Ecological significance of morphometric variation in three sympatric 
Phylloscopus warblers

Juha Tiainen


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 siterenacious 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.

Juha Tiainen, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland (permanent address), and Max-Planck-Institut für Verhaltensphysiologie, Vogewarte Radolfzell, Schloss, D-7760 Radolfzell-Möggingen, Federal Republic of Germany.

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
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 Mögglingen. 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 moulting, 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 covert.
- 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.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Sex</th>
<th>Ph. sibilatrix</th>
<th></th>
<th></th>
<th>Ph. trochilus</th>
<th></th>
<th></th>
<th>Ph. collybita</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(x)</td>
<td>SD</td>
<td>CV %</td>
<td>(x)</td>
<td>SD</td>
<td>CV %</td>
<td>(x)</td>
<td>SD</td>
</tr>
<tr>
<td>Weight</td>
<td></td>
<td>9.77</td>
<td>0.530</td>
<td>5.4</td>
<td>22</td>
<td>9.65</td>
<td>0.513</td>
<td>5.3</td>
<td>139</td>
</tr>
<tr>
<td>Wing length</td>
<td></td>
<td>9.65</td>
<td>0.590</td>
<td>6.1</td>
<td>13</td>
<td>8.64</td>
<td>0.487</td>
<td>5.6</td>
<td>78</td>
</tr>
<tr>
<td>Wing pointedness</td>
<td></td>
<td>79.1</td>
<td>1.61</td>
<td>2.0</td>
<td>22</td>
<td>71.4</td>
<td>1.46</td>
<td>2.0</td>
<td>198</td>
</tr>
<tr>
<td>Wing symmetry</td>
<td></td>
<td>75.0</td>
<td>1.36</td>
<td>1.8</td>
<td>22</td>
<td>71.4</td>
<td>1.46</td>
<td>2.0</td>
<td>198</td>
</tr>
<tr>
<td>Partial length of 1st</td>
<td></td>
<td>96.5</td>
<td>0.635</td>
<td>5.4</td>
<td>16</td>
<td>65.7</td>
<td>0.047</td>
<td>8.5</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>28.7</td>
<td>12.93</td>
<td>44.8</td>
<td>16</td>
<td>7.4</td>
<td>3.55</td>
<td>48.0</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24.4</td>
<td>11.76</td>
<td>48.0</td>
<td>12</td>
<td>6.9</td>
<td>2.09</td>
<td>30.4</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-3.9</td>
<td>1.48</td>
<td>37.9</td>
<td>16</td>
<td>4.0</td>
<td>1.66</td>
<td>41.5</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-3.4</td>
<td>1.84</td>
<td>52.6</td>
<td>11</td>
<td>3.7</td>
<td>1.89</td>
<td>51.1</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>53.5</td>
<td>1.90</td>
<td>3.5</td>
<td>17</td>
<td>55.9</td>
<td>2.26</td>
<td>4.0</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>49.7</td>
<td>2.12</td>
<td>4.3</td>
<td>17</td>
<td>51.0</td>
<td>2.50</td>
<td>4.9</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td></td>
<td>17.8</td>
<td>2</td>
<td>1.01</td>
<td>5</td>
<td>19.9</td>
<td>0.91</td>
<td>5.1</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>17.6</td>
<td>2</td>
<td>1.89</td>
<td>5</td>
<td>18.9</td>
<td>0.91</td>
<td>5.1</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>23.9</td>
<td>2</td>
<td>2.95</td>
<td>5</td>
<td>25.7</td>
<td>2.98</td>
<td>3.8</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24.4</td>
<td>0.82</td>
<td>3.4</td>
<td>7</td>
<td>25.3</td>
<td>0.59</td>
<td>2.3</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.8</td>
<td>2</td>
<td>1.06</td>
<td>5</td>
<td>12.0</td>
<td>0.61</td>
<td>5.1</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.6</td>
<td>0.75</td>
<td>6.0</td>
<td>7</td>
<td>11.9</td>
<td>0.66</td>
<td>5.5</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.2</td>
<td>2</td>
<td>0.32</td>
<td>5</td>
<td>3.2</td>
<td>0.16</td>
<td>5.0</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.2</td>
<td>2</td>
<td>0.30</td>
<td>5</td>
<td>3.2</td>
<td>0.10</td>
<td>2.7</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.6</td>
<td>2</td>
<td>0.37</td>
<td>5</td>
<td>3.6</td>
<td>0.10</td>
<td>2.7</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.7</td>
<td>2</td>
<td>0.37</td>
<td>5</td>
<td>3.7</td>
<td>0.10</td>
<td>2.7</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.48</td>
<td>0.049</td>
<td>3.3</td>
<td>17</td>
<td>1.28</td>
<td>0.052</td>
<td>4.0</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.51</td>
<td>0.058</td>
<td>3.8</td>
<td>17</td>
<td>1.29</td>
<td>0.023</td>
<td>1.8</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.44</td>
<td>0.22</td>
<td>8.2</td>
<td>2</td>
<td>3.66</td>
<td>0.169</td>
<td>4.6</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.42</td>
<td>3</td>
<td>0.49</td>
<td>5</td>
<td>3.78</td>
<td>0.138</td>
<td>3.7</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.95</td>
<td>2</td>
<td>4.00</td>
<td>5</td>
<td>3.95</td>
<td>0.213</td>
<td>4.0</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.53</td>
<td>2</td>
<td>3.23</td>
<td>5</td>
<td>3.53</td>
<td>0.213</td>
<td>4.0</td>
<td>5</td>
</tr>
</tbody>
</table>
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 Möggingen. 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 measure-
ments 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 nesting period, the age of the
nestlings was determined from their wing lengths (Tiainen
1978, see also 1983a).

