

Ecological significance of morphometric variation in three sympatric *Phylloscopus* warblers

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Measurements of 11 morphometric characteristics of coexisting populations of the willow warbler *Phylloscopus trochilus*, the wood warbler *Ph. sibilatrix*, and the chiffchaff *Ph. collybita* revealed the following results: (1) the willow warbler and the chiffchaff resemble each other much more than they do the wood warbler; (2) all three species are significantly sexually size dimorphic, the degree of dimorphism decreasing from the small chiffchaff to the large wood warbler; (3) the chiffchaff males and the willow warbler females were the same size, while the wood warbler females fell between the willow and wood warbler males; (4) measurements of the body size were more dimorphic than those of the bill, which, on the other hand, were intrasexually more variable; (5) males occupying territories in the deciduous and mixed woodland of the study area were significantly larger than those in the nearby spruce-dominated woodland; and (6) larger males were more site-tenacious than smaller ones in the deciduous and mixed woodland of the study area.

These results suggest that in these warblers, the sexual size dimorphism is more a result of sexual selection than of intraspecific competition. Furthermore, at least in the willow warbler, spacing of territories fits Fretwell's ideal despotic habitat distribution model, and food competition is expected to be more intense between the willow warbler and the chiffchaff than between the wood warbler and either of the other two species, if there is any significant competition.

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1. Introduction

The morphology of a species is an adaptation to environments encountered by individuals during the annual cycle, and to the specific form of life (Mayr 1963). Models developed by Pyke (1978) and Case (1979) predict that animals have an optimal body size which maximizes the energy intake for particular resources. The body size can also be selected, however, by pressure from several other factors, like prey densities (Schoener 1969), interspecific competition for food (e.g. Hutchinson 1959, Lack 1971, Diamond 1973, 1975), intraspecific competition for food (e.g. van Valen 1965, Rothstein 1973a, b) or other resources like nest sites (Dhondt et al. 1979), size-selective predation upon the species (Case 1979), and intraspecific social systems (e.g. Lack 1968, Searcy 1979a, b). Competition for food should also exert selective pressure on single morphometric characteristics (e.g. Schoener 1965, Lack 1971), and more on trophic than other features (Rothstein 1973a). Because there are many different selective

pressures, which may act in opposite directions, the overall morphology of a species tends to be a compromise, especially in variable and unpredictable environments (Schmalhausen 1949, Mayr 1963).

In this paper I examine the intraspecific and interspecific variation in morphology of three sympatric *Phylloscopus* warblers, the willow warbler *Ph. trochilus*, the wood warbler *Ph. sibilatrix*, and the chiffchaff *Ph. collybita*, in order to interpret the significance of the above selection pressures on them in two local communities.

2. Study areas

Warblers were caught for ringing and measuring in southern Finland and in the southwest of the Federal Republic of Germany.

In Finland, birds were caught at Lammi Biological Station (61° 03' N, 25° 03' E) during a population study in 1972-1978 (Tiainen 1983a). The main study area consisted of about 21.5 ha of forest. The southern part (about 17 ha) had rich grass-herb forest vegetation dominated by deciduous trees, mainly birches *Betula* spp. The northern and eastern

parts (4.5 ha) contained almost pure Norway spruce *Picea abies* (L.) Karst., or spruce-dominated stands. A more detailed description of the study area can be found in Tainen (1983a).

The willow warbler population was almost stable in the southern part of the area (18–20 pairs in 1972–1978, coefficient of variation 4.6%), with a mean density of 1.15 pairs/ha, while in the northern and eastern parts the population was somewhat more variable (4–7 pairs, CV 27.8%) with a mean density of 0.83 pairs/ha (Tainen 1983a). The wood warbler population was 0–2 pairs in the first years, but then increased steadily to 12 pairs in the final years (unpubl.). The chiffchaff population was stable at 2–3 pairs throughout the 1970s. Generally speaking, the willow and wood warbler territories were distributed over the entire study area with the exception of the spruce forest habitats. The chiffchaff inhabited spruce forests and spruce-dominated parts, but many territories partly extended into other habitats.

In the Federal Republic of Germany, chiffchaffs and willow warblers were caught near the village of Möggingen and Lake Mindelsee (47° 46' N, 9° 01' E) near Radolfzell on Lake Constance. The habitats were more variable here, ranging from low lake-shore bushes (*Rhamnus cathartica* L. and *Salix* spp.) to tall deciduous stands. Chiffchaffs inhabited all habitats of the study area abundantly, while the willow warbler was concentrated in lake-side habitats; it outnumbered the chiffchaff only in bushy habitats.

3. Material and methods

A total of 252 willow warblers, 45 wood warblers and 23 chiffchaffs were measured for this study in Lammi, and 16 willow warblers and 35 chiffchaffs in Möggingen. Only adult individuals (at least 1 year old) were included here. Most birds belonged to the local populations, but in Lammi some of the willow warblers caught in May have been passing migrants.

The birds were sexed according to behaviour, form and size of the cloacal protuberance (Svensson 1975), and the brood patch (the females' patch is totally bare from the beginning of the breeding period until the postnuptial moult, while males have always at least some feathers especially on the sides of the patch; cf. Svensson 1975). Sexing was usually based on all three characteristics. A few individuals caught early in the season could not be sexed in the field. Their sex was later determined according to wing length (see Fig. 1). The age of most adult warblers could not be determined exactly. However, returning males were measured to find out whether wing length increased with increasing age.

