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Morphological variation in sympatric and allopatric populations of European Willow Warblers and Chiffchaffs

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The geographical variation of Willow Warbler *Phylloscopus trochilus* and Chiffchaff *Ph. collybita* males was studied in Finland (sympatry, but separated by breeding habitat), SW Germany (sympatry, in the same habitats) and Hungary (Chiffchaff only). The 32 external characters measured were treated as three functional complexes, the flight apparatus, foot and feeding apparatus. In the Willow Warbler, there was little geographical variation although the German birds differed from the three Finnish populations in the size of the flight apparatus and the shape of the feeding apparatus, and there were also significant differences among the Finnish populations. In the Chiffchaff, the differences between the Finnish, German and Hungarian populations were clear, the Hungarian population being intermediate between the other two. The less marked geographical differences in the Willow Warbler morphology are assumed to be connected with the similarity of its habitats and migratory habits in Finland and Germany. Finnish Chiffchaffs, breeding in spruce forest, did not seem to have special morphological adaptations to this habitat. The morphological difference between the Willow Warbler and Chiffchaff was greater in Germany than in Finland. The geographical variation of the Willow Warbler is so slight that the appropriateness of the currently recognised subspecies may be questioned. In the Chiffchaff the variation is more extensive and recognition of subspecies has more justification.

1. Introduction

Two widespread Eurasian species of the large passerine genus *Phylloscopus*, the Willow Warbler *Ph. trochilus* and the Chiffchaff *Ph. collybita*, are superficially fairly similar in both morphology and ecology. Naturally there are interspecific character differences, but the species also differ largely in the amount of intraspecific geographic variation in many traits. Hence only three subspecies are usually recognised in the Willow Warbler, but 6–8 in the Chiffchaff (Ticehurst 1938, Williamson 1974).

In this paper we study morphological variation in the Willow Warbler and Chiffchaff in Northern and Central Europe, where both of them are common and abundant (or fairly abundant) breeding species. In this area, two subspecies of both species are usually recognised, the northern *Ph. t. acredula* and *Ph. c. abietinus*, and the southern *Ph. t. trochilus* and *Ph. c. collybita* (Ticehurst 1938).

Our analysis is based on field data from areas where

1) both species coexist, but mainly in different habitats (southern Finland),
2) both species coexist largely in the same habitats (southwestern Germany), and
3) only the Chiffchaff occurs (Hungary; south of the range of the Willow Warbler).

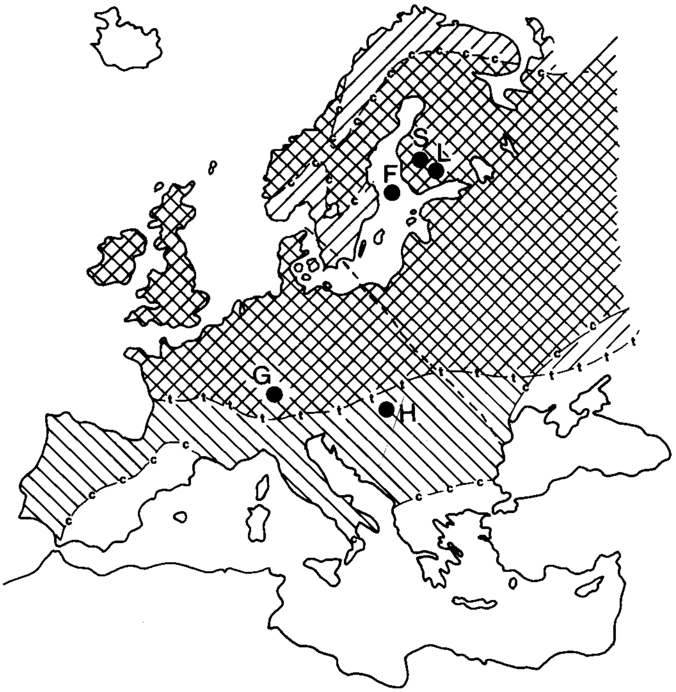


Fig. 1. Sampling sites (F = Föglö, S = Seitseminen, L = Lammi, G = SW Germany, H = Hungary) in relation to the European breeding ranges of the Willow Warbler (hatching from SW to NE) and Chiffchaff (hatching from NW to SE). The dashed line shows the approximate range limit between the subspecies of the Willow Warbler and Chiffchaff.

Using principal component analyses of 32 characteristics of the external morphology of three functional complexes, we shall try to relate the morphological variation with variation in the ecology of the species combined with possible geographical variation. For this purpose we have also analysed the Goldcrest *Regulus regulus*, a specialist of coniferous and especially spruce forests (e.g. Leisler & Thaler 1982).

2. Study areas, material and methods

2.1. Sampling

Our study is based on 212 Willow Warbler, 132 Chiffchaff and 7 Goldcrest males caught in 1981–87. The study areas are shown in relation to the ranges of the subspecies in Fig. 1. The birds were adult males defending their territories in the early part of the breeding season or feeding nestlings. The only exceptions were our sample of juvenile Chiffchaffs (n = 27), in which a few females may be included due to possible sexing errors (juveniles were sexed by wing length; see Tiainen & Hanski 1985) and three Goldcrest females. The Finnish breeding season study areas have been described by Tiainen (1982, Tiainen et al. 1983), and Haila & Hanski (1987), and the German site by Tiainen (1982, Tiainen & Bastian 1983). The Hungarian sites were in deciduous woods on the northwestern borders of Budapest and at Ocsa about 40 km south of Budapest. The Finnish juvenile Chiffchaffs were caught in August and September during the autumn migration and the Goldcrests in November from the local prewinter population in Southern Finland. The birds were released after measurements and individual marking with standard aluminium rings; breeding adults also received a unique combination of colour rings.

2.2. Measurements and statistical analyses

We made 32 measurements on each bird (Table 1). The methods of measurement are explained in Leisler (1977), Tiainen (1982), Svensson (1984)

Table 1. Characteristics measured on the birds. All measurements are in mm (wing area in sq. mm).

Flight apparatus

1. Length of closed wing
2. Square root of wing area calculated from outline of spread wing
3. Maximal wing breadth from wing outline
4. Tail length
5. Length of notch in inner web of second primary
6. Distance from tip of first primary to primary coverts.

