habitats of each species was measured by weighting each habitat in proportion to its use by the species in question. For species codes see Fig. 1.

whole bird community, and it varied only slightly with season (Table 6). It is more interesting to consider overlaps within particular guilds, since competition is most likely to occur between species with similar resource use patterns. For most guilds, habitat overlap, conforming to habitat breadth, was smaller in early summer than in late summer. The difference was significant (t-test, $P < 0.05$) for foliage-gleaners at Oulu. Gallinaceous birds were the only exception, displaying maximum habitat overlap in early summer.

Among resident foliage-gleaners, habitat overlaps were larger in winter than in the summer periods, the difference being significant at Lammi ($P < 0.05$). On the other hand, habitat overlap among gallinaceous birds was much smaller in winter than in any other season (all differences significant, $P < 0.05$).

Table 6. Average habitat overlaps (C_{xy}) within each guild, and habitat overlap measured by the within-habitat component of diversity (Exp H') for the whole bird community. For species included see Tables 2 and 3.

	Winter	Spring	Early summer	Late summer	Autumn
OULU					
Residents					
Foliage-gleaners	0.77/0.76	—	0.55	0.71	0.67
Resident and migrants					
Foliage-gleaners	—	—	0.65	0.68	—
Ground passerines	—	—	0.58	0.67	—
All species					
Within-habitat diversity	0.70/0.62	—	0.69	0.75	0.64
LAMMI					
Residents					
Foliage-gleaners	0.58	0.49	0.42	0.49	—
Gallinaceous birds	0.47	0.72	0.75	0.67	—
Residents and migrants					
Foliage-gleaners	—	—	0.48	0.49	—
Ground passerines	—	—	0.63	0.66	—
Flycatchers	—	—	0.67	0.82	—
All species					
Within-habitat diversity	0.85	0.83	0.79	0.82	—

Table 7. Average habitat overlaps C_{xy} between congeneric and noncongeneric passerines at Lammi. Asterisks indicate the significance of the difference from noncongeners (for significance levels and numbers of species see Table 5).

	Winter		Spring		Early summer		Late summer	
	C_{xy}	*S.D.*	C_{xy}	*S.D.*	C_{xy}	*S.D.*	C_{xy}	*S.D.*
Noncongeners	0.67	0.20	0.69	0.13	0.50	0.28	0.67	0.17
Congeners	0.52	0.24	0.44***	0.21	0.39°	0.31	0.50**	0.26
Parus	0.52	0.24	0.45***	0.24	0.36	0.28	0.41**	0.24
Sylvia	—		—		0.53	0.36	0.92	—
Phylloscopus	—		—		0.37	0.33	—	
Turdus	—		0.40***	0.14	0.32	0.33	0.67	0.10

Congeneric versus noncongeneric species

Habitat overlaps between congeneric passerines were significantly smaller than those between noncongeners in spring and in late summer (Table 7). During the breeding season, although overlaps were at their smallest for congeners, the difference was only marginally significant as the overlaps between noncongeners were much smaller in early summer than in other seasons. In winter the difference in habitat overlaps of the two groups was of the same magnitude as in the summer periods, but the small number of species prevents any firm conclusions.

Five species of tits (*Parus*) form a resident genus, and they appeared to have smaller habitat overlaps than noncongeners throughout the year, significantly so in spring and late summer. Among the migratory foliage-gleaning genera, *Phylloscopus* warblers overlapped little, but *Sylvia* warblers overlapped as much as noncongeners. Thrushes (*Turdus*) overlapped little in their habitat use in spring and early summer, but in late summer had large habitat overlaps.

3.5. Variation in habitat selection from year to year

Soveri (1940) censused all his study plots over two years, and I measured the variation in habitat selection between the two years for the most abundant bird species (Table 8). *Regulus regulus* was the only species with a significant difference in habitat selection during the breeding season (i.e. early summer) between the two years. In 1934, the density of *R. regulus* was higher than in the other year of study, and its habitat use was widened to include mixed coniferous forests. For *Parus cristatus* the estimate of annual variation is greatest, but not significant, in early summer. *P. cristatus* is a very early breeder (von Haartman 1969), the young leaving the nests well before the end of Soveri's census period in early summer, and the results from early summer refer to the post-breeding season in this species.

Of seven summer visitors, five showed significant annual changes in habitat use in late summer, but none in early summer. Altogether it appears that habitat selection is more fixed from year to year during the breeding season than in late summer, though changes do occur during the breeding season, too.

4. Discussion

4.1. Competition and habitat selection

Interspecific competition is more likely between closely related than between unrelated species with different morphological structure

Table 8. The change in habitat selection between two consecutive years for each season at Lammi measured by components of diversity (V %) with Exp H' (* = habitat shift significant, $P < 0.05$, chi square test).