The weight and the wing length were measured as standard procedure in the field; from 1975 the tail length and wing formula were also measured. Several additional characters were measured from 1978. The measurements were made to the nearest mm with a ruler, if not otherwise stated. The following methods were used:

The *weight* was recorded to an accuracy of 0.1 g using a 30-g Pesola spring balance.

The *wing length* was measured from the wrist bend to the tip of the longest primary, using the maximum method, where the wing is flattened and straightened sideways (Svensson 1975).

The *wing formula* was recorded by measuring the distances of the second (outermost) to the eighth primaries, inclusive, from the wing tip. The formula was used to calculate two indices, an index of wing pointedness, as the sum of the distances standardised by division by the wing length, and an index of wing symmetry as a ratio of sums of distances of primaries ascendantly and descendantly from the tip, respectively (cf. Busse 1967).

The *partial length of the first primary* (outermost) was measured as the distance from its tip to the tip of the longest primary coverts.

The *tail length* was measured from the tip of the longest feathers to the back ('Operation Baltic' method, see Busse 1974). The tail was bent at right-angles to the back, and the

Table 1. Morphometric characteristics of the three *Phylloscopus* warblers studied in Lammi. Wing pointedness and wing symmetry are given as indices based on the wing formula. Weight is expressed in grams, other measurements in mm.

Characteristic	Sex	<i>Ph. sibilatrix</i>				<i>Ph. trochilus</i>				<i>Ph. collybita</i>			
		\bar{x}	SD	CV %	N	\bar{x}	SD	CV %	N	\bar{x}	SD	CV %	N
Weight	♂	9.77	0.530	5.4	22	9.65	0.513	5.3	139	8.18	0.509	6.2	14
	♀	9.65	0.590	6.1	13	8.64	0.487	5.6	78	7.52	0.556	7.4	9
Wing length	♂	79.1	1.61	2.0	22	71.4	1.46	2.0	138	66.7	1.49	2.2	14
	♀	75.0	1.36	1.8	21	65.7	1.46	2.2	117	59.7	0.92	1.5	9
Wing pointedness	♂	0.65	0.035	5.4	16	0.55	0.047	8.5	40	0.43			3
	♀	0.63	0.053	8.4	12	0.54	0.059	10.9	19	0.38			3
Wing symmetry	♂	28.7	12.83	44.8	16	7.4	3.55	48.0	40	2.8			3
	♀	24.4	11.76	48.0	12	6.9	2.09	30.4	19	3.6			3
Partial length of 1st primary	♂	-3.9	1.48	37.9	16	4.0	1.66	41.5	40	6.5			2
	♀	-3.4	1.84	52.6	11	3.7	1.89	51.1	19	5.0			3
Tail length	♂	53.5	1.90	3.5	17	55.9	2.26	4.0	72	53.4	1.75	3.0	11
	♀	49.7	2.12	4.3	17	51.0	2.50	4.9	56	48.4	2.32	4.8	7
Tarsus length	♂	17.8			2	19.9	1.01	5.1	5	19.4	0.54	2.8	6
	♀	17.6			3	18.9			2	18.5			2
Foot span	♂	23.9			2	25.7	0.98	3.8	7	—			0
	♀	24.4	0.82	3.4	7	25.3	0.59	2.3	6	24.1			2
Bill length	♂	12.8			2	12.0	0.61	5.1	8	11.5	0.32	2.8	8
	♀	12.6	0.75	6.0	7	11.9	0.66	5.5	6	10.9			2
Bill depth	♂	3.2			2	3.2	0.16	5.0	5	—			0
	♀	3.2			3	3.0			2	2.8			2
Bill breadth	♂	3.6			2	3.7	0.10	2.7	5	—			0
	♀	3.7			3	3.7			2	3.7			2
Wing/tail length ratio	♂	1.48	0.049	3.3	17	1.28	0.052	4.0	72	1.25	0.036	2.8	11
	♀	1.51	0.058	3.8	17	1.29	0.023	1.8	53	1.23	0.056	4.5	7
Wing/tarsus length ratio	♂	4.44			2	3.66	0.169	4.6	5	3.45	0.096	2.8	6
	♀	4.22			3	3.49			2	3.27			2
Bill length/depth ratio	♂	4.01			2	3.78	0.138	3.7	5	—			0
	♀	3.95			3	4.00			2	3.95			2
Bill length/breadth ratio	♂	3.53			2	3.28	0.131	4.0	5	—			0
	♀	3.29			3	3.23			2	2.95			2

ruler placed on the base of the tail while this was gently pulled.

The *tarsus* (tarsometatarsus) length was measured using a caliper to the nearest 0.1 mm from the notch on the back of the intertarsal joint to the lower edge of the last complete scale before the toes diverge (Svensson 1975).

The *foot span* was measured from the tip of the middle claw to the tip of the hind claw (Leisler 1977).

The *bill length*, *depth* and *breadth* were recorded to the nearest 0.1 mm with a slide caliper. The length was recorded from the tip to the skull, the depth and the breadth at the posterior ends of the nostrils (see Svensson 1975).