7.–12. Distances between tips of the first (outermost) and fifth to eighth primaries (fifth not used in analyses of the Chiffchaff because it usually equals zero)

Foot

1. Tarsus length
2. Foot span between tips of middle and hind claws
3. Foot span between tips of middle and hind toes

4.–7. Lengths of toes
8.–11. Lengths of claws

Feeding apparatus

1. Bill length from tip to feathers
2. Bill length from tip to anterior edge of nostrils
3. Bill length from tip to edge of skull
4. Bill length from tip to corner of mouth
5. Bill height at hind edge of nostrils
6. Bill width at anterior edge of nostrils
7. Bill width at hind edge of nostrils
8. Bill width at corner of mouth
9. Length of longest rictal bristles

and in Table 1. We grouped the measurements into three functional complexes (Leisler 1977, Bairlein 1980): the flight apparatus (wing and tail), foot (foot and tarsus), and feeding apparatus (bill and rictal bristles).

The analyses were performed with the BMDP statistical package. We carried out principal component analyses of the morphological data with correlation matrices (Wiens & Rotenberry 1980, Somers 1986), taking each functional complex separately. As the values of the traits were approximately normally distributed (checked by plotting original variables against expected normal values), all the analyses were done on untransformed data (e.g. Morrison 1983, Schluter & Smith 1986). For the sake of brevity, the principal components of the flight apparatus will be denoted by W, those of the foot by F, and those of the feeding apparatus by B. These abbreviations are combined with 1, 2 or 3, which denote the first, second or third principal component of each of the functional complexes.

In comparisons of mean factor scores, a one-way ANOVA and Tukey multiple comparison test were used. When reporting a difference between two groups, we imply statistical significance of at least $P < 0.05$.

3. Patterns of morphological variation

In all the principal component analyses, the first PC axis of every functional complex was interpreted to represent mainly size (with minor shape variation), because the loadings on the variables were mostly high and positive (e.g. Pimentel 1979). In the case of the flight apparatus, however, wing length, breadth and area, and tail length can logically be considered to be the main size indicators. High loadings of feather tip distances from the wing tip represent shape, and Tables 2, 3 and 4 show that in all cases large wings are also sharp (note that positive loadings for primaries to WT indicate short feathers). In all the analyses, the second and third axes were related to shape (Tables 2, 3 and 4). The interpretation of the components was based on the magnitude and direction (positive or negative) of correlations between the morphological variables and principal components.

3.1. Willow Warbler

The morphological differences between the Willow Warbler populations were small. The only significant differences were found in the flight apparatus; the German population scored significantly smaller values for the first component than two of the Finnish populations (Fig. 2, cf. Appendix). In the other functional complexes no significant differences were found in the first component between the Willow Warbler populations.

W2 (Table 2) can be interpreted to represent shape, ranging from a long tail, and long broad rounded wings with long inner and short outer primaries at one end to a short tail, and short

Table 2. Factor loadings of morphological variables with Willow Warbler data. WT = wing tip, prim. = primary, BL = bill length, BW = bill width.

	Factor 1	Factor 2	Factor 3
Flight apparatus (W)			
Wing length	711	439	223
Wing breadth	464	530	319
Wing area	454	255	271
Tail length	367	596	309
Notch of 2nd primary	338	102	477
1st prim. to primary coverts	20	–441	739
1st prim. to WT	389	660	–486
2nd prim. to WT	22	418	–537
5th prim. to WT	574	–439	–172
6th prim. to WT	706	–487	–206
7th prim. to WT	808	–381	–190
8th prim. to WT	796	–353	–152
Cumulative % of variance explained	28.7	48.8	63.3
Foot (F)			
Tarsus	503	–253	–637
Foot span with claws	891	–18	–92
Foot span without claws	753	–461	–70
Hind toe	560	–476	–262
Inner toe	542	–460	148
Middle toe	566	–382	289
Outer toe	407	–390	637
Hind claw	605	556	–6
Inner claw	517	604	35
Middle claw	612	578	42
Outer claw	581	652	101
Cumulative % of variance explained	36.8	59.1	68.3
Feeding apparatus (B)			
BL to feathers	821	–139	60
BL to nostrils	822	–230	–64
BL to skull	740	–347	101
BL to mouth corner	850	–182	159
Bill height	231	529	487
BW at anterior edge of nostrils	493	691	–188
BW at hind edge of nostrils	449	684	–260
BW at mouth corner	162	–372	–578
Rictal bristles	– 23	–165	654
Cumulative % of variance explained	35.0	52.9	65.6

Table 3. Factor loadings of morphological variables with Chiffchaff and Goldcrest data. For symbols, see Table 2.

	Factor 1	Factor 2	Factor 3
Flight apparatus (W)			
Wing length	943	14	–180
Wing breadth	849	–146	–356
Wing area	884	–173	–298
Tail length	857	– 87	–342
Notch of 2nd primary	567	39	–304
1st prim. to primary coverts	–107	–789	– 85
1st prim. to WT	763	572	– 41
2nd prim. to WT	– 50	845	– 41
6th prim. to WT	691	–244	546
7th prim. to WT	622	0	698
8th prim. to WT	743	10	550
Cumulative % of variance explained	49.6	65.8	80.0
Foot (F)			
Tarsus	242	–426	752
Foot span with claws	864	– 94	259
Foot span without claws	723	–489	26
Hind toe	600	–421	–143
Inner toe	497	–422	–187
Middle toe	684	–301	–280
Outer toe	479	–293	–330
Hind claw	582	535	–242
Inner claw	677	563	3
Middle claw	624	400	360
Outer claw	593	683	31
Cumulative % of variance explained	37.9	57.8	67.5
Feeding apparatus (B)			
BL to feathers	653	502	
BL to nostrils	458	702	
BL to skull	726	246	
BL to mouth corner	795	217	
Bill height	180	–576	
BW at anterior edge of nostrils	719	–370	
BW at hind edge of nostrils	701	–443	
BW at mouth corner	730	–189	
Rictal bristles	–407	448	
Cumulative % of variance explained	39.3	58.8	

Table 4. Factor loadings of morphological variables with Willow Warbler and Chiffchaff data. For symbols, see Table 2.

	Factor 1	Factor 2
Flight apparatus (W)		
Wing length	974	19
Wing breadth	667	512
Wing area	810	256
Tail length	819	275
Notch of 2nd primary	630	223
1st prim. to primary coverts	–717	14
1st prim. to WT	941	66
2nd prim. to WT	–405	705
6th prim. to WT	927	–282
7th prim. to WT	941	–241
8th prim. to WT	946	–223
Cumulative % of variance explained	66.6	77.0
Foot (F)		
Tarsus	421	–158
Foot span with claws	883	118
Foot span without claws	803	–433
Hind toe	709	–372
Inner toe	643	–338
Middle toe	695	–395
Outer toe	505	–208
Hind claw	272	785
Inner claw	467	680
Middle claw	453	683
Outer claw	428	771
Cumulative % of variance explained	35.8	61.4
Feeding apparatus (B)		
BL to feathers	783	–333
BL to nostrils	838	–311
BL to skull	765	–324
BL to mouth corner	834	–241
Bill height	569	404
BW at anterior edge of nostrils	655	529
BW at hind edge of nostrils	594	553
BW at mouth corner	417	–168
Rictal bristles	–310	–439
Cumulative % of variance explained	44.1	59.0

narrow sharp wings with short inner and long outer primaries at the other. W3 adds to the symmetry of the wing, as it represents varying lengths of the feathers anterior to the wing tip (Table 2). The only significant difference in W2 was found between the German and one of the Finnish populations (Fig. 3).

