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The habitat and spatial relations of breeding Phylloscopus warblers and the goldcrest Regulus regulus in southern Finland

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The habitat and spatial relations of 762 territories of willow warblers *Phylloscopus trochilus*, chiffchaffs *Ph. collybita*, wood warblers *Ph. sibilatrix*, and goldcrests *Regulus regulus*, as well as the intraspecific and interspecific effects on the habitat selection, were studied in two large forest areas in southern Finland. The occurrence of the species in 12 subareas depended on the forest fragmentedness, and the amount of spruce forests and forest edges. The habitat distribution of all four species differed significantly from the availability of different habitat types. When the habitats were classified according to the characteristics of vegetation, the preferences of different species were different, although chiffchaff and goldcrest resembled each other. However, all the species preferred habitats which were characterised by a high density of birds. The habitat amplitude of the abundant willow warbler did not vary much between subareas, but in the other species, an increase in the population density seemed to lead to acceptance of less preferred habitats. There was a possible effect of the goldcrest on the habitat amplitude of the chiffchaff. Association indices, which take the availability of different habitat types into account, revealed that the greatest differences in habitat utilisation patterns were between the willow warbler and both the chiffchaff and goldcrest, as well as between the goldcrest and wood warbler. However, a nearest neighbour analysis showed a slight association between the willow warbler and chiffchaff, which was due to differences in their territory size.

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1. Introduction

The warblers *Phylloscopus* spp. and *Sylvia* spp., the goldcrest *Regulus regulus*, tits *Parus* spp., the pied flycatcher *Ficedula hypoleuca*, and the chaffinch *Fringilla coelebs* belong to the most common breeding bird species in southern Finnish forest habitats, and form the main body of the foliage-gleaning guild of insectivorous birds. Of these, the *Phylloscopus* warblers and the goldcrest form a smaller coherent group on the basis of their small body size and foraging behaviour. Their mobility and agility more or less differ from those of other foliage-gleaners, as does the relative importance to them of foliage at different heights in the habitats (Pielowski 1961a, b, Kopp 1970, Lack 1971) or in different horizontal and vertical parts of the trees, and of different prey searching and capture methods (Ulfstrand 1976, 1977, Alatalo 1982, Sæther 1982). Also with respect to morphology (e.g. Bairlein 1981) they form a coherent group of species.

In a study of population dynamics and ecological interactions between species, a quantitative description of their habitats and spatial relations is necessary. In this paper, we analyse the habitat distribution and interspecific associations of the willow warbler *Phylloscopus trochilus*, chiffchaff *Ph. collybita*, wood warbler *Ph. sibilatrix* and goldcrest in two heterogeneous southern Finnish study areas on the basis of a large-scale territory mapping census program. The rare greenish warbler *Ph. trochiloides* is also included in pooled data. We pose the following questions: (1) Do the habitat distributions result from autecological preferences only? (2) How is the habitat amplitude affected by the population size (e.g. v. Haartman 1971, Fretwell 1972)? (3) Does the occurrence of other species affect the habitat distribution and density of a species?

Table 1. Total area (ha) and forest area (ha, percentage of the total in parentheses), and the amount of edges between forests and open habitats in different parts of the study area. Note that the forest areas do not include cultural habitats (CUL) whose total area is 45.0 ha in Subareas B-K (-L) (see Table 2). In Subarea L, the length of edges has not been measured because definition of the edges is very difficult there due to the heterogeneity and patchiness of the habitats. Edges km/km² calculated per forest area only.

Subarea	Total area	Forest area	Edges km	Edges km/km²
A	200	0 (0)	-	-
B	338	11.5 (3)	1.6	13.9
C	82	25.0 (29)	5.6	22.4
D	191	41.4 (22)	11.6	28.0
E	111	55.6 (50)	3.5	6.3
F	61	50.8 (83)	3.4	6.7
G	146	96.4 (66)	11.1	11.5
H	90	63.9 (71)	6.3	9.9
I	54	51.9 (96)	1.4	2.7
J	56	36.9 (66)	4.1	11.1
K	30	24.0 (80)	2.0	8.3
L	164	150.0 (91)	—	—
Totals				
A-L	1523	607.4 (40)	—	-
B-K	1159	457.4 (39)	50.6	11,1

2. Study areas

Breeding land birds were censused in the surroundings of Lammi Biological Station (61° 03′ N, 25° 03′ E) and in Porkkala (60° 05′ N, 24° 33′ E) in Kirkkonummi near the northern coast of the Gulf of Finland (see Tiainen et al. 1980, 1982, Pakkala et al. 1983). The study areas and their subareas (see below) are described in Tables 1, 2 and 3.

The whole study area in Lammi was about 13.6 km², comprising 457 ha of forests, the rest being fields (638 ha), lake shore meadows and peatland (41 ha), three small lakes (10 ha), and human settlements (213 ha). The forests were mostly closed, mature, and spruce-dominated, with smaller areas dominated by deciduous trees. A bushy understory of spruce and deciduous trees was characteristic. The soil is mostly fertile, giving rise to a more productive and luxuriant vegetation than average in southern Finland (see Jauhiainen 1972). The forests were divided, mainly by fields and roads, into smaller areas and patches. We divided the study area into smaller subareas according to their habitat characteristics (proportion of forest in total area, and degree of fragmentedness) as follows (Subareas A-K in Lammi, L in Porkkala.

Subarea A, the main (church) village and centre of Lammi municipality. A rural village with about 500 houses, gardens, meadows, some small fields, and parks and other plantations, but without real forest.

Subarea B, Jahkola and Vanha-Kartano. Large fields surrounded by forest (not included in the study area), small bush and forest islands, as well as small villages and single houses surrounded by gardens and parks.

