INTRODUCTION

The existence of age- or sex-related differences in the wing morphology of passerines is a feature which shows intraspecific differences related to the timing of migration (Gauthreaux, 1982; Lövei, 1983; Hedenström & Pettersson, 1986; Mulvihill & Chandler, 1990, 1991) and also reveals migration patterns among sedentary and migratory populations (Mulvihill & Chandler, 1991; Pérez-Tris & Tellería, 2001; Tellería et al., 2001), residence status of wintering birds (Senar et al., 1994) or show variations among individuals of different geographic origin (Lövei, 1983; Tiainen & Hanski, 1985; Lo Valvo et al., 1988; Wiedenfield, 1991; Copete et al., 1999). These features reveal intraspecific differences in the wing shape of short-distance migrants such as pre-Saharan migrants (e.g. Blackcaps Sylvia atricapil...
Intraspecific variation in wing morphology has been hypothesised to be due to a trade-off between selection forces on wing shape in relation to manoeuvrability and migration demands (e.g. Alatalo et al., 1984; Pérez-Tris & Tellería, 2001). This trade-off is predicted to have a different outcome in different age classes or in populations with different migration patterns. Juveniles should have shorter and more rounded wings than adults, giving more manoeuvrability because their naivety makes them more vulnerable to the attacks of predators (Kullberg et al., 1996). This natural selection might favour more manoeuvrable, short and rounded wings in the juvenile plumage (Alatalo et al., 1984), hence improving juvenile survival at the expense of a somewhat impaired migration performance.

On the other hand, birds that migrate different distances (i.e. occupying different areas in a breeding range large enough) would also differ in wing shape due to similar selection forces acting on them. Birds should have the most manoeuvrable wing given the cost of migration they have to pay in relation to distance travelled. This hypothesis poses two testable predictions: (i) juveniles should have shorter and more rounded wings than adults and (ii) populations migrating shorter distances should have shorter and more rounded wings than those moving longer distances. Both predictions have received empirical support in short distance migrant species, but not in long-distance migrants such as the Reed Warbler (Acrocephalus scirpaceus). This paper studies the effect of age and migratory distance on wing shape of Reed Warblers through the analysis of temporal variations of the wing shape of the birds trapped in a Mediterranean area. This area is particularly suitable for this type of analysis since it is used by both local and migrating populations with different migratory distances (Peiró, 1997a).

**MATERIAL AND METHODS**

Reed Warblers were trapped in reed beds (Phragmites australis) at El Hondo Natural Park, Alicante province, south-eastern Spain (38°16′N 00°41′W). The population of this species consists mainly of breeding birds, with additions of migrants during both spring (March-May) and autumn (August-October) according to the recaptures of birds ringed abroad (Peiró, 1997a). Wing shape was characterised by measuring the wing length and the wing formula for each individual. Wing length (maximum chord method; Svensson, 1992) was recorded to the nearest 0.5 mm and the wing formula of the left wing was recorded to the nearest 0.5 mm by measuring the primary distances from the wing-tip (P3) to the tip of each one of the nine primaries (P2-P10, numbered in ascending order) on the folded wing using a transparent ruler. Primary lengths were calculated by subtracting each primary distance from the wing length (Evered, 1990).

As juveniles and adults undergo a partial body moult in summer and complete their moult at their winter quarters, full-grown birds with juvenile plumage were distinguished from adults in mid summer mainly by a fresh plumage in juveniles and a worn or abraded one in adults (Svensson, 1992). In spring it was not possible to differentiate between adult and juvenile birds due to the complete winter moult of both age classes. In the late summer and autumn, other features, such as the colour of bare parts, were also used to age birds (Karlsson et al., 1988).