	Winter	Spring	Early summer	Late summer
Residents				
Parus cristatus	6.2*	0.4	4.1	2.4
Parus montanus	0.1	0.2	0.0	0.1
Regulus regulus	0.5	0.5	2.5*	0.2
Summer visitors				
Turdus iliacus	—	—	0.3	4.3*
Turdus philomelos	—	—	0.8	3.7*
Erithacus rubecula	—	—	0.1	0.7
Phylloscopus trochilus	—	—	0.7	0.7
Ficedula hypoleuca	—	—	0.4	4.6*
Carduella spinus	—	—	0.1	2.2*
Fringilla coelebs	—	—	0.1	0.2*
Average	2.3	0.4	0.9	1.9

and ecological adaptations (see Lack 1971, Grant & Abbott 1980). Without competitive effects we could expect closely related species to overlap more in their habitat use than unrelated species, since they have more similar basic feeding adaptations. Consequently, the observed pattern (viz. that passerines of the same genus had smaller habitat overlaps and breadths than noncongeners) is likely to be due to interspecific competition between congeneric species. Further evidence for the importance of interspecific competition is given by the negative relation between the habitat breadth of foliage-gleaners and the number of other species of the guild encountered by each species in its habitats.

Interspecific competition may be at work either currently in ecological time, or it may have had its effects in the past, during the evolution of feeding adaptations of the species. There is considerable evidence that tit species are better adapted to the exploitation of the resources in their preferred habitats than in other habitats (Partridge 1976, 1978). Tits in coniferous forests have finer beaks than tits in deciduous forests (see also Snow 1954). Herrera (1978) and Grant (1979) provide evidence that the absence of other tit species has led to morphological changes in the tits present, and such changes, accompanied by habitat shifts, can reasonably be attributed to interspecific competition. Interspecific territoriality between some bird species (see e.g. Orians & Willson 1964, Davies 1978) is the best example of interspecific competition affecting habitat selection in ecological time.

In the absence of intraspecific competition, all individuals of the same species should select the same optimal habitat. However, owing to intraspecific competition some individuals settle in habitats which are originally less suitable (see Brown 1969, Fretwell 1972, Davies 1978). This may be due either to decreased suitability of the optimal habitat as a consequence of the high number of other individuals there (ideal free model of Fretwell 1972), or to other individuals directly preventing the settlement of newcomers in the optimal habitat (ideal despotic model). Among foliage-gleaners, species which were abundant in a particular habitat were also the ones with the widest distribution over all habitats. This might be attributable to intraspecific competition. All individuals of rare species can settle in the habitat for which they are best adapted, but abundant species also make use of other habitats.

An alternative explanation is that different individuals of the same species are adapted to different habitats (Van Valen 1965, Roughgarden 1972). This can also be explained by intraspecific competition. Apart from evidence for sexual dimorphism for differential feeding within habitats (Selander 1966, Hogstad 1976), the evidence for differential adaptation of bird individuals is scanty and controversial (see Partridge 1978). The best example in favour of this hypothesis is provided by Grant et al. (1976). In *Ficedula hypoleuca* (Lundberg et al. 1981) and *Parus major* (Ulfstrand et al. 1981) differential habitat selection during the breeding season did not appear to be due to differential adaptation, but was rather a consequence of existing intraspecific competition. The latter hypothesis is also supported by the observations that *Parus major* (Kluyver & Tinbergen 1953) and *Fringilla coelebs* (Glas 1960) occupied suboptimal habitats relatively more often in years of high population numbers, as appeared to be the case for *Regulus regulus* at Lammi.

4.2. Restrictive habitat selection during the breeding season

The habitat breadths of birds tended to be smallest during breeding. Might this be due to special habitat needs at that time? Constraints on breeding season habitat selection have been pointed out, for example by Lack & Venables (1939) and Glowacinski (1975). Birds have to select habitats providing suitable nest-sites, singing posts, and shelter (Hildén 1965). Birds are certainly highly vulnerable to predation during incubation and nestling periods (Connell 1975). Fretwell (1972) found that habitat preferences within a passerine community were partly regulated by nest predation.

Examples of restricted habitat selection during breeding include *Regulus regulus* which nests only in spruce (von Haartman 1969), although it also commonly forages in pine in mixed coniferous forests in summer (Alatalo 1980). *Turdus iliacus* and *T. philomelos* do not have suitable nest-sites in pure pine forests, but frequently forage there in late summer. Open pine forests presumably provide less shelter against nest predation, and might therefore be used less during the breeding season than in late summer (see also Soveri 1940). Hole-nesting birds are largely restricted to habitats with deciduous trees, as conifers are not equally suitable for the excavation of holes, and, since hole-nesting reduces predation risk (Nice 1957), this is an example of the effects of predation on habitat selection.