All measurements were made by myself in M \ddot{o} ggingen. Of all birds in Lammi, 200 willow warblers, 43 wood warblers and 13 chiffchaffs were measured by me. Thirty-nine of the other 67 birds were measured at least once by T. Solonen, and the remaining 28 birds by four other ringers with less experience. We tried to standardise the measuring techniques by training. To confirm the repeatability of the wing measurements, I compared the records of willow warblers measured by me on several occasions, or by me and another measurer. In 51 % of 79 cases the result was the same, and in a further 41 % of the cases the difference was only ± 1 mm, which is fully acceptable because of the possibility of different rounding off to the nearest mm (no systematic trend was found in rounding off). Many comparisons were also done on birds measured repeatedly in different years, and in different phases of the season, when the birds may have had differentially worn feathers. The measurements were repeatable when birds with badly worn wings were excluded. The tail length measurements were not as repeatable, which results in a greater standard deviation of the mean, and therefore I used only my own records. Tarsus and beak measurements were done only by me and another ringer, foot span measurements only by me.

The stage of breeding was known exactly for many birds from records of egg-laying, or hatching of their young. If the nest was not found before the nestling period, the age of the nestlings was determined from their wing lengths (Tiainen 1978, see also 1983a).

4. Results

4.1. Morphometric characteristics

Results of measurements are presented in Table 1 for Lammi and in Table 2 for Radolfzell. For females, only weight records from before May 27 and June 20 — August 3 were used in order to

Table 2. Morphometric characteristics of willow warbler (*N* = 16) and chiffchaff (*N* = 35, except bill length where *N* = 32) males in Radolfzell. Explanations as in Table 1.

Characteristic	<i>Ph. trochilus</i>			<i>Ph. collybita</i>		
	\bar{x}	$\pm SD$	CV %	\bar{x}	$\pm SD$	CV %
Weight	9.48	± 0.594	6.3	7.87	± 0.337	4.3
Wing length	70.1	± 1.43	2.0	62.3	± 1.63	2.6
Wing pointedness	0.55	± 0.040	7.3	0.36	± 0.042	11.8
Wing symmetry	6.6	± 1.38	20.8	2.1	± 0.61	29.5
Partial length of 1st primary	4.1	± 1.33	32.8	6.5	± 1.13	17.5
Tail length	54.0	± 1.81	3.3	51.3	± 1.75	3.4
Tarsus length	20.0	± 0.40	2.0	20.1	± 0.65	3.3
Bill length	12.4	± 0.50	4.1	11.6	± 0.52	4.5
Wing/tail length ratio	1.30	± 0.025	1.9	1.22	± 0.031	2.5
Wing/tarsus length ratio	3.50	± 0.101	2.9	3.11	± 0.106	3.4

Table 3. Male/female ratios of some morphometric characteristics in adult *Phylloscopus* warblers in Lammi. Means from Table 1 were used. Level of significance (*P*) of the difference between means of males and females also shown where a test was possible (t-test).

Characteristic	<i>Ph. sibilatrix</i>		<i>Ph. trochilus</i>		<i>Ph. collybita</i> ¹	
	ratio	<i>P</i>	ratio	<i>P</i>	ratio	<i>P</i>
Weight	1.01	NS	1.12	0.001	1.10	0.01
Wing length	1.06	0.001	1.09	0.001	1.11	0.001
Tail length	1.08	0.001	1.10	0.001	1.11	0.001
Tarsus length	1.01	—	1.06	—	1.05	—
Foot span	0.98	—	1.02	NS	—	—
Bill length	1.02	—	1.01	—	1.06	—
Bill depth	1.00	—	1.07	—	—	—
Bill breadth	0.97	—	1.01	—	—	—

¹ Ratios calculated from Schönfeld (1978; *N* = 43 for males and 74 for females): wing length 1.12, tail length 1.11, tarsus length 1.06.

avoid the inclusion of gravid females and therefore an increased mean weight (Tiainen, unpubl.).

Sexual dimorphism

Many characters of all three warbler species were sexually dimorphic (Tables 1 and 3, Figs. 1 and 2). This sexual difference becomes evident in the wing length and weight already in nestlings under 10 days old (Tiainen 1983b). The sexual

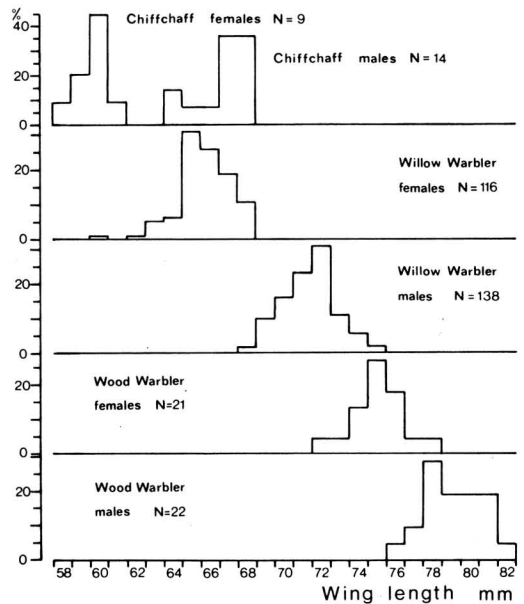


Fig. 1. Frequency distribution of the wing length of *Phylloscopus* warblers.