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).

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

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.

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.

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

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

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

avoid the inclusion of gravid females and therefore
an increased mean weight (Tiainen, un-
publ.).
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 (Levene 1960). Variation in weight was not compared because of different dimensionality ($\text{Cl}_{\text{wing}}$ may be up to 3$\text{Cl}_{\text{wing}}$ depending on the perfectness of correlation between the weight and the wing length: Lande 1977).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>$\text{Ph. sibilatrix}$</th>
<th>$\text{Ph. trachius}$</th>
<th>$\text{Ph. collybita}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail length</td>
<td>*</td>
<td>**</td>
<td>—</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>—</td>
<td>**</td>
<td>—</td>
</tr>
<tr>
<td>Foot span</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Bill length</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Bill depth</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Bill breadth</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

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-
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.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Ph. sibilatrix</th>
<th>Ph. trochilus</th>
<th>Ph. collybita</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td>37.0</td>
<td>35.2</td>
<td>33.5</td>
</tr>
<tr>
<td>Tail length</td>
<td>25.0</td>
<td>23.3</td>
<td>26.3</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>8.3</td>
<td>8.4</td>
<td>9.3</td>
</tr>
<tr>
<td>Foot span</td>
<td>11.2</td>
<td>11.5</td>
<td>12.1</td>
</tr>
<tr>
<td>Bill length</td>
<td>6.0</td>
<td>5.9</td>
<td>5.6</td>
</tr>
<tr>
<td>Bill depth</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5</td>
</tr>
<tr>
<td>Bill breadth</td>
<td>1.7</td>
<td>1.7</td>
<td>1.8</td>
</tr>
</tbody>
</table>