F2 represents the gradient of long claws and short toes to short claws and long toes (Table 2). F3 refines the relationship between outer toe and tarsus length, having high loadings for long toe and short tarsi at the one end and short toe and long tarsi at the other (Table 2). One of the Finnish populations differed significantly from all the other populations on F2, and one Finnish population differed from the German and another Finnish population on F3 (Fig. 3).

In the analysis of the feeding apparatus, B2 represents an axis with short, stout bills at one end and long, slender bills at the other (Table 2). On B3, birds with a high bill which is narrow at the corner of the mouth and with long rictal bristles take their place at one end and birds with a low and broad bill and short bristles at the other. The shape of the bill was the most variable of the functional complexes. On B2, German birds differed significantly from all the Finnish populations, possessing longer and more slender bills. Two Finnish populations also differed from each other on B2, as the Lammi birds had shorter and stouter bills than the Seitseminen birds. On B3 the German birds differed from all the Finnish groups, having broader and lower bills with short rictal bristles (Fig. 3).

3.2. Chiffchaff

We performed the analyses on three populations, but the Finnish population was represented separately by adult territorial males and first-year males caught in late summer and early autumn when the autumn migration had already started (hence the juveniles may not be representatives of the local breeding population). The decision to use juveniles was made because we had few adult males from Finland, and it was expected that adults and juveniles would differ from each other only in wing variables, the latter not yet having undergone their first complete moult or possibly

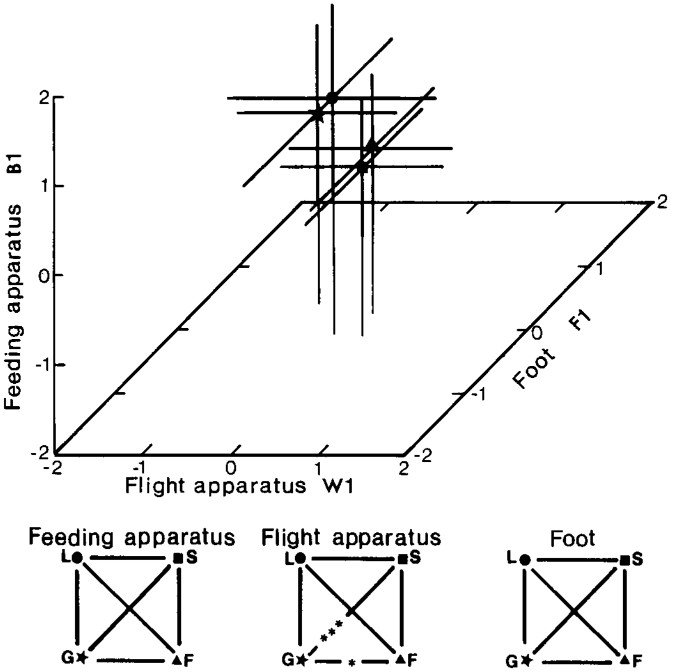


Fig. 2. Means ± SD (thick lines) of factor scores of Willow Warblers on the first axes of PCA of the three morphological functional complexes studied. Statistical significances of differences between population means (S = Seitseminen, F = Föglö, L = Lammi, G = German) shown in the lower part of the figure (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

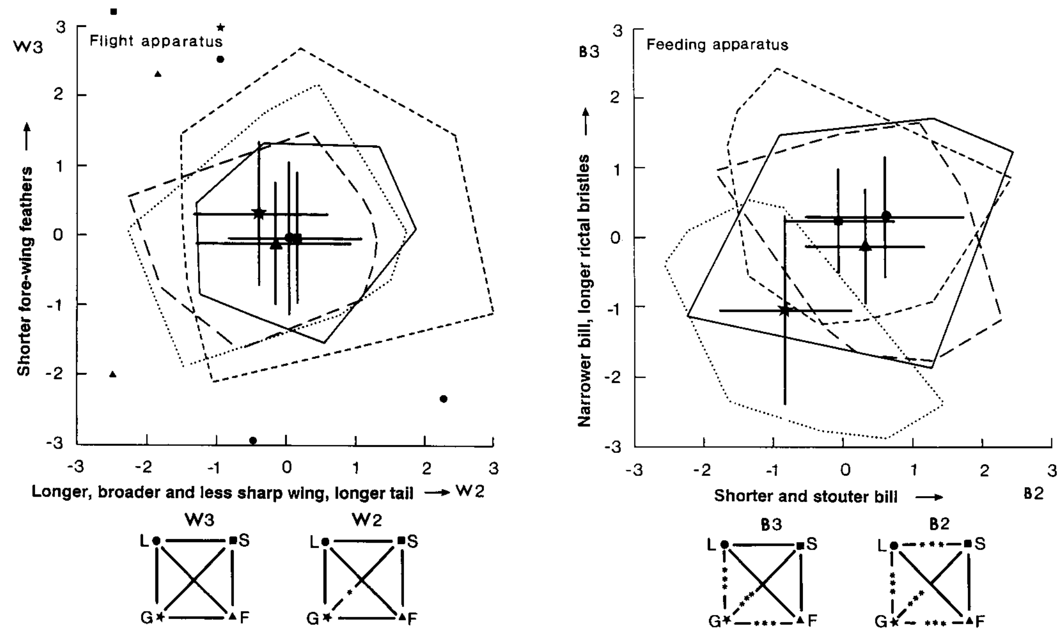
selective first-winter mortality. The dimensions of foot and bill can be supposed to be independent of age. We also included the Goldcrest, a specialist of spruce forests, which are the breeding habitat of Finnish Chiffchaffs, to find out whether there are any adaptive shifts in the Chiffchaff towards a morphology appropriate to spruces. However, we will not compare these two species in more detail in this paper. We chose the Goldcrest because its genus is close to *Phylloscopus*, and we use it only as an example of a species morphologically adapted to conifers (Leisler & Thaler 1982).