Subarea C, Pappilanlahti and Lamminjärvi. Deciduous groves and mixed stands of pine and deciduous trees on moisture soil between fields and lake shore meadows, or peatland.

Subarea D, Oinen, Letku, Pappilankylä and Pikku-Pappila. Transition zone between large fields and forest areas. Fields of different sizes fragmented by numerous narrow strips of forest and small forest islands. Both deciduous and spruce, as well as mixed stands.

Subarea E, Uusitalo. Two larger and one smaller forest areas with mainly mixed, but also pure deciduous and spruce stands; mainly surrounded by fields or Lake Pääjärvi.

Subarea F, Rantala. A uniform forest area mainly surrounded by fields or Lake Pääjärvi. Mainly spruce-dominated, but also mixed stands.

Subarea G, Jyrkänmäki and Lehtimäki. Larger forest areas, but somewhat fragmented by small fields and roads. Mainly spruce-dominated, but also mixed and deciduous stands.

Subarea H, Kaunisniementie and Rinnekoti. Large forest areas divided by small fields into two parts. Mainly pure spruce, but also spruce-dominated mixed stands.

Subarea I, Ahomäki. Quite uniform spruce forest with less spruce-dominated mixed stands. One clear-cut area of 2-3 ha.

Subarea J, Ahomäen lehto and Lampellonjärvi. A luxuriant grass-herb forest and tall spruce stands on fertile soil. Half of the boundaries border larger forests, the rest being a fragmented zone bordering fields.

Subarea K, the area of the Biological Station. Mainly deciduous-dominated, variably luxuriant grass-herb forest, but also pure spruce, or spruce-dominated, stands. Mainly bordered by fields and Lake Pääjärvi.

Subarea L, the whole area of Porkkala, added 1.6 km² to the study area. Part of larger forests. Two main forest types, often intermingled in a mosaic-like manner: (i) mainly closed, mature, spruce-dominated stands on mesotrophic soils and (ii) light, barren, pine-dominated forests on rocky hills. Deciduous trees and bushes were less common than in Lammi, and the bush layer was not so dense or continuous. The area enclosed some small meadows and open fens, and the edges of a few fields and of a larger open bog.

The subareas are referred to below by their capital letters.

The habitats of the study areas were classified in two different ways. Firstly, in Lammi, eight forest types were recognised in the field according to the characteristics of the vegetation (age of the forest and tree species composition). The ninth type comprised cultural habitats (human settlements) (Table 2). Secondly, nine habitat types were later recognised according to the density of the bird community (on the basis of

Table 2. Habitat type distributions (ha) in different parts of the study area. Habitats were classified according to the vegetation as follows: (1) Coniferous forests (100-80 % spruce; CON), (2) mixed coniferous-dominated forests (80-50 % spruce; MCON), (3) deciduous and mixed deciduous-dominated forests (50-0 % spruce; DEC), (4) grass-herb forests (GRA), (5) heterogeneous forests (patches of different types and successional stages, often thin stands, mainly spruce; HET), (6) young mixed forests (YMIX), (7) young deciduous forests (YDEC), (8) brush (BRU), and (9) yards, gardens and parks (cultural habitats, CUL). These habitats were only described in subareas B-J.

Subarea	CON	MCON	DEC	GRA	HET	YMIX	YDEC	BRU	CUL
B	1.5	0	2.1	0	3.2	1.1	2.8	0.8	22.5
C	1.9	1.9	2.4	0	2.1	3.1	12.7	0.9	0
D	9.0	8.9	9.7	0	4.6	0.6	3.0	5.6	12.3
E	19.1	7.3	2.0	0	11.2	14.8	1.0	0.2	2.9
F	21.2	22.5	2.0	0	5.1	0	0	0	1.0
G	24.2	34.6	8.8	6.2	12.2	9.4	0.4	0.6	3.7
H	50.6	6.0	0	0	5.8	0	1.0	0.5	1.3
I	44.5	4.4	0	0	1.0	0	0	0	0
J	11.4	6.3	5.1	7.9	2.9	0	2.3	1.0	0.3
Total	183.4	91.9	32.1	14.1	48.1	29.0	23.2	9.6	44.0

Table 3. Habitat type distributions (ha) in different parts of the study area. Habitats were classified here according to the density of the forest bird community in each of the one-hectare quadrats in subareas B–J and L (numbers of pairs indicated; only one pair/square counted from colonies of the Fieldfare *Turdus pilaris*). Note that the areas do not correspond with the forest areas, as many quadrats also include fractions of field and other open habitats. Quadrats with no breeding birds were excluded.

Subarea	Density of the bird community (territories/ha)									
	1	2	3	4	5	6	7	8	≥9	Total
B	47	30	10	11	2	2	2	3	2	109
C	11	15	9	13	2	3	2	1	0	56
D	29	21	18	11	10	4	6	6	6	111
E	11	11	9	10	11	4	13	7	7	83
F	2	11	10	12	8	6	5	2	2	58
G	15	10	21	17	19	16	14	6	8	126
H	9	10	12	9	12	4	8	6	3	73
I	0	5	13	9	7	9	2	4	2	51
J	3	2	11	7	5	8	2	6	6	49
L	13	19	23	24	24	15	12	9	23	164
Total	140	134	136	123	100	71	66	50	59	877

the census results) (Table 3). These will be referred to below as HAB_I and HAB_{II}, respectively. Both were based on one-hectare squares of the 50 × 50 m grid system (see Sect. 3).

Habitat types of the first classification were 'real', as revealed by a detrended correspondence analysis (Hill 1979, Gauch 1981) based on the structure of the bird community. This analysis separated the habitat types well in the two-dimensional space of the first two axes (unpubl. data and M. Vickholm, in prep.).

The second classification is based on the assumption that the size of the forest bird community of each one-hectare quadrat is positively correlated with the productivity of the habitat (Palmgren 1930, Nilsson 1979). It also takes into account the edge effect.