The restricted habitat selection during breeding is supported by lower variation in habitat use in early summer than in late summer from year to year. The alternative explanation for small habitat breadths during breeding might be increased interspecific competition in early summer. However, the habitats of gallinaceous birds overlapped most in early summer, even though habitat breadths were at their smallest. The general decrease in habitat overlaps during the breeding season was mostly due to the drastic reduction in the habitat breadths of noncongeneric passerine species (Tables 5,7). If interspecific competition were to increase during breeding, we would expect clearer changes in the habitat overlaps and breadths of congeneric species. Nor is reduced intraspecific competition likely to explain the small habitat breadths during breeding, as territorial behaviour is most common at that time.

4.3. Seasonal variation in habitat overlap and breadth

In temperate and cold regions there is more food available to forest birds in summer than in winter, and populations are likely to be limited by food supply in winter (e.g. Lack 1966, Fretwell 1972). In support of this hypothesis foliage-gleaners may consume a considerable part of the available food in the course of the winter (Betts 1955, Gibb 1958, 1960, 1966, Solomon et al. 1976, Askenmo et al. 1977), whereas in summer the consumption is very low compared to the resources (Betts 1955, Tinbergen 1960, Gibb & Betts 1963, Lack 1966).

Habitat overlap among gallinaceous birds was clearly smaller in winter than in summer. The clear habitat segregation is correlated with differences in their winter diet: *Tetrao urogallus* - pine needles, *Lyrurus tetrix* - birch catkins, *Tetrastes bonasia* - catkins of alder and birch and buds (Seiskari 1962, von Haartman et al. 1963—72). In summer, the three species have much more similar diets (Siivonen 1957, von Haartman et al. 1963—72), and this change might be a result of more abundant food resources in summer (buds, shoots, leaves, seeds and berries of ground vegetation) than in winter with snow cover.

The habitat overlap of foliage-gleaners was smaller in summer than in winter. Foliage-gleaners, in contrast to gallinaceous birds, include many numerous summer visitors. The number of species sharing the food resources is high in summer, and diffuse competition (MacArthur 1972) might therefore increase (cf. Ulfstrand 1977). At Oulu, however, when foraging site segregation within habitats (division within trees in particular) is also taken into account, the multidimensional resource utilization overlap of foliage-gleaners was smaller in winter than in summer (Alatalo 1980). Some other studies also report reduced resource use overlap in winter (Gibb 1954, Betts 1955 according to Baker & Baker 1973, Haftorn 1956), but Gibb (1960) found no seasonal trends and Ulfstrand (1977) showed increased overlap in winter.

The reduced habitat overlap among foliage-gleaners during the breeding season does not appear to bear any relation to interspecific competition. It might rather be a consequence of the restricted habitat selection during breeding, which leads to reduction in habitat breadth. If the special requirements of breeding habitat are different for each species, the result will be reduced habitat overlap.

Seasonal changes in habitat breadth and overlap can be expected to be positively correlated if habitats are continually used equally widely by the whole bird community. In fact both habitat breadth and overlap were at their smallest during breeding, which appears to be explicable by the restricted habitat selection at that time. In late summer, bird populations are at their highest, and increased intraspecific competition might partly explain the diverse habitat use during that time. However, at Lammi, habitat breadths were already equally high in spring before breeding, when population levels are at their lowest.

Acknowledgements. My thanks are due to R. H. Alatalo, O. Järvinen, A. Lundberg, E. Pulliainen, S. Sulkava and S. Ulfstrand for valuable comments on the manuscript, and to T. Turpeenniemi for help in the preliminary field work. The study was supported by grants from the Emil Aaltonen Foundation and Tauno Tönning Foundation. Part of the work was carried out at the Department of Zoology, University of Oulu, Finland and at the Edward Grey Institute of Field Ornithology, Oxford University (visit supported by the British Council).

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Appendix. Seasonal habitat selection of birds at Oulu. Selectivity measured by density in each habitat divided by the average density in the whole forest, which is also given. Abbreviations: Wi = winter, ES = early summer, LS = late summer, Au = autumn, Ye = year, P = pine forest, S = spruce f., PS = mixed coniferous f., SD = spruce-deciduous f., PSD = mixed f., W = wooded swamp, Y = young forest.