The morphological variation in the Chiffchaff populations was more extensive than in the Willow Warbler. The first component of all the functional complexes appears as a size factor with high positive loadings for almost all the variables (rictal bristles and two wing variables being the notable exceptions; Table 3). All the Chiffchaff groups differed significantly from each other in W1, except for the Finnish adults and juveniles (Fig. 4). The Finnish birds had the largest and the German birds the smallest flight apparatuses (cf. Appendix). It might be argued that the high cumulative percentage of variance explained by W1 can be due to the inclusion of the Goldcrest, but when the analysis was performed without that species, the proportion of variance accounted for by the principal components did not change; the main difference was that W2 and W3 were interchanged, and the interpretation of the new W2 was slightly changed.

As regards the foot, the German birds differed significantly from the Hungarian ones and the Finnish juveniles, but not from Finnish adults (Fig. 5). The German Chiffchaffs had the smallest feet but the longest tarsi (F1; see Appendix). The size of the feeding apparatus was larger in the German Chiffchaffs and their rictal bristles were shorter than in Hungarian birds and Finnish juveniles. The German birds also differed, though not significantly ($P < 0.10$), from the Finnish adults (Fig. 5, Appendix).

As regards the flight apparatus, W3 appears to be the main shape factor, representing narrow- and sharp-winged birds with a short tail at the one end and round-winged birds with a broad wing base and a long tail at the other (Table 3).

W2 places birds with short first and second primaries at one end and birds with long ones at



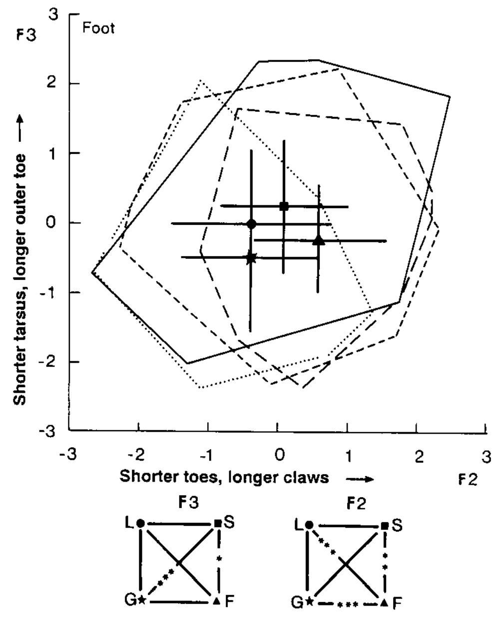


Fig. 3. Means ± SD of factor scores of Willow Warblers on the second and third axes of PCA of the three functional complexes studied. Except for the more deviating points (shown as small population-specific symbols), the lines (continuous = Seitseminen; long dashes = Föglö; short dashes = Lammi; dotted = German) show ranges in the factorial plane. For statistical significances, see Fig. 2.

the other (Table 3). On W3 Finnish adults differed from the remaining Chiffchaff groups, among which there were no significant differences (Fig. 5); the Finnish adults possess clearly sharper and narrower wings than the others. On W2 adult Chiffchaffs did not differ from the others, but the German and Hungarian birds differed from Finnish juveniles (Fig. 5), the juvenile Chiffchaffs having the shortest feathers at the fore edge of the wing. On W3, the Finnish adults resembled the Goldcrests.

In the foot analysis, F2 clearly places birds with relatively long claws and short toes at one end and those with short claws and long toes at the other (Table 3). On F3, the birds are mainly ordinated according to tarsal length, but to some extent also according to toes and claws. Having the largest scores on F2, the Hungarian Chiffchaffs differed from the Finnish juveniles and German birds (Fig. 5). The Hungarian Chiffchaffs had absolutely the longest claws and shortest tarsi (Appendix). On F3 the German birds differed from Hungarian birds and Finnish juveniles

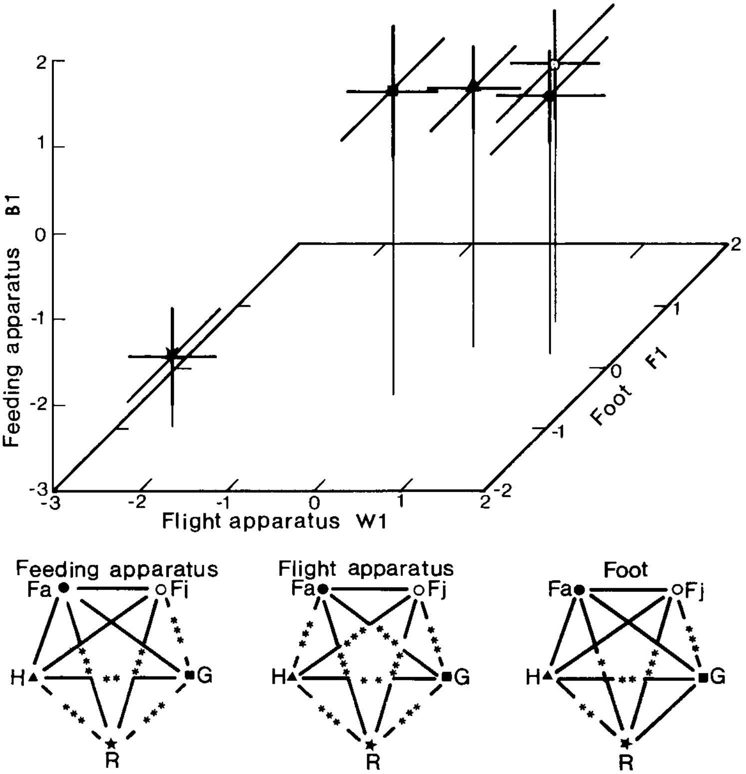


Fig. 4. Means ± SD (thick lines) of factor scores of Chiffchaffs (Fa = Finnish adults, Fj = Finnish juveniles, G = SW German, H = Hungarian) and Goldcrests (R) on the first axes of PCA of the three morphological functional complexes studied. For statistical significances, see Fig. 2.

(Fig. 5). Among Chiffchaffs the German birds had absolutely the longest tarsi (Appendix).