3. Material and methods

The censuses were mainly performed using the mapping method (Anon. 1969, see also Tomiałojć 1980) (Table 4). A grid system of 50 × 50 m was established in the study area, and marked in the field for exact registration of observations of birds on visit maps. Advancing slowly (10–20 min/ha), and systematically (the observer's routes were never more than 100 m and usually only 50–60 m apart), we recorded all singing males, and all other contacts with birds indicating the possible existence of a territory. Movements of birds were also marked on the maps.

From visit maps, the observations were transferred onto species maps. We interpreted the territories according to the following principles. A cluster of observations had to contain at least three registrations (two where five visits were made) from different days, and to be separated from other clusters in the close vicinity (relative to territory size according to our own field experience and available literature) by simultaneous registrations, before it could be accepted as representing a territory. Where the density was high, clusters separated by simultaneous registrations from close vicinity clusters on two or more sides were not accepted if all separating registrations came from different visits and these close vicinity clusters were separated on some visit(s) by simultaneous registrations over the cluster concerned. We find this strict interpretation crucial in reliable estimation of population sizes by the mapping method. This underlines the necessity of careful field work in which special attention is paid to observing and registering the birds simultaneously. Tests done by simultaneous mapping and colour-ringing of territorial males have shown that the mapping method is accurate for censusing the willow warbler in mountain birch forests in Lapland (Enemar et al. 1979), and both the willow warbler and the chiffchaff in southwest German conditions (Tiainen & Bastian 1983). Similar tests (in collaboration with I. K. Hanski and J. Mehtälä) in Lammi have shown the same for both the willow warbler and chiffchaff, and the wood warbler. No similar tests have been done for the goldcrest. Its territory size was about 2–2.5 ha in a spruce study plot examined by Palmgren (1932).

Our average census efficiency was most probably slightly weaker in 1979 than in later years because of the later start of censuses (this does not, however, concern *Phylloscopus* warblers because they do not settle down before the first (chiffchaff) or second (willow and wood warblers) thirds of May); we were also more careful about registering simultaneous observations in these later years. The efficiency, however, was probably not weaker for the species studied in this paper, because they are generally more easily censused than most other forest bird species due to their active singing (especially the *Phylloscopus* warblers).

A total of 762 territories of *Phylloscopus* warblers and the goldcrest were registered in 1979–1982. Each territory was located in the one-hectare square of the grid system where most observations of the particular territory had been made.

Table 4. Censuses performed using the mapping method in different subareas. Subarea A was visited only once (in two parts) on June 6 and 8, 1979. Data for Subarea K originate from separate population studies on *Phylloscopus* warblers (Tiainen 1983a, and unpubl.) and partly from Solonen (1981). The areas visited were always smaller parts of the subareas shown in Table 1.

Subarea	Census period	Visits
B, partly C	May 12–July 3, 1979	5
C–J	May 12–July 3, 1979	9
F and J	April 28–June 27, 1980	12
L	April 22–June 28, 1980	12
F	May 8–June 26, 1982	10

4. Results

4.1 Occurrence and densities in different subareas

The willow warbler was the only species occurring in all subareas. Except for the rare greenish warbler, all species studied occurred together in only six subareas (Table 5). The density of the willow warbler was always highest,

Table 5. Numbers (N) and densities (territories/km², of forest; D) of *Phylloscopus* warblers and the goldcrest, as well as their proportions of all these species (in per cent, p) in different parts of the study areas (A–K in 1979, L in 1980).

Subarea	Willow warbler			Chiffchaff			Wood warbler			Greenish warbler			Goldcrest			Total	
	N	D	p	N	D	p	N	D	p	N	D	p	N	D	p	N	D
A	12	-	100	0	0	0	0	0	0	0	0	0	0	0	0	12	-
B	10	87	100	0	0	0	0	0	0	0	0	0	0	0	0	10	87
C	29	116	100	0	0	0	0	0	0	0	0	0	0	0	0	29	116
D	39	94	95	0	0	0	0	0	0	0	0	0	2	5	5	41	99
E	46	83	81	2	4	4	0	0	0	0	0	0	9	16	16	57	103
F	17	34	49	3	6	9	6	12	17	0	0	0	8	16	23	34	69
G	66	73	68	8	9	8	6	7	6	2	2	2	15	17	16	97	107
H	31	49	53	9	14	15	0	0	0	0	0	0	19	30	32	59	92
I	25	50	51	5	10	10	2	4	4	0	0	0	17	34	35	49	98
J	28	76	54	3	8	6	14	38	27	0	0	0	7	19	13	52	141
K	23	96	59	2	8	5	12	50	31	0	0	0	2	8	5	39	163
L	38	25	41	7	5	8	5	3	5	0	0	0	42	28	46	92	61
Total	364	-	64	39	-	7	45	-	8	2	-	0.4	121	-	21	571	-

comprising at least half of the pooled density of the species studied except in Subarea L where the density of the goldcrest exceeded that of the willow warbler. In all, the willow warbler was three times as numerous as the goldcrest, eight times as numerous as the wood warbler, and nine times as numerous as the chiffchaff. In the whole data, only the chaffinch exceeded the density of the willow warbler (unpubl.).

The chiffchaff occurred in all areas with larger continuous forests. The densities were highest in areas containing much spruce forest (Table 5, cf. Table 2). Four small forest islands surrounded by fields (2.0, 2.8, 3.3, and 4.7 ha in Subarea D) were not accepted by the chiffchaff even though they comprised spruce, spruce-dominated, habitats on fertile soil where the density was highest elsewhere. Two of these areas (2.8 ha and 4.7 ha) had been visited each year since 1974. The chiffchaff has never had permanent territories there, and it was only once observed there (in the larger island) during the breeding season (early July 1981).