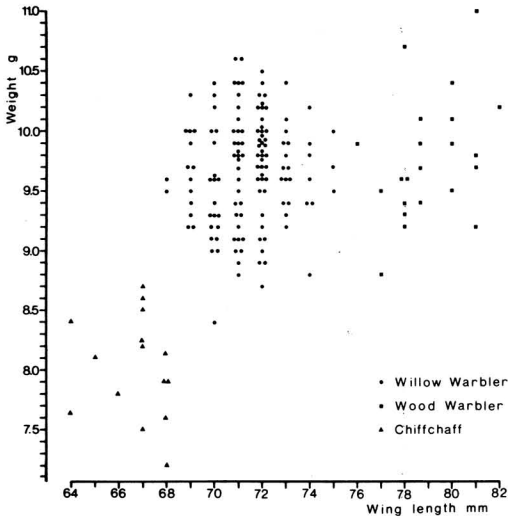


Fig. 2. Relationship between wing length and weight in males of *Phylloscopus* warblers.

differences were greatest in characters related to body size, i.e. in weight (willow warbler and chiffchaff), and wing and tail lengths (all three species). The difference between the sexes tended to increase with decreasing body size, i.e. the chiffchaff showed the highest degree of sexual dimorphism. My results on the sexual dimorphism of the chiffchaff are based on scanty data but are strongly supported by the measurements of Schönfeld (1978; see Table 3).

Intrasexual variation

The intrasexual variation of all characters could not be examined with the available data. Of linear measurements, the relative length of the first primary, as well as lengths of other primaries used to calculate the wing form indices, were very variable (Table 1, Fig. 2). The wing length varied less than any other character (Table 4). The greater variability in the tail than in the wing length may be due to the less accurate measurement technique (see Methods). The coefficients of variation for tail, tarsus and bill lengths may be reduced in male chiffchaffs because the skewed wing length distribution suggests that the sample includes mainly large individuals (see Fig. 1). Intrasexual variation of the other characters did not differ significantly in pairwise comparisons. There were no consistent interspecific differences in the intrasexual variation of different characters (exception: male chiffchaffs, see above).

Table 4. Results of tests on whether the variability of the wing length is smaller than that of other traits. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, — = $P > 0.05$, no sign = test not possible. Coefficients of variation from Table 1 were tested with *F*-statistics (Lewontin 1966). Variation in weight was not compared because of different dimensionality (CV_{weight} may be up to $3CV_{wing}$ depending on the perfectness of correlation between the weight and the wing length; Lande 1977).

Characteristic	<i>Ph. sibilatrix</i>		<i>Ph. trochilus</i>		<i>Ph. collybita</i>	
	♂	♀	♂	♀	♂	♀
Tail length	**	***	***	***	—	**
Tarsus length			***		—	
Foot span		*	**	—		
Bill length		***	***	***	—	
Bill depth		**				
Bill breadth			—			

The mean wing length of returning males and females of the willow warbler did not differ from their means when breeding for the first time.

Interspecific differences

Morphologically all the three warbler species were similar. In my measurements, they usually formed a regular order in which the willow warbler fell between the wood warbler and the chiffchaff, but the tail and tarsus lengths and the foot span of the wood warbler deviated from this pattern (Table 1). My data do not allow proper multivariate analysis because all measurements were taken from only a few individuals. Consequently, the different measurements are treated separately below.

The wood warbler was the largest, the willow warbler intermediate, and the chiffchaff the smallest species, as indicated by the weights and wing lengths (Table 1, Figs. 1 and 3). The weights and wing lengths did not, however, correlate linearly within the genus (Fig. 3). The weight of the willow and wood warblers overlapped greatly, but the species differed in wing length. This was due to the sharper, more pointed and more asymmetrical wing tip in the wood warbler (Fig. 2 and Table 1). On the other hand, the willow warbler and the chiffchaff differed in weight (Table 1 and Fig. 3), but the wing length of female willow warblers and male chiffchaffs overlapped (Fig. 1 and Table 1). The wing of the chiffchaff was more symmetrical and less pointed than that of the willow warbler, but these species did not differ much from each other compared to their differences from the wood warbler (Fig. 2 and Table 1).

In relation to body size, the tail and tarsal length and the foot span of the wood warbler were less than in the willow warbler and in the chiff-

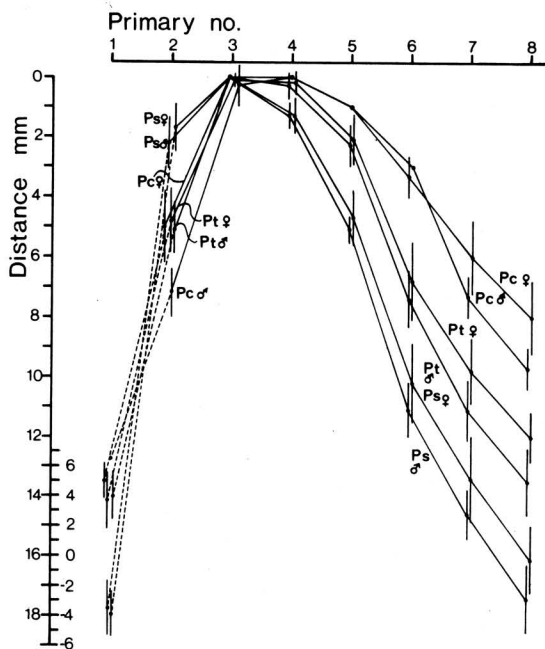


Fig. 3. Distance of the first primary from the tip of primary coverts (scale on the right side of y-axis), and distances of primaries 2-8 from the tip of the wing (scale on the left side) in the wood warbler (Ps), willow warbler (Pt), and chiffchaff (Pc).