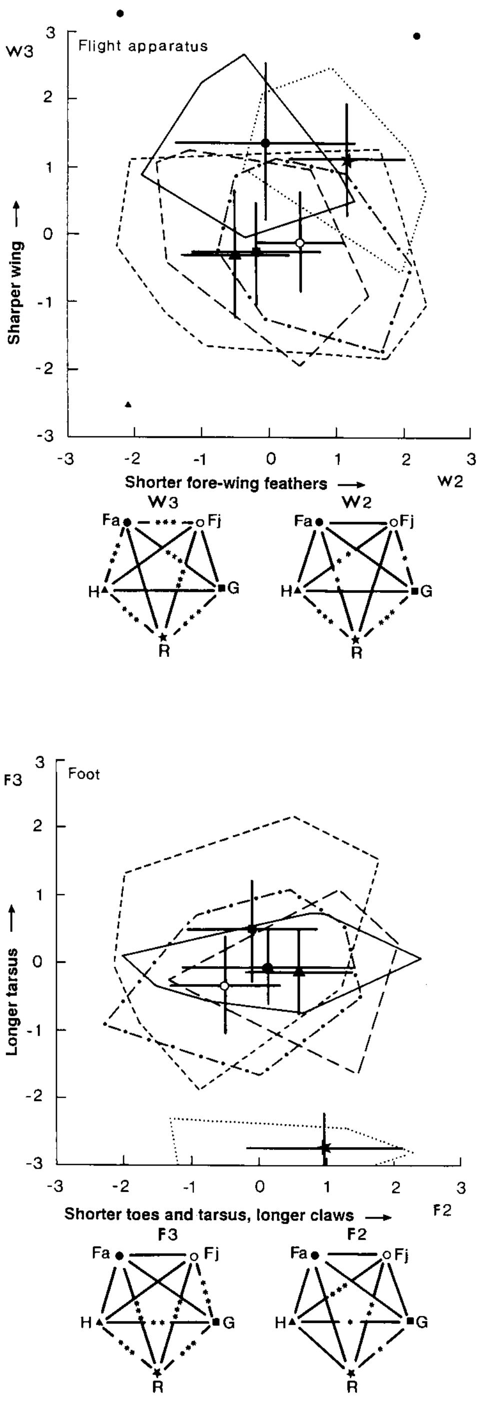
As regards the feeding apparatus, B2 places birds with a long and slender bill and long rictal bristles at one end and birds with the opposite characters at the other (Table 3). B3 did not significantly add to the cumulative percentage of the variance explained. The German birds differed on B2 from all the other Chiffchaffs and the Hungarian birds from the Finnish juveniles (Fig. 5). The Finnish Chiffchaffs, which had the shortest and stoutest bills and the shortest rictal bristles, were the most different from the Goldcrests.

4. Hypotheses for explaining the patterns

Let us summarise our main findings:

(1) There was little geographic variation in the Willow Warbler in either size or shape between S Finland and SW Germany. Two of the Finnish populations differed significantly in the size of the flight apparatus from the German population, but not in the size of the other two functional complexes (Fig. 2). Shape differences in the flight apparatus were found only between one Finnish and the German population (Fig. 3). In the foot morphology, shape differences were found between the German and some of the Finnish populations and among the Finnish populations as well (Fig. 3). The shape of the feeding apparatus differed most consistently between the German and Finnish populations, but some difference was also found among the Finnish populations (Fig. 3).

(2) In the Chiffchaff all three populations differed from each other in both size and shape. Between the Hungarian and Finnish populations size differences were found in the flight apparatus, but the German population showed size differences from both the Hungarian one and the Finnish juveniles in all three functional complexes, and from the Finnish adults in one com-



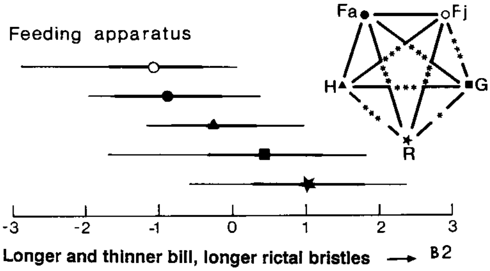


Fig. 5. Means ± SD of factor scores of Chiffchaffs on the second and third axes of PCA of the three functional complexes studied. Except for the more deviating points (shown as small population-specific symbols), the lines (continuous = Finnish adults, dotted and dashed = Finnish juveniles, long dashes = German, short dashes = Hungarian, dotted = Goldcrest) show ranges in the factorial plane. For statistical significances, see Fig. 2.

plex (Fig. 4). Wing shape differences existed between the Central European and either Finnish juveniles (W2) or adults (W3), but not between German and Hungarian Chiffchaffs (Fig. 5). Foot shape differences were found between the two Central European populations and between them and the Finnish juveniles (Fig. 5). In respect of the feeding apparatus, the German population differed from all others, but there was also a difference between the Finnish juveniles and Hungarian birds (Fig. 5).

How can these patterns be explained? Four types of explanations may be recognised (e.g. Zink & Remsen 1986): the differences between the populations may be

1) merely a developmental response to environmental conditions,
2) due to intra-individual seasonal or life-historic morphological variation,
3) adaptive to the conditions of the locality or region of the population, or
4) due to some other, non-adaptive, possibly random factors.

The last alternative lies outside the scope of this study.

4.1. Phenotypic patterns without genotypic components?

Most studies show that regional differences in birds have a genetic component. Whether there is also a significant environmentally determined component can only be discovered by means of manipulative experiments. Thus, James (1983) showed with transporting experiments that the size and shape variation of the Red-winged Blackbird *Agelaius phoeniceus* was partly produced by the local conditions of the growth area. However, in the Pied Flycatcher *Ficedula hypoleuca*, a species taxonomically, ecologically and life-historically fairly similar to *Phylloscopus* warblers, cross-fostering experiments between territories of varying quality showed that the heritability component of tarsus length was more significant than the environmental component (Alatalo & Lundberg 1986). Alatalo & Gustafsson (1988) showed that geographical differences in the Coal Tit *Parus ater* between Gotland and the Swedish mainland were inherited. The morphological characteristics of the Great Tit *Parus major* are also highly hereditary (van Noordwijk 1980, Boag & van Noordwijk 1987). For *Phylloscopus* warblers, the only comparisons available were made of the weight increment between N Swedish and S Finnish Willow Warbler chicks and between S Finnish and S German Wood Warbler *Ph. sibilatrix* chicks, and no significant geographical differences were found (Tiainen 1978).

4.2. Intra-individual variation?

After the juvenile growth has been completed, only the morphologies of the flight and feeding apparatuses are likely to vary during the lifetime of an individual passerine bird. The morphology of the feathered part of the flight apparatus varies because of wear and moults. In species which handle hard objects or substrates the bill is also likely to suffer from wear (Gosler 1987), but this does not affect our warblers.

Willow Warblers and Chiffchaffs have finished their juvenile growth by the time of autumn migration (Gwinner 1969, Winkler 1979, Tiainen 1983a). At that time they still possess their first wing and tail feathers, which are shorter and narrower than the ones developed after the first complete moult (Gwinner 1969, Svensson 1984). Willow Warblers undergo the first complete moult already in their first winter, but Chiffchaffs not before the second autumn (e.g. Svensson 1984). These moulting patterns cause intra-individual lifetime variation in the size and shape of the flight apparatus (e.g. Norman 1983). An additional factor is the wear of remiges and rectrices, which averages 0.1–0.3 mm/month in the Willow Warbler during the breeding season (Norman 1980).