In 1979 in Lammi, most of the territories of the wood warbler were aggregated in two large concentrations (in Subareas J and K). Three of the territories in Subarea G formed a small group. Most of the remaining territories adjoined these concentrations at greater distances. Only one territory was completely isolated (500 m from the closest neighbour). It was clear that the densest concentrations occurred in the richest and most fertile habitats, around which there were less densely distributed territories in suitable sites.

The goldcrest was numerous everywhere there were spruce forests. It even occurred in the 2.8 and 3.3 ha forest islands in Subarea D. In other years, it has also been recorded in the 4.7 ha forest island.

The willow warbler population increased in Subarea F from 1979 to 1980, and from 1980 to 1982, but decreased in Subarea J from 1979 to 1980 (Table 6). The change from 1980 to 1982 in Subarea F was mainly connected with a habitat change caused by felling.

To analyse whether habitat characteristics explained density differences between subareas, the data were subjected to regression analyses. The density of the willow warbler correlated positively with the amount of edges (Fig. 1), which explained 43 % (r^2) of the variation. Densities of the chiffchaff and goldcrest correlated negatively with the amount of edges; the wood warbler did not show significant correlation. They were, however, absent from subareas with more edges than 13 km/km², except for the goldcrest in one subarea (D). The relative amounts of coniferous and mixed coniferous-dominated forests explained 68 and 81 % of the density variation in the chiffchaff and goldcrest, respectively, and 81 % in the willow warbler (negative correlation) (Fig. 2). In a multiple regression analysis, the two above variables explained 86 % of the density variation in the willow warbler.

Table 6. Number of pairs of *Phylloscopus* warblers and goldcrest in two subareas where the mapping census was carried out in more than one year. The boundaries of the subareas slightly differ from those used elsewhere in this paper.

Species	Subarea F			Subarea J	
	1979	1980	1982	1979	1980
Willow warbler	16	21	27	27	18
Chiffchaff	3	2	2	3	2
Wood warbler	6	5	5	14	13
Goldcrest	8	11	10	8	10

4.2 Habitat distributions and preferences

The willow warbler reached its highest densities in young, especially deciduous, forests, and in grass-herb and deciduous forests (Table 7). Coniferous, and mixed coniferous-dominated forests, however, were more important for the

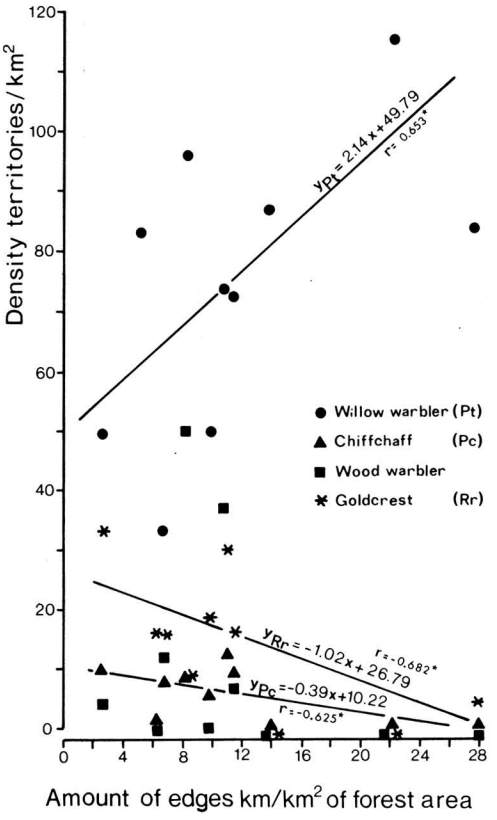

Fig. 1. Relationships between the densities of *Phylloscopus* warblers and the golderest, and the relative amount of edges between forests and open habitats in ten subareas in Lammi.

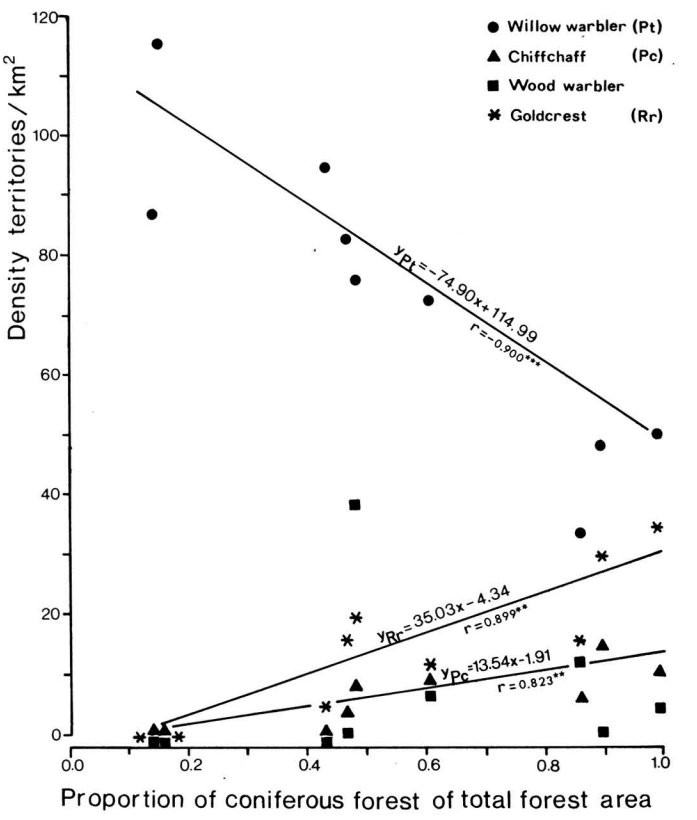

Fig. 2. Relationship between the densities of *Phylloscopus* warblers and the goldcrest, and the proportion of coniferous and mixed coniferous-dominated forests of total forest area in nine subareas in Lammi.

population of the study area, even though the densities were lower there, because these habitat types dominated the study area. The chiffchaff and goldcrest were almost entirely concentrated into these two coniferous forest types. These forest types were also important for the wood warbler, although its densities were much higher in grass-herb forests and deciduous forests.