chaff. However, absolute measurements were quite similar in the large wood warbler and the small chiffchaff (Table 1). The pattern of bill length was similar to that of body size, i.e. the wood warbler had the longest, and the chiffchaff the shortest bill (Table 1). Accordingly, the wood warbler had the broadest, and the chiffchaff the narrowest bill, as indicated by the length/breadth ratio (Table 1). The absolute depth of the bill seems to have decreased slightly from the wood warbler through the willow warbler to the chiffchaff. The relative depth was similar in all three species, as indicated by the length/depth ratio (Table 1).

To confirm the above result, which suggested that the form of the wood warbler is different from that of the willow warbler or chiffchaff, the linear measurements were transformed into measurements independent of size by dividing them by the cube root of the body weight (see Amadon 1943, Bairlein 1981, cf. also e.g. Leisler 1980). Also in relation to the body size, the wood warbler had a clearly longer wing, shorter tail, tarsus and foot span, and a somewhat longer beak than the willow warbler or chiffchaff (Table 5).

Table 5. Linear measurements of *Phylloscopus* warblers in Lammi standardised by dividing the original figures by the cube root of the weight.

Characteristic	<i>Ph. sibilatrix</i>		<i>Ph. trochilus</i>		<i>Ph. collybita</i>	
	♂	♀	♂	♀	♂	♀
Wing length	37.0	35.2	33.5	32.0	33.1	30.5
Tail length	25.0	23.3	26.3	24.9	26.5	24.7
Tarsus length	8.3	8.4	9.3	9.2	9.6	9.4
Foot span	11.2	11.5	12.1	12.3	—	12.3
Bill length	6.0	5.9	5.6	5.8	5.7	5.6
Bill depth	1.5	1.5	1.5	1.5	—	1.4
Bill breadth	1.7	1.7	1.7	1.8	—	1.9

Morphometric characteristics of southwest German warblers

The measurements of some characteristics of southwest German willow warbler and chiffchaff males are presented in Table 2. These Central European warblers were smaller than those in Lammi, but the difference was greater in the chiffchaff than in the willow warbler. In relation to body size, the southwest German chiffchaffs had a shorter wing and tail, but a longer tarsus than the Finnish ones (Tables 5 and 6). The Finnish chiffchaffs also had a more pointed and more symmetrical wing tip than the Central European ones (Tables 1 and 2). Similarly, the southwest German willow warblers had a shorter tail, but a longer bill and less symmetrical wing tip than the Finnish ones. However, all these differences were only slight.

4.2. Ecological correlates of the body size of willow warbler males in Lammi

Mate selection

The wing length of those willow warbler males whose exact phase of breeding was known were plotted against the date of the first egg in the nest to examine whether large males obtained a mate earlier than small ones (Fig. 4). A close correlation

Table 6. Linear measurements of willow warbler and chiffchaff males in Möggingen standardised by dividing the original figures by the cube root of the weight.

Characteristic	<i>Ph. trochilus</i>	<i>Ph. collybita</i>
Wing length	33.1	31.3
Tail length	25.5	25.8
Tarsus length	9.4	10.1
Bill length	5.9	5.8

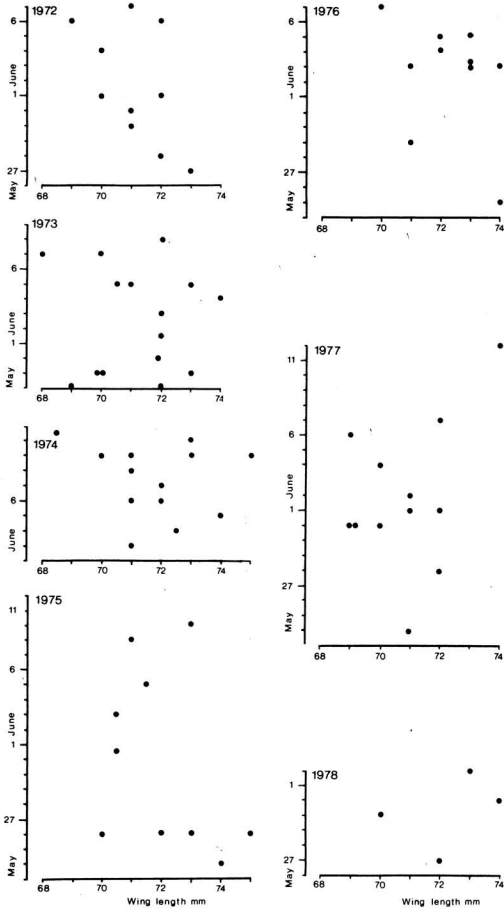


Fig. 4. Correlation between the wing length of willow warbler males and the date of the first egg in the nest in different years.

between the formation of a pair bond and the beginning of breeding was assumed. This assumption presumes that the first breeding attempts can be separated not only from genuine second clutches, but also from repeated attempts after failure of the first attempts. Because the accurate breeding history of each pair was not always known, I excluded only very late nests from the analysis. The asynchrony of commencement in known nests (especially in 1975 and 1977) indicates that the first and other attempts could not always be separated.