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 Möögingen standardised by dividing the original figures by the cube root of the weight.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Ph. trochilus</th>
<th>Ph. collybita</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td>33.1</td>
<td>31.3</td>
</tr>
<tr>
<td>Tail length</td>
<td>25.5</td>
<td>25.8</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>9.4</td>
<td>10.1</td>
</tr>
<tr>
<td>Bill length</td>
<td>5.9</td>
<td>5.8</td>
</tr>
</tbody>
</table>
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 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 ($t=2.926$, $P < 0.005$, $df = 119$).
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 Fonstad & 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 Fonstad & 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 Hespenheide (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, Payevskii 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 chifchaff (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 chifchaff, 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 chifchaff 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, Sulikava 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 suitability 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 suitability 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 chifchaff 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 chifchaff 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 chifchaff. The situation between the willow warbler and the chifchaff is not clear. I have no observations of direct hostile encounters, but in a few cases early arriving chifchaff males occupied a territory in an area where there had usually been a willow warbler territory (in Finland, the chifchaffs 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 chifchaff 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 chifchaff 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, 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 chifchaff 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 chifchaff 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 chifchaff 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 its "...its life history, sibilatrix 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).

Acknowledgements. I wish to express my gratitude to Harri Makkonen, Jarmo Piirioinen, Tapio Solonen, Seppo Varjonen and Lasse Vilhunen for their help in the field, to Yrjö Haala, Ilkka Hanski, Olli Järvinen, Gerald Niemi, Sven G. Nilsson, Tapio Solonen and Kari Vepsäläinen for commenting upon the manuscript, and to Ludwik Tomiałojć for help with the Russian articles. Good working facilities were provided by Lammi Biological Station, University of Helsinki, and Vogelwarte Radolfzell, Max-Planck-Institut für Verhaltensphysiologie. The work was supported by the Finnish Cultural Foundation in its critical final phases and by a fellowship from Deutscher Akademischer Austauschdienst for completion. The English was corrected by Nigel Billany.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight ratio</th>
<th>Wing length ratio</th>
<th>Bill length ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lammari</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pt / Ps</td>
<td>1.01</td>
<td>1.11</td>
<td>1.07</td>
</tr>
<tr>
<td>Pt / Pc</td>
<td>1.19</td>
<td>1.19</td>
<td>1.11</td>
</tr>
<tr>
<td>Pt / Pt</td>
<td>1.18</td>
<td>1.07</td>
<td>1.04</td>
</tr>
<tr>
<td>Pt / Ps / Pt</td>
<td>1.00</td>
<td>1.05</td>
<td>1.05</td>
</tr>
<tr>
<td>Pt / Ps / Pc</td>
<td>1.06</td>
<td>0.99</td>
<td>1.03</td>
</tr>
<tr>
<td>Radolfzell</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pt / Ps</td>
<td>1.20</td>
<td>1.13</td>
<td>1.09</td>
</tr>
</tbody>
</table>
References


Buse, P. 1967: Application of the numerical indexes of the wing-shape. — Notatki Ornithol. 8: 3-18. (Polish with English summary.)


Hogstad, O. 1978: Sexual dimorphism in relation to winter foraging and territorial behaviour of the three-toed woodpecker Picoides tridactylus and three Dendrocopos species. — Ibis 120: 198-203.

Hutchinson, G. E. 1959: Homage to Santa Rosalia or why are there so many kinds of animals? — Amer. Nat. 93: 143-159.


Opdam, P. 1973: Inter- and intraspecific differentiation with respect to feeding ecology in two sympatric species of the genus Acipenser. — Ardea 65: 30-54.

Payevski, V. A. 1981: Survival in chalklinches (Frangilla coelebs) which attained sexual maturity, with special respect to the date of their hatching and the brood size. — Zool. Zhurnal 60: 109-114. (Russian with English summary.)


Schoener, T. W. 1963: The evolution of bill size differences


Sulkava, P. 1972: Varpushaukan, Accipiter nisus (L.), pesimäobiologiasta ja pesimäaikaisesta ravinnosta. — Manuscript, Dept. of Zoology, Univ. of Helsinki. (In Finnish.)


Received 26 VII 1982
Printed 30 XII 1982