The willow warbler was the only species studied which occurred in young deciduous forests, brush and cultural habitats. These three habitat types comprised 16 % of the total area of forest and cultural habitats in Subareas B–J, and 15 % of the willow warbler population occurred there (17 % in Subareas A–K). Only in cultural habitats (9 % in B–J) of these three habitats, the willow warbler did occur (4 % of the population in B–J) less than expected on the basis of the habitat availability (cf. Tiainen et al. 1982).

The habitat distributions of all species studied differed significantly (χ^2-tests) from the availability (Table 8). The willow warbler preferred deciduous and young forests (DEC, GRA, YMIX and YDEC), the wood warbler older, luxuriant

Table 7. (Densities territories/km²) of *Phylloscopus* warblers and the goldcrest in different habitats classified according to vegetation in subareas B–J in Lammi.

Species	CON (183.4 ha)	MCON (91.9 ha)	DEC (32.1 ha)	GRA (14.1 ha)	HET (48.1 ha)	YMIX (29.0 ha)	YDEC (23.2 ha)	BRU (9.6 ha)	CUL (44.0 ha)
Willow warbler	44	64	100	114	69	90	121	52	27
Chiffchaff	10	9	3	0	4	3	0	0	0
Wood warbler	5	5	22	50	0	0	0	0	0
Goldcrest	33	13	0	0	8	3	0	0	0

Table 8. Preferences by *Phylloscopus* warblers and goldcrest for forest habitats classified according to the vegetation. The observed and expected numbers are numbers of territories in each habitat. Habitat types were combined (as shown with square brackets) to increase the expected numbers. If all other habitats except the first two were combined, $\chi^2 = 8.73$ for the chiffchaff ($p<0.05$, d.f. = 2).

Species	CON	MCON	DEC	GRA	HET	YMIX	YDEC	BRU	χ^2
Willow warbler									
Observed	80	59	32	16	33	26	28	5	36.0***
Expected	123.7	62.0	21.7	9.5	32.4	19.6	15.6	6.5	
Chiffchaff									
Observed	18	8	[1	0]	[2	1	0	0]	6.8°
Expected	12.8	6.4	2.3	1.0	3.3	2.0	1.6	0.7	
Wood warbler									
Observed	9	5	[7	7]	[0	0	0	0]	60.7***
Expected	11.9	6.0	2.1	0.9	3.1	1.9	1.5	0.6	
Goldcrest									
Observed	60	12	[0	0]	4	1	[0	0]	44.8***
Expected	32.7	16.4	5.9	2.6	8.6	5.2	4.1	1.7	

(grass-herb) deciduous forests, and the chiffchaff and the goldcrest coniferous forests.

The densities of all species studied increased with increasing density of the whole forest bird community (Table 9). As more than one pair of these species (never more than two) only seldom occurred in a single one-hectare square (willow warbler 18 times, wood warbler twice, goldcrest three times), these densities are also close to occurrence frequencies. All species highly significanty preferred habitats with many birds (Table 10). The observed density matched the expected in habitats with 3 pairs of birds for the willow warbler, in habitats with 3–5 pairs for the goldcrest, in habitats with 3–4 pairs for the chiffchaff, and in habitats with 4 pairs for the wood warbler. That the species differed with respect to their acceptance of the low-density end of the habitat scale was also shown by the fact that 62 % of willow warblers, 65 % of chiffchaffs and goldcrests, and 82 % of wood warblers occurred in habitats where bird density was at least 5 pairs/ha (excluding the species in concern).

4.3 Habitat amplitudes

As a measure of the habitat amplitude, we used

$$B' = X^2 / [A \sum_{i}^{n} (x_i^2/a_i)]$$

where X is the total population of a species in the study area, A is the total area of the study area, and x_i and a_i the number of territories in, and area of, the habitat type i, respectively (Hurlbert 1978, Eq. 29). This measure allows for variation in the area (a_i) of a habitat type, and can take on values ranging from $1/n$ (when only a single habitat type is used; $1/9 = 0.11$ in this case) to 1.00 (when each habitat type is utilised in proportion to its abundance) (Hurlbert 1978).

The habitat amplitude of the willow warbler was broadest, and that of the wood warbler narrowest (Table 11). In spite of considerable variation in the density, the habitat amplitude of the willow warbler was also consistently broad in all subareas, with few exceptions. The amplitude for HAB_I was low in Subarea B, where the habitats were often split into fragments which were too small and the sample size was also small, and in Subarea J, where the density was disproportionately high in grass-herb forests. The amplitude for HAB_{II} was low in subareas where there were many low-density squares.

The habitat amplitudes of other species were more variable (Table 11). This variability may be a consequence of either (1) an intraspecific response to varying density of populations in different subareas, or (2) interspecific interactions which may have an effect on habitat selection. These alternatives were examined more closely with correlation analysis. In the first case, wer expect to find a positive correlation between habitat amplitude and density. In the second case, we are interested in correlations between the

Table 9. Densities (territories/km^2) of *Phylloscopus* warblers and goldcrest in different habitats classified according to the density of the whole bird community (HAB_{II}) in each of the one-hectare squares in subareas B–J and L in Lammi and Porkkala.

Species	Density of the bird community (territories/ha)								
	1	2	3	4	5	6	7	8	≥9
Willow warbler	3	14	28	41	47	68	71	58	80
Chiffchaff	0	0	3	4	4	10	11	6	12
Wood warbler	0	0	1	1	4	7	9	12	17
Goldcrest	0	4	7	14	11	24	29	30	44

Table 10. Preferences by *Phylloscopus* warblers and goldcrest for habitats with varying density of the bird community (the species in concern excluded). The observed and expected numbers are numbers of territories in each habitat. Habitat types were partly combined (as shown with square brackets) to increase the expected numbers.