	P	S	PS	SD	PSD	W	Y	Ind/km^2
Parus montanus								
Wi78	0.85	0.15	1.14	0.91	1.56	1.20	0.59	7.1
Wi75-76	0.96	0.74	1.50	1.18	1.61	0.50	0.57	15.6
ES75	0.67	0.25	1.37	1.54	1.35	0.87	0.87	18.2
LS75	0.60	1.38	1.54	1.28	1.89	0.42	0.50	56.5
Au75	1.17	0.12	1.03	0.89	2.18	0.75	0.22	39.3
Ye75—76	0.85	0.76	1.38	1.18	1.82	0.57	0.49	27.2
Parus cristatus								
Wi78	1.29	0.00	2.00	0.00	0.90	1.62	0.56	2.0
Wi75-76	1.25	1.06	1.08	1.35	1.62	0.00	0.61	3.1
ES75	2.27	1.28	1.74	1.30	0.49	0.00	0.00	3.6
LS75	1.60	2.27	1.54	0.46	1.56	0.19	0.00	10.1
Au75	1.65	0.00	3.32	0.36	1.07	0.00	0.54	6.5
Ye-75-76	1.59	1.27	1.83	0.81	1,33	0.07	0.30	5.0
Regulus regulus								
Wi78	1.25	0.00	0.43	0.00	1.16	2.43	0.71	1.2
Wi75-76	1.70	0.00	2.87	0.20	1.32	0.00	0.59	4.3
ES75	0.16	1.06	1.44	2.16	2.84	0.00	0.00	8.6
LS75	0.14	2.87	1.56	2.39	1.80	0.05	0.09	39.9
Au75	0.95	1.34	2.45	1.36	1.48	0.11	0.15	34.2
Ye75-76	0.63	1.79	2.04	1.72	1.72	0.06	0.17	16.4
Phylloscopus trochilus								
ES75	0.09	0.51	0.14	1.24	1.67	1.97	1.13	44.9
LS75	0.43	0.38	1.02	0.81	1.34	1.63	1.21	97.6
Ye75-76	0.34	0.40	0.75	0.91	1.44	1.79	1.14	25.8
Fringilla coelebs								
ES75	0.47	2.15	1.08	2.24	1.47	0.57	0.17	40.5
LS75	0.96	0.99	0.77	1.29	2.43	0.18	0.27	32.4
Ye75-76	0.68	1.65	0.91	1.83	1.91	0.39	0.21	13.0
Turdus iliacus								
ES75	0.30	2.31	1.22	2.61	0.78	0.44	0.79	17.9
LS75	0.51	0.73	1.77	1.25	0.55	1.12	1.45	31.5
Au75	2.04	0.91	0.20	0.69	0.52	1.16	0.69	30.3
Ye75-76	1.05	1.15	1.05	1.34	0.59	0.98	1.01	13.8
Turdus philomelos								
ES75	0.34	1.45	0.99	1.77	1.55	0.50	1.00	15.8
LS75	0.57	0.97	1.06	0.99	0.37	1.09	2.09	23.5
Au75	1.03	1.40	0.47	1.24	0.94	0.60	1.34	13.1
Ye75-76	0.26	1.23	0.89	1.29	0.87	0.79	1.58	9.1
Anthus trivialis								
ES75	1.41	1.25	1.13	0.53	0.79	1.16	0.72	22.0
LS75	1.16	0.98	1.00	0.42	0.50	1.96	0.88	28.0
Ye75-76	1.29	1.07	1.03	0.45	0.62	1.65	0.79	8.9
Erithacus rubecula								
ES75	0.00	1.23	1.25	2.19	1.65	0.79	0.71	7.4
LS75	0.00	0.00	0.17	0.91	2.16	2.53	0.69	17.9
Ye75-76	0.00	0.31	0.42	1.25	1.82	2.37	0.65	5.2
Emberiza rustica								
ES75	0.00	0.00	0.00	0.21	1.27	4.81	0.16	11.0
LS75	0.39	0.33	0.45	1.70	0.26	2.29	1.41	13.7
Ye75-76	0.18	0.47	0.53	1.03	1.01	3.00	0.72	5.1
Muscicapa striata								
ES75	1.32	1.28	0.44	2.61	1.23	0.00	0.25	7.1
LS75	1.51	1.35	2.02	1.92	0.41	0.23	0.21	17.0
Ye75-76	1.57	1.28	1.49	2.05	0.63	0.16	0.21	4.3
Carduelis flammea								
Wi78	0.10	0.00	0.10	5.28	1.32	0.41	0.17	6.4
Wi75-76	0.00	0.00	0.00	1.14	4.45	0.00	0.58	4.4
Au75	0.00	0.00	0.27	2.28	3.06	0.60	0.00	22.9
Ye75-76	0.00	0.00	0.17	2.36	3.41	0.47	0.19	6.5

Received 15.I.1981
Printed 6. X. 1981