We have ruled out most of the possible effect of the intra-individual component on our results, as we sampled mostly territorial males in the early part of the breeding cycle, with the exception of the Finnish juvenile Chiffchaff males, which were caught in the autumn. Hence all first-autumn juveniles and about 60% of spring males (corresponding to the annual mortality rate of adult males; Tiainen, unpubl., see also Tiainen 1983b) still possess their first primaries. This heterogeneity of the Chiffchaff samples may fully explain the shape difference of the flight apparatus (W3 in Fig. 5) of Finnish adults and juveniles, which is due to the relatively shorter sixth, seventh and eighth primaries of the adults (longer distance from the primary tip to the wing tip; Appendix).

Among the Finnish Chiffchaffs there is another source of between-group variation. The juveniles have not yet experienced their first winter, when they may be subjected to mortality disproportionate for their morphological characters (Johnston & Fleischer 1981). However, the only significant difference we found between the factor scores of Finnish juveniles and adults was in W3 (Fig. 5), which can be explained by the moulting pattern (see above). Hence we could not detect directional selection in the juvenile morphology.

Hence the only source of variation due to morphological changes during the lifetime of an average individual is the moulting pattern. This probably provides an adequate explanation of the difference between Finnish juveniles and adults in W3.

4.3. Adaptive geographic variation?

How do the ecological conditions experienced by the warblers vary? In the broad ecology of the species the breeding habitats of the Willow Warbler are fairly similar in all parts of the European range, whereas there is a major difference in the Chiffchaff habitats between N and Central Europe. The Willow Warbler inhabits all kinds of light deciduous forests or forests with an admixture of deciduous trees, mainly living at forest edges. The Chiffchaff dwells in the interior and edges of spruce forests or spruce-dominated mixed forests in N Europe, but in central and southern parts of Europe it lives in many kinds of light deciduous forests and woods, avoiding the interior parts. These habitat patterns are related to the migratory habits (Tiainen & Hanski, unpubl.): the Willow Warblers from the whole range are long-distance migrants to tropical Africa south of the Equator, but of the European Chiffchaffs, only the northern ones are long-distance migrants, overwintering in Africa south of the Sahara, while the Central European populations migrate to western Europe, the Mediterranean basin and Northern Africa.

On the basis of these ecological and migratory patterns one may predict that:

1) the Willow Warbler morphology will vary less than that of the Chiffchaff;
2) northern warblers, migrating longer migratory distances, will have longer and sharper wings (Leisler & Winkler 1985);
3) the Finnish Chiffchaffs will show morphological adaptations to their spruce-dominated habitats, while the Willow Warbler will not differ morphologically between Finland and Germany, since the breeding habitats are roughly similar;
4) if the Willow Warbler and Chiffchaff are ecological competitors (Tiainen 1983c, Tiainen et al. 1983), either
   a) the Hungarian Chiffchaffs will respond to the release from competition resulting from the absence of the Willow Warbler, or
   b) German Willow Warblers and Chiffchaffs will adapt morphologically to coexistence in same habitats.

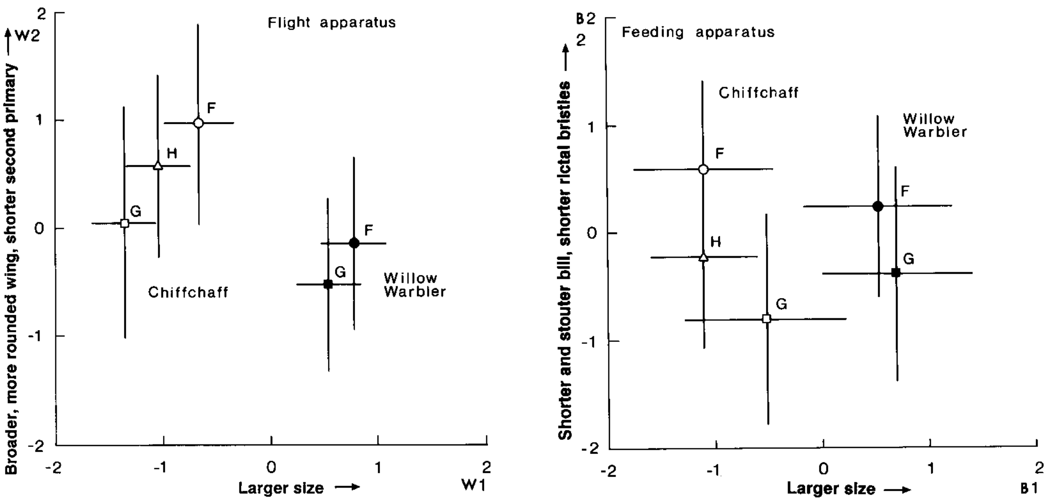
The first two predictions were supported by our results. In the Willow Warbler the average factor scores of the individual functional complexes differed little between SW Germany and S Finland and there were as large differences among the Finnish populations as between some of the Finnish populations and the German one. However, the flight apparatus of Finnish birds (in two populations) was larger than that of German birds. A slight trend was also apparent in the form of the flight apparatus when W2 and W3 were examined in combination (Fig. 3). The wing of Finnish Willow Warblers was longer, but not sharper than that of the German birds.

The third prediction is only partly fulfilled because the shape of the feeding apparatus of German Willow Warblers differs from that of all the Finnish populations. However, it is not at all clear whether this is an adaptive response to feeding conditions. The flight and foot apparatuses, which are used in moving in the habitats, do not show any clear patterns. In the Chiffchaff, the only character in which the Finnish Chiffchaffs resembled Goldcrests more than the German or Hungarian birds was the wing sharpness (W3). Hence the Finnish Chiffchaffs are probably not morphologically specialised to their habitat, as far as can be concluded from the weak similarity to the spruce-forest specialist Goldcrest, a representative of a closely related genus. This conclusion disagrees with the third prediction.

For the evaluation of the fourth prediction, we performed an additional PCA, in which the groups were Finnish and German Willow Warblers, and Finnish, German and Hungarian Chiffchaffs (Fig. 6).

If the first part of the fourth prediction were true, the Hungarian Chiffchaffs should show more variation than other Chiffchaff populations and/or deviate from them. This was mostly not the case, as they did not vary more, and they resembled the German Chiffchaffs in their flight apparatus and were intermediate between the Finnish and German birds in their feeding apparatus. Only in the foot morphology did they differ from other populations.