Species	Density of the bird community (territories/ha) 0-1	2	3	4	5	6	7	8	≥9	χ^2
Willow warbler										
Observed	23	40	52	43	48	45	35	25	49	63.5***
Expected	63.2	56.9	54.4	40.4	37.1	26.8	20.9	9.2	18.0	
Chiffchaff										
Observed	0	4	5	4	[7	7]	[3	3	4]	14.3*
Excepted	6.4	5.7	5.7	5.1	4.3	3.0	2.6	2.2	2.2	
Wood warbler										
Observed	0	1	1	4	[8	3]	[7	3	6]	30.1***
Expected	5.7	5.0	5.0	4.7	3.8	2.6	2.5	1.7	2.1	
Goldcrest										
Observed	5	9	17	11	17	19	18	8	15	59.6***
Expected	21.1	18.5	19.3	15.6	14.2	9.8	8.7	7.4	4.8	

habitat amplitude of one species and density of the other. We cannot expect that correlation analyses can directly show the effects of interspecific interactions, but they may give useful hints. If the species have different habitat optima, the habitat amplitude of both species, or at least of the socially or ecologically inferior species, or at least with increasing density of the other species, i.e. there should be a negative correlation. If, on the other hand, the species have same habitat optima, increasing density of the superior species should increase the habitat amplitude of the other species if that species' density remains unchanged. If the density of the inferior species is depressed, its habitat amplitude can be expected to remain unchanged or to decline.

In all cases but one (wood warbler), there was a positive significant or nearly significant intraspecific correlation, suggesting that intrapopulation processes are important (Table 12). Interspecifically, there were significant correlations only between the density of the goldcrest and the habitat amplitude of both the chiffchaff and wood warbler. As the goldcrest and the chiffchaff have similar habitat preferences, interspecific relations may be important. The correlations between the wood warbler and the goldcrest for the two kinds of habitat classifications were contradictory; as the species have different habitat preferences, the result may be only coincidental with regard to interspecific relations.

4.4 Interspecific associations

The interspecific associations were first examined on the population level by correlating the densities from different subareas (Table 13). A negative correlation was found between the willow warbler and both the chiffchaff and goldcrest, which, in turn, were positively correlated.

A closer examination was made using the similarity index

$$L = (A/XY) \sum_{1} (x_i y_i / a_i)$$

where A is the area of the whole study area, X and Y the total populations of two species, x_i and y_i the

Table 11. Habitat amplitudes of *Phylloscopus* warblers and goldcrest in Lammi and Porkkala. The indices were calculated for both the whole study area in Lammi (B-J) and the whole pooled data of Lammi and Porkkala (B-J, L), as well as for each subarea separately. HAB_I and HAB_{II} refer to habitat classification according to the characteristics of vegetation, and the density of the bird community in each of the one-hectare quadrats, respectively.

Subarea	Willow warbler		Chiffchaff		Wood warbler		Goldcrest	
	HAB_I	HAB_{II}	HAB_I	HAB_{II}	HAB_I	HAB_{II}	HAB_I	HAB_{II}
B-J	0.85	0.59	0.72	0.45	0.29	0.25	0.58	0.53
B-J, L	-	0.70	-	0.53	-	0.34	-	0.59
B	0.51	0.23	-	-	-	-	-	-
C	0.83	0.79	-	-	-	-	-	-
D	0.84	0.53	-	-	-	-	0.33	0.11
E	0.85	0.71	0.33	0.26	-	-	0.74	0.40
F	0.84	0.74	0.41	0.13	0.53	0.30	0.52	0.46
G	0.87	0.77	0.78	0.30	0.39	0.28	0.46	0.52
H	0.83	0.64	0.68	0.60	-	-	0.92	0.53
I	0.92	0.84	085	0.41	0.89	0.13	0.86	0.73
J	0.69	0.77	0.55	0.28	0.58	0.40	0.47	0.49
L	-	0.56	-	0.31	-	0.27	-	0.47

Table 12. Correlations between the habitat amplitudes of the chiffchaff, wood warbler and goldcrest with densities of the willow warbler and themselves. HAB_I and HAB_{II} refer to different habitat classifications (see Table 11).

Species		df	Willow warbler	Chiff-chaff	Wood warbler	Gold-crest
Chiffchaff	HAB_I	6	-0.15	0.73°	-0.51	0.68°
	HAB_{II}	7	-0.04	0.82*	-0.21	0.74*
Wood warbler	HAB_I	4	-0.31	0.51	-0.17	0.94*
	HAB_{II}	5	0.35	-0.37	0.79°	-0.75°
Goldcrest	HAB_I	7	-0.50	0.47	-0.50	0.87**
	HAB_{II}	8	-0.54	0.58	-0.32	0.65°

Table 13. Interspecific correlations of densities of *Phylloscopus* warblers and the goldcrest in subareas B-L. In 'All' the densities of the chiffchaff, wood warbler, goldcrest and greenish warbler were pooled. The data of repeated censuses in Subareas F and J were not used, because they are not independent, as a result of site tenacity (df=10).

	Willow warbler	Gold-crest	Wood warbler
Chiffchaff	-0.507°	0.770**	0.313
Wood warbler	0.154	-0.061	
Goldcrest	-0.795**		
All	-0.387		

Table 14. Interspecific associations for cooccurence in different subareas and in different habitat types. HAB_I and HAB_{II} refer to different habitat classifications (see Table 11). The index values express the multiple of the probability of interspecific encounter compared to what it would be if both species were uniformly distributed with respect to the area of the various subareas or to the areas of the various habitats (Hurlbert 1978).