A significant negative correlation ($P < 0.05$) between the male wing length and the date of the first egg was found in 1972, and also in 1976 if the two earliest nests were excluded (this is justified because there was a long cold spell at the end of May in this year which interrupted the arrival of

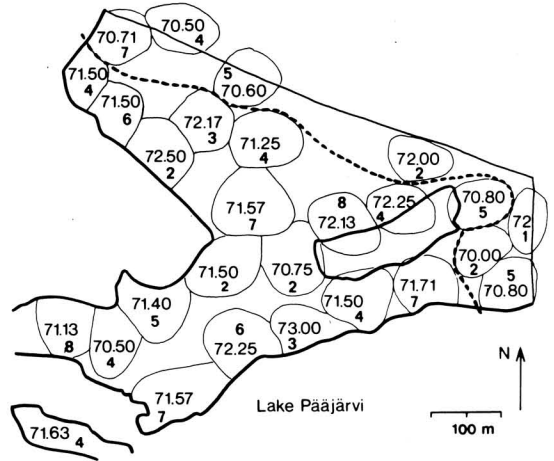


Fig. 5. Mean wing length of willow warbler males in various territories in 1972-1977 (second figures give N). The overall mean in the spruce-dominated part of the study area (east and north of the broken line; 70.7 ± 1.27 (SD) mm, $N = 26$) was significantly smaller ($t = 2.798$, $P < 0.01$) than in the deciduous-dominated part (south of the broken line; 71.6 ± 1.42 mm, $N = 95$). Thick line shows where the study forest borders on open habitats, or the lake.

females and all breeding activities of such pairs which had not yet commenced) (see Fig. 4). In the other year, no significant correlations could be found.

Pair formation was nonassortative as to individual size in the population (there was no correlation between male and female wing lengths of established pairs).

Between-habitat body size differences

To test whether there were differences in the size of willow warbler males in different parts of the study area, the wing lengths of the occupants of 27 different territories (whose locations were persistent from year to year) were compiled from the 7 years of study. Not all territory owners were trapped and measured, and many males were on the same or a nearby territory in two or more years. Not all sites of territories were occupied every year, and territory boundaries did not always fully coincide with those presented in Fig. 5. A total of 121 records or an average of 4.5/territory were available. Means calculated for each territory suggested that owners in the spruce-dominated part of the study area had shorter wings than those in the deciduous-dominated part (Figs. 5 and 6). Means of the pooled data from these two sub-areas were significantly different ($t = 2.926$, $P < 0.005$, $df = 119$).

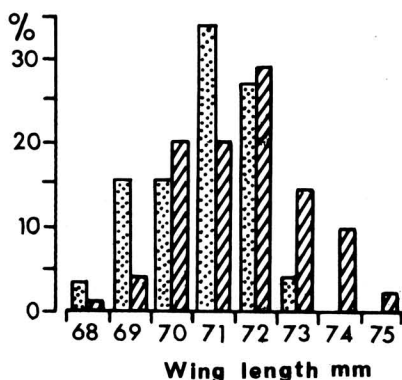


Fig. 6. Frequency distributions of the wing of willow warbler males in the spruce-dominated (stripped) and deciduous-dominated (hatched) parts of the study area.

Site tenacity

There was a difference in the return to the territory of the previous year between larger and smaller males in the deciduous part of the study area (Table 7). The males returning to the same or adjacent territory had a longer wing length (71.9 ± 1.44 , $N = 22$) than those returning to a more distant territory (70.2 ± 0.58 , $N = 4$; $t = 2.236$, $P < 0.05$). The only male moving from the spruce-dominated part to the deciduous-dominated one was larger than the average in the population, and was one of the largest in the spruce-dominated part. The longest observed distance moved by a territorial male between two successive years was by a small male (wing length

Table 7. Relationship between the size of willow warbler males (indicated by the wing length) and the tenacity to the territory of the previous year. Figures indicate numbers of observations.

Wing length mm	Southern part		Northern and eastern part	
	same or neighbouring territory	more distant territory	same or neighbouring territory	more distant territory
68	—	—	1	—
69	1	—	—	1
70	2	3 ^{1,3}	1	—
71	7	1 ³	—	—
72	3	—	2	1 ²
73	6	— ³	—	—
74	3	—	—	—
75	—	—	—	—

¹ Returned to the northern part; previous-year territory was occupied by two larger males.

² Returned to the southern part.

³ Apart from the males indicated, one male which was absent in the second year returned in the third year.

70 mm) from the deciduous-dominated to the spruce-dominated part (600 m). Its territory from the previous year was occupied by two larger males (wing lengths 72 and 74 mm).