As regards the second part of the fourth prediction, it is interesting to compare the interspecific difference in Finland and in Germany. The difference is mostly greater in Germany. It may be noted that the difference in B2 was similar, but in the opposite direction. Except in F2, the Hungarian Chiffchaffs were intermediate between the Finnish and German Chiffchaffs. Hence the results support the prediction at least partly. However, there is another possible explanation for the



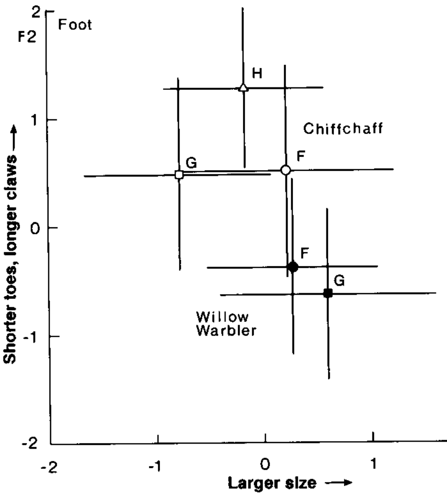


Fig. 6. Means ± SD of factor scores of Willow Warblers (black) and Chiffchaffs (open) on the first and second axes of PCA of the three functional complexes studied (F = Finnish, G = German, H = Hungarian).

differing German Chiffchaffs. Other factors than the impact of Willow Warbler competition may shape them, and the Hungarian birds may represent an intermediate population between the Finnish and German birds. If the Hungarian birds are different from the German birds because of release from competition, we might expect Chiffchaffs of other allopatric populations to differ from the German birds as well. This does not seem to be the case in a small sample of eight males measured in southern Cevennes in southern France by JT in spring 1988.

5. Subspeciation

Of our populations, the Finnish Willow Warblers belong to the subspecies *Ph. t. acredula* and the German ones to *Ph. t. trochilus*, and the Finnish Chiffchaffs to the subspecies *Ph. c. abietinus* and both the German and Hungarian ones to *Ph. c. collybita* (Ticehurst 1938; see Fig. 1). Ticehurst showed that, according to the plumage colouration, there were two extreme, stable forms, the darkest and most olive green and yellow *Ph. t. trochilus* in the west and the most grey-brown and white *Ph. t. yakutensis* in Far Eastern Siberia. "In Poland and South Sweden *t. trochilus* grades into a paler, brighter and a little larger form — *acredula* — which is more or less stable over the southern and western part of its distribution, but in the north from Finnmark to the Yenisei the form is unstable, some being quite as typical *acredula*, some almost as *yakutensis*, and every intergrade between these is found" (Ticehurst 1938: 38). To us it seems that there is only clinal variation in the plumage colouration in the whole range of the Willow Warbler (Tiainen 1991). Salomonsen (1945) supported the distinction of *Ph. t. trochilus* and *Ph. t. acredula* by demonstrating the change of plumage colouration from Central Europe to the Kola Peninsula, but we consider this change to be only a gradual cline. The measurements given by Ticehurst (1938) for the subspecies of the Willow Warbler do not differ significantly from each other. Ticehurst notes that *Ph. t. trochilus* is slightly smaller than *acredula*, which is slightly smaller than *yakutensis*, and Fonstad & Hogstad (1981) show that there is a gradual cline in the wing length from Southern to Northern Scandinavia. The morphological differences between the Central and Northern European Willow Warblers found by us are also small and mostly insignificant, and the differences among the Finnish populations are similar to those between the Finnish and German ones (see also Tiainen 1982, Tiainen & Hanski 1985). Hence it seems that all the geographical variation found in the Willow Warbler is minor and probably clinal (the latter probability cannot be tested with our own data from only two localities). In conclusion, it is difficult to support the division of the species into subspecies on the basis of the morphology, at least not in the western part of the range (Tiainen 1991). Salomonsen (1945), an advocate of the subspecific division, in fact also demonstrated a gradual cline in the plumage colouration of the Willow Warbler from northern Central Europe to the Kola Peninsula.

In the Chiffchaff differences between subspecies in both the morphology and colouration are more obvious than in the Willow Warbler (Ticehurst 1938). However, because of intergrades and overlapping of characters in the populations, it is difficult to determine the subspecies of single individuals of *Ph. c. collybita* and *Ph. c. abietinus* (Ticehurst 1938). Our results show that the morphological differences between the German and Finnish Chiffchaffs are fairly clear, but the Hungarian Chiffchaffs were intermediate, differing significantly in many respects from both the other populations. Whether these birds represent an intergradation zone between the two subspecies, also recognised by Ticehurst in the Silesian Carpathians, or a basic "*Ph. c. collybita* type" free from the probable selection pressure caused by competing Willow Warblers, must remain unanswered until more point samples are available from eastern Europe.

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Selostus: **Pajulinnun ja tiltaltin morfologian maantieteellinen muuntelu Euroopassa**

Huolimatta monista pienistä erottavista piirteistä ovat pajulintu ja tiltaltti kokonsa, muotonsa ja ekologiansa suhteen hyvin toistensa kaltaisia. Maantieteellisen muuntelun määrän suhteen ne kuitenkin eroavat selvästi. Niinpä tiltaltista erotetaan useampia alalajeja kuin pajulinnusta.

Tutkimme työssämme pajulintu- ja tiltalttikoiraiden maantieteellistä muuntelua Suomesta, Lounais-Saksasta ja Unkarista kerätyn aineiston perusteella (Fig. 1, Appendix). Kaikki näytteet koskevat vain pesimäaikaisia koiraita lukuun ottamatta Suomesta myös loppukesällä nuorista tiltalttikoiraista kerättyä näytettä. Molemmat lajit esiintyvät Suomessa ja Saksassa, mutta Unkari on pajulinnun levinneisyysalueen eteläpuolella. Suomessa lajit esiintyvät erilaisissa ympäristöissä, mutta Saksassa paljolti samassa ympäristössä (lehtimetsien reunat). Unkarissa tiltaltin ympäristö on samanlainen kuin Saksassa.

Tarkastelimme erikseen kolmea toiminnallista kokonaisuutta, (i) siipeä ja pyrstöä, (ii) jalkaa sekä (iii) nokkaa ja suupielisukasia (muuttujia oli yhteensä 32, Table 1). Suomalaisten (kolme populaatiota) ja saksalaisten pajulintujen välillä oli hyvin vähän eroja (Table 2; Fig. 2, joka kuvastaa lähinnä kokoa, ja Fig. 3, joka kuvastaa toiminnallisten kokonaisuuksien muotoa). Tulkitsemme tämän johtuvan hyvin samankaltaisista elinympäristöistä. Sen sijaan kaikkien kolmen tutkitun alueen tiltaltit erosivat sekä kokonsa että muotonsa puolesta toisistaan; unkarilaiset tiltaltit olivat suomalaisten ja saksalaisten välimuotoja (Table 3, Fig. 4, Fig. 5).