Association in subareas		Chiff-chaff	Wood warbler	Gold-crest
B-L	Willow warbler	0.88	1.21	0.80
	Chiffchaff		1.17	1.16
	Wood warbler			0.85
B-J (HAB_I)	Willow warbler	0.80	1.17	0.72
	Chiffchaff		0.79	1.33
	Wood warbler			0.85
B-J (HAB_I)	Willow warbler	0.80	1.17	0.72
	Chiffchaff		0.79	1.33
	Wood warbler			1.91
B-K, L (HAB_{II})	Willow warbler	1.25	1.76	1.56
	Chiffchaff		2.10	1.82
	Wood warbler			2.19

populations sizes of two species in a subarea or habitat type i and a_i its area (Hurlbert 1978, Eq. 11). The index value is 1 if both species occur in each subarea or use each habitat type in proportion to its area (a_i), >1 if both species occur in certain subareas more often or use certain habitat types more intensively than other types in a similar fashion, and <1 if the species differ in these respects (Hurlbert 1978).

As shown by the association indices, the occurrence of the willow warbler in different subareas (B-L) differed from that of the chiffchaff and the goldcrest ($L<1$), whose occurrence also differed from that of the wood warbler ($L<1$) (Table 14). There was an association in the occurrence of the wood warbler and both the willow warbler and the chiffchaff ($L>1$), and of the chiffchaff and the goldcrest ($L>1$). Associations were similar at the habitat level when examining HAB_I, except that now also the chiffchaff and wood warbler differred. The utilisation of different habitats of HAB_{II} coincided in all comparison, but least for the willow warbler and chiffchaff. The difference between the willow warbler and chiffchaff was even less when Porkkala (Subarea L) was included than in Lammi alone.

The interspecific associations were also examined using a nearest neighbour method. In subareas where both of the two compared species occurred, the nearest neighbour for each territory was recorded by measuring the distance between their centres (in Lammi). These were arranged in a 4 × 4 segregation table

		Species of neighbour A	B	Σ
Species of base territory	A	a	b	m
	B	c	d	n
	Σ	r	s	N

from which the index

$$S = 1 - N(b + c) / (ms + nr)$$

was calculated according to Pielou (e.g. 1977: 226-228). If there is no segregation between the species, $S = 0$. If $b = c = 0$, or the populations are fully segregated, $S = 1$. If $a = d = 0$, or the nearest neighbour always belongs to the other species, $S = -1$.

In our study area, the wood warbler and goldcrest were most segregated from each other, and the chiffchaff and goldcrest most associated with each other (Table 15). There was also slight segregation between the chiffchaff and wood warbler, and slight association between the chiffchaff and willow warbler.

Table 15. Interspecific segregation values according to the nearest neighbour analysis (upper triangle). Numbers of comparisons given in the lower triangle (these do not correspond with the numbers in Table 5 because territories were also included close to the boundaries of the study area when the nearest neighbour was known). A value of +1 indicates total segregation, and of -1 total association.

	Willow warbler	Chiff-chaff	Wood warbler	Gold-crest
Willow warbler		-0.17	-0.05	-0.09
Chiffchaff	226		0.19	-0.40
Wood warbler	222	56		0.38
Goldcrest	279	106	112	

5. Discussion

5.1 Habitat of Phylloscopus warblers and the colcrest

The general patterns of habitat selection of Finnish forest birds are well known (e.g. Palmgren 1930, Soveri 1940, Merikallio 1946, Haapanen 1965, Haila et al. 1980, Ukkonen & Toivanen 1980, Toivanen et al. 1981, see also v. Haartman et al. 1963-1972), and the present results are in good accordance with previous ones. The willow warbler and the wood warbler reach their highest densities in deciduous forests, the former in younger, open forests near edges (see also Kuusisto 1941), and the latter in mature, often more luxuriant forests. The chiffchaff and the goldcrest, on the other hand, are species of spruce, and spruce-dominated mixed forests.

Tiainen (1981) quantitatively studied the habitat preferences of these species (and eight other common forest passerines) by examining their distributions on four habitat dimensions in Lammi. Of them, the willow warbler was least, and the goldcrest most, selective for the coverage of the tree layer. The willow warbler and the wood warbler were least selective for the foliage structure (measured by the product of tree species diversity and the proportion of deciduous trees), the former tending, however, towards deciduous-dominated forests. The goldcrest clearly, and the chiffchaff to a lesser extent, preferred spruce. The wood warbler inhabited the highest forests, all the other species reaching their peaks in moderately high forests. And finally, the willow warbler was a clear edge species, while the others had no clear preference for the distance from the nearest forest edge. Combining these results revealed that the habitat niche width (or amplitude) of the wood warbler was largest, and that of the goldcrest narrowest; the intermediate willow warbler and chiffchaff did not markedly differ from each other. The four-dimensional habitat overlaps were quite high between the chiffchaff and goldcrest, low between the willow warbler and goldcrest, and quite low between the willow warbler and wood warbler; otherwise the overlaps were intermediate with respect to those prevailing in the whole community of 12 species.

These results surprisingly showed that the wood warbler was the second most generalised species, with regard to habitat requirements, in the whole community (after the redwing *Turdus iliacus*, but before the chaffinch). This may have been due to (1) variation in habitat requirement from year to year according to the fluctuations in the population size, the study year (1978) having been a 'good' one, or (2) specialisation for habitat features other than those measured. Anyhow, it is suggested that biological factors other than habitat requirements restrict its abundance (the Finnish population is only about 5 % of that of the willow warbler, and is about the same size as that of the chiffchaff; Järvinen & Väisänen 1983) (Tiainen 1981). As the species has a tendency to aggregation (e.g. Svärdson 1949, this study) a small population size leads 'automatically' to a restricted habitat distribution.