5. Discussion

5.1. Sexual dimorphism

The intraspecific morphological variation in all three species was increased by sexual dimorphism. Male/female character ratios similar to those in Table 3 can be calculated from, or were calculated by, Salomonsen (1928), Niemeyer (1969), Bährmann (1976), and Fongstad & Hogstad (1981) for the European subspecies *trochilus* and *acredula* of the willow warbler.

Whether or not sexual dimorphism reduces intraspecific (intersexual) competition (e.g. Van Valen 1965, Selander 1966, Rothstein 1973a, b, Hogstad 1978) remains open, because the bill did not exert the same degree of dimorphism as characters more related to the body size (Table 3; this was found also by Fongstad & Hogstad 1981). In addition, intrasexual variability of the bill length was larger than that of the wing length (Table 4). It may be noted, however, that Hespeneide (1971) found that the mean (insect) prey size increased with predator size, but not clearly with bill size, within each foraging type of some flycatchers, vireos, and swallows. In birds, traits related to the body size are often more dimorphic than those related to the food (e.g. Johnston & Klitz 1977, Smith & Zach 1979, Wiens & Rotenberry 1980). Theoretically, neither intraspecific nor interspecific differences of small predators such as *Phylloscopus* warblers should imply any great differences in mean prey size or prey size distributions (Schoener 1969, Wilson 1975). Schoener's model also predicts that feeding consequences should not select for markedly increased sexual dimorphism in warbler-like solitary predators which do not spend a large proportion of their feeding time in pursuing.

While competitive avoidance may have played some role in the evolution of sexual dimorphism in the willow and wood warblers and the chiffchaff (there is no direct or indirect evidence for this hypothesis), Darwinian sexual selection (e.g. Selander 1965, 1972, Trivers 1972, Halliday 1978, Searcy 1979b, Weatherhead 1980) is supported somewhat by the present results. Observations on the habitat distribution and differential site-tenacity among willow warbler males of different sizes (see Sect. 5.2) show that there is competition for preferential sites. The spruce-dominated parts of the study area, however, were

by no means marginal habitats for the willow warbler. Their productivity is also high. Consequently, the start of laying was not significantly later there than in the deciduous part, and the reproductive output did not differ between the two parts of the study area (Tiainen 1983a).

Early pairing may be advantageous for a male if young from early nests survive better than those from late ones (cf. the great tit *Parus major*, e.g. Perrins 1979, and the chaffinch *Fringilla coelebs*, Payevski 1981), and because, in the case of nest losses, there may still be enough time to make a repeated attempt (early beginning of breeding becomes especially important as the time is apparently short for the warblers in the northern summer; e.g. Tiainen 1981). Because the mate is chosen by the female, characteristics proving vigour (and good fitness) of the male, like large body size, will be favoured (Searcy 1979a). In the willow warbler population studied, it was not possible to demonstrate any advantage of large male body size in terms of earlier beginning of breeding (Fig. 4).

We have a few observations of bigamy in the willow warbler, and also indications that bigamy may be a common feature in the breeding systems of the chiffchaff (J. Tiainen, J. Mehtälä & I.K. Hanski, unpubl., T. Wesołowski, pers. comm., see also Schönfeld 1978), as it is in the wood warbler (Aschenbrenner 1966, Fouarge 1968, Herman 1971, Wesołowski 1980). Sexual selection for larger male size should be strong in polygamous species. The situation is not consistent in *Phylloscopus* warblers, where the degree of dimorphism is least in the wood warbler (Table 3). Compared with the chiffchaff, the strategy for bigamy is, however, different in the wood warbler males, as it is in the pied flycatcher *Ficedula hypoleuca* (von Haartman 1951), another passerine species with no notable degree of sexual size dimorphism. In these species the males establish a new territory after the first female is engaged in breeding affairs. This does not necessarily select for increased body size. The chiffchaff males establish large territories where both/all females breed.

At least one probable opposing factor can be suggested to limit the body size of willow warbler males. The present size of *Phylloscopus* warblers seems to be relatively safe from predation. Their proportions in the diet of the three potential predators, the pygmy owl *Glaucidium passerinum*, the Tengelmalm's owl *Aegolius funereus*, and the sparrow hawk *Accipiter nisus*, are lower than their availability in Finland. Moreover, the goldcrest *Regulus regulus* (5–6 g) and many species weighing 9–13 g were preyed upon in the same proportions as their availability (the goldcrest only be the pygmy owl), and many species weighing 11–16 g

more often (Kellomäki 1977, Korpimäki 1981, Sulkava 1972, who also checked the prey list from remains by collecting data at nests before the prey animals were eaten). In Central European studies on the food of the pygmy owl (see Kellomäki 1977 for references) and sparrowhawk (Uttendörfer 1939, 1952, Opdam 1975 and references therein), the proportion of *Phylloscopus* warblers is also always low. Only occasionally are *Phylloscopus* warblers caught by some larger predators (e.g. *Strix aluco*, Mikkola 1970, *S. uralensis*, Eskelinen & Mikkola 1972). I argue that the low energetic profitability of small *Phylloscopus* warblers is the reason for their rarity as prey, because they are probably not less conspicuous than other forest passerines, and may be equally available.