Populaatioiden väliset erot voivat olla (1) puhtaasti ympäristön aikaansaamia, (2) yksilön elämänvaiheiden mukanaan tuomasta vaihtelusta johtuvia, (3) sopeumia paikallisiin tai laajemmalla alueella vallitseviin olosuhteisiin tai (4) satunnaisista seikoista johtuvia. Pidämme vaihtoehtoa (1) epätodennäköisenä. Vaihtoehto (2) ei selitä tuloksia aineistomme rajauksen ansiosta. Vaihtoehtoa (4) emme voi tarkastella, koska siihen tarvittaisiin lisäaineistoa.

Elinympäristöjen ja muuttotapojen perusteella voidaan ennustaa, että pajulinnun morfologia muuntelee vähemmän kuin tiltaltin ja että pohjoisemmilla populaatioilla on pitemmät ja teräväkärkisemmät siivet kuin eteläisillä; aineistomme tukee näitä ennusteita. Lisäksi suomalaisilla tiltalteilla tulisi olla sopeumia kuusikkoiseen elinympäristöönsä. Tutkiaksemme tätä sisällytimme hippiäisen tiltalttianalyyseihimme, mutta tulokset eivät olleet ennusteen mukaisia (Table 3, Fig. 4, Fig. 5). Suomalaisten ja saksalaisten pajulintujen taas ei tulisi erota toisistaan, kuten ne eivät eronneetkaan. Lopuksi, jos pajulintu ja tiltaltti ovat ekologisia kilpailijoita, tulisi tämän näkyä unkarilaisten, pajulinnun kilpailusta vapaiden tiltalttien morfologiassa joko muuntelun lisääntymisenä tai jonain suuntauksena, mutta tällaista ei havaittu (Table 4, Fig. 6). Edelleen saksalaisten lintujen tulisi sopeutua rinnakkaiseen eloon yhteisissä ympäristöissä morfologisesti. Tästä saatiin viitteitä, sillä lajien väliset erot olivat yleensä suurempia Saksassa kuin Suomessa. Siten populaatioiden välinen muuntelu selittyy ainakin osittain sopeutumisella paikallisiin oloihin.

Lopuksi otamme kantaa eurooppalaisten pajulintujen ja tiltalttien alalajikysymyksiin. Nähdäksemme tiltaltilla alalajit *Ph. c. abietinus* ja *Ph. c. collybita* eroavat niin selvästi toisistaan, että alalajien erottaminen on järkevää. Pajulinnun alalajien *Ph. t. acredula* ja *Ph. t. trochilus* erot (myös höyhenpuvun värityksessä) ovat taas niin vähäisiä, että alalajien erottaminen on kyseenalaista.

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Appendix. Mean values of the original variables in the four Willow Warbler (F = Föglö, L = Lammi, S = Seitseminen G = SW Germany) and four Chiffchaff groups (Fa = Finnish adults, Fj = Finnish juveniles, H = Hungarian), and the Goldcrest (R); sample sizes are shown in parentheses. WT = wing tip, BW = bill width. All measurements are in mm, except for the wing area, which is the square root of the area measured in sq. mm.

	Willow Warbler				Chiffchaff				Goldcrest
	F	L	S	G	Fa	Fj	H	G	R
Variable	(39)	(36)	(105)	(32)	(14)	(27)	(23)	(68)	(7)
Flight apparatus									
Wing length	70.7	71.1	71.4	70.3	65.1	65.2	62.7	61.8	54.1
Wing breadth	50.3	50.2	50.6	50.4	50.2	50.1	50.2	48.1	41.0
Wing area	19.3	19.0	19.3	18.9	18.6	18.6	18.6	17.7	14.8
Tail length	54.5	54.9	55.1	54.4	52.5	53.2	51.2	51.2	40.9
Notch of 2nd primary	18.0	17.9	17.8	17.5	16.9	17.1	16.7	16.5	15.4
1st primary to coverts	3.5	3.7	3.7	4.3	5.7	5.6	6.6	6.6	5.5
1st primary to WT	38.0	38.3	38.5	37.0	33.2	33.1	31.1	30.9	28.9
2nd primary to WT	5.6	5.6	5.6	5.3	6.4	6.9	6.3	6.6	7.6
5th primary to WT	2.4	2.3	2.5	2.2	–	–	–	–	–
6th primary to WT	7.7	7.6	7.5	7.3	3.7	2.6	2.3	2.0	1.1
7th primary to WT	11.2	10.9	11.1	10.7	7.1	5.8	5.4	5.2	4.8
8th primary to WT	13.5	13.1	13.3	13.1	9.1	8.3	7.8	7.5	6.6
Foot									
Tarsus length	19.9	19.8	19.7	20.2	19.6	19.7	19.4	20.0	16.7
Foot span with claws	26.9	26.7	26.6	27.1	26.6	26.9	26.5	26.1	24.7
Foot span without claws	19.2	19.3	19.0	19.4	18.3	18.9	18.2	18.1	17.7
Hind toe	6.7	6.7	6.6	6.8	6.2	6.7	6.3	6.3	6.3
Inner toe	5.9	6.0	6.0	6.3	5.8	5.9	5.9	5.8	5.8
Middle toe	10.0	10.1	10.1	9.8	9.7	9.9	9.4	8.9	9.0
Outer toe	6.6	6.7	6.7	6.7	6.6	6.7	6.6	6.5	6.4
Hind claw	5.3	5.1	5.1	5.3	5.6	5.6	5.8	5.5	5.8
Inner claw	3.6	3.4	3.5	3.4	3.7	3.6	3.8	3.4	3.4
Middle claw	4.5	4.3	4.5	4.5	4.5	4.6	4.7	4.5	4.2
Outer claw	3.5	3.2	3.3	3.3	3.4	3.4	3.6	3.3	3.4
Feeding apparatus									
Bill to feathers	7.3	7.5	7.4	7.5	6.9	6.7	6.8	7.3	6.4
Bill to nostrils	6.3	6.4	6.4	6.5	5.8	5.8	5.9	6.2	6.1
Bill to skull	12.2	12.5	12.2	12.5	11.6	11.5	11.7	11.9	10.5
Bill to mouth corner	13.7	13.9	13.8	13.8	12.9	13.0	13.0	13.4	12.1
Bill height	3.0	3.0	3.0	2.7	2.7	2.7	2.5	2.5	2.4
BW at anterior edge of nostrils	2.7	2.8	2.6	2.6	2.4	2.5	2.5	2.5	2.1
BW at hind edge of nostrils	3.7	3.8	3.6	3.6	3.5	3.6	3.4	3.5	2.9
BW at mouth corner	6.8	6.5	6.7	7.1	6.5	6.5	6.6	6.6	5.6
Rictal bristles	4.3	4.2	4.4	4.1	4.3	4.6	4.6	4.9	5.8