According to Tiainen (1981), the willow warbler was less generalised than the wood warbler in the fourdimensional habitat niche space (intermediate in the whole community). This was mainly due to its clear preference for edges. The edge effect was studied more closely by ordinating the most common forest bird species of our study area in Lammi using a detrended correspondence analysis (Hill 1979, Gauch 1981) (unpubl. and M. Vickholm in prep.). Each of the one-hectare squares was classified into one of four groups according to the distance from forest edge, in addition to the habitat classification based on the characteristics of the vegetation. All species were nicely ordinated on the first correspondence axis, which was clearly a forest edge — forest interior axis. In this ordination, the chiffchaff, wood warbler and goldcrest were clearly separated, as forest interior species, from the willow warbler, an edge species. The second axis reflected a gradient from deciduous to coniferous forests and differentiated between the wood warbler (deciduous) and the chiffchaff and goldcrest (coniferous).

5.2 Selection of habitat

Our results showed that there are habitat types which are first inhabited by the species studied. For the chiffchaff, wood warbler and goldcrest, we could show correlations between the habitat amplitude and density, suggesting that population pressure leads to acceptance of less preferred habitats, as well.

For an examination of possible interspecific interaction, the following species pairs are most interesting:

(1) *Willow warbler and chiffchaff.* Both species are ecologically and morphologically very similar (Lack 1971, Gaston 1974, Burnhauser 1978, Laursen 1978, Bairlein 1981, Sæther 1982, Tiainen 1982 and unpublished). Direct conflicts between them have been observed at least in England (Howard 1920), southern Germany (Burnhauser, pers. comm., JT's own obs.) and Norway (Sæther 1983a, b) during the early breeding season. Sæther (1983a, b) showed interspecific territoriality between them in a

Norwegian grey alder *Alnus incana* wood where their territories were exclusive.

In our study area, the willow warbler and chiffchaff were negatively associated with regard to the different subareas and habitat types. While the habitat amplitude of the willow warbler was not variable, that of the chiffchaff was, but its variation was not correlated with (or explained by) the variation in the density of the willow warbler. These two species always occurred in close proximity to each other and their territories often overlapped to some extent. In fact, the nearest neighbour of a chiffchaff was never another chiffchaff when these two species were compared. This is due to the large territory size of the chiffchaff in relation to that of the willow warbler. Although the two species are separated by habitat and distance from the forest edge, there is always a willow warbler territory close to a chiffchaff territory in the conditions of Lammi.

Other studies (Tiainen, Hanski and Mehtälä, unpubl.) have indicated that interspecific interactions between the willow warbler and chiffchaff may to some extent affect the location of chiffchaff territories, although the main factor for its observed habitat distribution is probably its adaptedness to those habitats where it is found.

(2) *Willow warbler and wood warbler.* Edington & Edington (1972) reported interspecific hostile encounters and exclusive spacing of territories between these species in England. Our results do not indicate any interspecific interactions.

(3) *Chiffchaff and goldcrest.* These species were associated with each other with respect to subareas, habitats, and spatial closeness. The habitat amplitude of both species became broader with increasng density of the respective populations, as shown by correlation analysis. The habitat amplitude of the chiffchaff was also positively correlated with the density of the goldcrest, but not vice versa. As both species had similar habitat requirements, such an interspecific correlation was predictable if the species interact and one of them is ecologically or socially superior (Sect. 4.3). As the densities of these species were also correlated (Table 13), we examined the effect of the densities of both species on the habitat amplitude of the chiffchaff with a multiple regression analysis. The multiple correlation was 0.759 for HAB_I and 0.896 for HAB_{II} (cf. Table 12). Thus, the coefficient of determination (r^2) increases from 53.6 % (density of chiffchaff alone as the independent variable) or 45.6 % (goldcrest) to 57.6 % (both) for HAB_I and from 67.6 % (chiffchaff) or 54.5 % (goldcrest) to 80.3 % (both) for HAB_{II}. Thus we conclude that the goldcrest may have a slight effect on the habitat amplitude of the chiffchaff when the habitats are classified according to the density of the bird community.

Does additional evidence suggest that the goldcrest is superior to the chiffchaff? These two species are certainly not interspecifically territorial; moreover, in such a case the chiffchaff would probably be stronger as it is some 50 % heavier than the goldcrest.

We suggest that there may be competition of some intensity between these two species for food resources. This is supported by two facts: (1) the goldcrest with its total population of 1.5 million breeding pairs is much more abundant in Finland than the chiffchaff with its 0.4 million breeding pairs (Järvinen et al. 1977, Järvinen & Väisänen unpubl.), although their ranges and favoured habitats are similar (von Haartman et al. 1963-1972, Tiainen, 1983b, Järvinen & Väisänen unpubl); and (2) during the past decades, of these two species, only the goldcrest has increased its population size as the amount of spruce forests has increased (Järvinen et al. 1977, Järvinen & Väisänen 1978). This suggested interspecific relation certainly deserves further study. In accordance with this idea, P. Helle (pers. comm.) observed that both the chiffchaff and the goldcrest preferred similar forests in Oulanka, northern Kuusamo (66° 22′ N, 29° 20′ E), but the former occurred within 100 m from forest edges and the latter in the forest interior. Although Helle's data for these two species are still small, this is what could be predicted for the northern, less productive conditions, if our idea is correct.

The explanation for the suggested ecological superiority of the goldcrest in comparison to the chiffchaff may be in their body sizes. These two species are the smallest of the common foliage-gleaners of Finnish forests. The goldcrest, as the smaller, is free from all competition by insectivorous birds in one direction, while the chiffchaff falls between the goldcrest in one direction and the other foliage-gleaners, including other *Phylloscopus* warblers, in the other (Tiainen 1978, 1981).

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