5.2 Territorial systems and habitat distribution

Fretwell & Lucas (1969) and Fretwell (1972) presented two alternative models to predict habitat distributions of birds. The ideal free distribution model predicts that birds first invade the most suitable habitat, the suitability of which for further newcomers then declines after every new settler. After the suitability of the first habitat has declined to the level of the second most suitable habitat, further newcomers may choose between either of the two habitats, whose suitabilities are simultaneously declining towards the suitability level of the third habitat, and so on. The alternative ideal despotic distribution model predicts that stronger residents of the more suitable habitat force weaker newcomers to accept territories in less preferred habitats before the suitabilities of these habitats have become equal. The test conducted by Lundberg et al. (1981) supported the latter model in the pied flycatcher *Ficedula hypoleuca*.

Movements of territorial willow warbler males between successive years and their smaller body size in the spruce-dominated than in the deciduous or mixed habitats in Lammi also agree with the ideal despotic distribution model (see Table 7 and Fig. 5). This was also supported by the results of Ebenman & Nilsson (1981) who found that willow warbler males were larger on the mainland than on small lake islands in southern Sweden. The islands probably formed a suboptimal habitat for the willow warbler, as collection of flying insects showed that the food abundance was lower there and because of this the density of birds was more variable than on the mainland. The skewed wing length distribution of chiffchaff males occupying territories in the study area suggests that the largest males are best able to settle down there and that, consequently, also

this species would fit the ideal despotic model (the wing length distribution of these territorial males was similar to that in Fig. 1, which includes some early migrants). The chiffchaff populations breeding in English farmland habitats also fitted the habitat distribution models. However, whether they fitted the ideal free model or the ideal despotic model was not tested (Osborne in O'Connor 1981).

In the *Phylloscopus* species studied by me in Lammi, there seems to be no interspecific territoriality between the wood warbler and the willow warbler or the chiffchaff. The situation between the willow warbler and the chiffchaff is not clear. I have no observations of direct hostile encounters, but in a few cases early arriving chiffchaff males occupied a territory in an area where there had usually been a willow warbler territory (in Finland, the chiffchaffs arrive about one week before the willow warblers; see Tiainen 1979). They later retreated after the arrival of a willow warbler male (J. Tiainen, J. Mehtälä & I. K. Hanski, Unpubl.). It cannot be excluded that this has been the result of territorial conflicts between them, taking into account the fact that rather few encounters during a spring may be sufficient to result in spatial segregation between species, and that selection should favour the avoidance of dominant individuals when the outcome is highly predictable (Morse 1974, Maynard Smith & Parker 1976, see also Morse 1976, Murray & Gill 1976). Thus, it can be hypothesised that the ideal despotic distribution model can also predict the outcome of territorial systems between the willow warbler and the chiffchaff in Finland.

5.3. Morphological relations between *Phylloscopus* warblers

Hutchinson (1959), Schoener (1965), Diamond (1973, 1975), and others have observed that the linear measurements of congeneric species coexisting in common habitats tend to differ by at least 1.2–1.4 : 1.0 (1.3 rule), and the weights by some 2.0 : 1.0 (see, however, Wiens & Rotenberry 1981, Simberloff & Boecklen 1981, Wiens 1982). Differences between even the largest wood warbler and the smallest chiffchaff were smaller (Table 8). Thus, the size pattern suggests that, if the above statement holds, the *Phylloscopus* warblers studied are not segregated enough to divide food resources according to prey size. The morphology of the wood warbler, however, differed in many respects from the other two species. These differences in the shape of the wing tip, and in the relative length of wing, tail, tarsus,

Table 8. Interspecific character ratios of *Phylloscopus* warblers (Ps, Pt Pc refer to wood warbler, willow warbler and chiffchaff, respectively).

	Weight	Wing length	Bill length
Lammi			
Ps ♂ / Pt ♂	1.01	1.11	1.07
Ps ♂ / Pc ♂	1.19	1.19	1.11
Pt ♂ / Pc ♂	1.18	1.07	1.04
Ps ♀ / Pt ♂	1.00	1.05	1.05
Pt ♀ / Pc ♂	1.06	0.99	1.03
Radolfzell			
Pt ♂ / Pc ♂	1.20	1.13	1.09

and foot span should be important to movement both in flight and on foot in the foliage (Norberg 1979). On the other hand, the willow warbler and the chiffchaff were more similar. The multivariate description by Bairlein (1981), based on 36 characteristics, also showed that among 38 European passerine species the willow warbler and the chiffchaff closely resembled each other with respect to the separate functional complexes of foot, feeding apparatus and flight apparatus, and also with respect to the overall morphology.

The morphological differences and similarities of the *Phylloscopus* warblers studied correspond with the observations on the feeding habits made in early May in the Białowieża National Park in eastern Poland (J. Tiainen, K. Vepsäläinen & E. Ranta, unpubl.). The willow warbler and the chiffchaff were similar to each other, while the wood warbler behaved plastically resembling the other two warbler species on cool cloudy, days and flycatchers (*Ficedula albicollis* and *F. hypoleuca*) on warm, sunny days. Similar observations on these warblers were made in Lammi (I. K. Hanski, J. Mehtälä & J. Tiainen, unpubl.). In fact, the wood warbler is peculiar in the whole *Phylloscopus* genus (about 30 spp.) for in "...its life history, *sibibatrix* is similar to other species of the genus, but its (morphological) properties suggest that it may be evolving into a separate adaptive zone. . ." (Gaston 1974).

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