A principal component analysis (PCA) on the correlation matrix of the standardised primaries was performed in order to estimate the main sources of variation in the feather length data and to obtain an independent and objective assessment of wing shape in Reed Warblers. Due to the existence of allometric variations in the lengths of feathers, which depended upon parameters related to the body size of each individual, primary lengths were corrected for body size.
size according to the growth model developed by Senar et al. (1994). The average wing length entered into the model was 64.7 mm. Age- and time-related differences in PCA scores, as well as its interaction, were tested by means of a two-way ANOVA (Sokal & Rohlf, 1981).

RESULTS

The wing length and wing formula were recorded from 384 first ringed Reed Warblers caught from March to October, 1992-1994. Only full-grown birds were included in the analyses. The results of the PCA on the standardised primary lengths extracted two components, which accounted for 83.26% of the total variance and were then used to evaluate the flight morphology of this species (Table 1). The first principal component (PC1) represents an axis of increasing length of the proximal primaries (P4-P9) and decreasing length of the distal primaries (P2), indicating a positive gradient of wing convexity. PC2 indicates an axis of decreasing length of the distal primary (P2) and increasing length of proximal primaries (P4-P8), thus indicating a gradient of increasing roundness at the leading edge of wing or wing-tip roundness.

![Table 1](image)

<table>
<thead>
<tr>
<th>PC1 PC2</th>
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<tbody>
<tr>
<td>Primary 2</td>
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<td>Primary 4</td>
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<td>Primary 5</td>
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<td>Primary 6</td>
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<td>Primary 8</td>
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<td>Primary 9</td>
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<td>Primary 10</td>
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<tr>
<td>Eigenvalue</td>
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<td>Variance explained (%)</td>
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</table>

The variation between age classes in the wing shape indicates that adults had a more elongated wing shape (higher wing convexity and roundness) and wing length than juveniles (Table 2; Fig. 2) independently of the component extracted. Wing length was not included as a covariate in the analysis of PC scores since the components extracted using PCA is usually independent of wing length. Hence, body size was not controlled for, although differences in relation to age in some parameters related to body size (e.g. tarsus length) have been found in this species at the study area (Peiró, 1995). Any confounding effect on differences in wing length could be related to morphologic adaptations among populations of such parameters related to breeding or migration distance (Cramp, 1992).

Variation in wing length was consistent with the presence of birds with longer wings, trapped from April to May and August-September in their passage from or towards northern areas, which differ from the local birds, which had shorter wings, trapped from June to July (Fig. 1). This pattern differs between age classes, as the increase in mean wing length of first-year birds took a month more than the increase of adults, a fact which is consistent with a latter passage of first year birds (Fig. 1). Variation of wing convexity was similar than variation in wing length. Wings were more rounded in the adults trapped in June-July (breeders) than in those trapped in passage, while juveniles trapped in passage show a more pointed wing than those trapped during the breeding period (Fig. 2). The wing-tip roundness pattern (as is indicated by PC2) is constant along the cycle, and it only differs among age-classes. Juveniles had more rounded wings than adults (Fig. 2).

DISCUSSION

Although due to the impossibility to differentiate all European populations of Reed Warblers by its biometry, the intraspecific differences in wing shape found in this study strongly suggested a differential migration pattern of such populations. This hypothesis stems from the temporal variations in wing length, degree of convexity and wing-tip roundness observed, since both wing length and wing shape are usually related to migration distance in...
many passerines (Mönkkönen, 1995). Results also support the hypothesis that the necessity to cover different distances implicates variable selection pressures that could cause intraspecific variation in the wing shape of long distance migrants.

On the other hand, age-related variations were in accordance with age effects in the tra-

Table 2

Results of ANOVAs testing for differences in wing length, wing convexity (PC1 scores) and wing-tip roundness (PC2 scores) in relation to age and month. Missing cells obliged to estimate age and month effects using a Type IV sum of squares (Goodnight, 1980). Interactions were estimated using the months in which individuals of both age classes were captured (June to September).

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>Age</th>
<th>Month</th>
<th>Age x Month</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td></td>
<td>1,365</td>
<td>6,365</td>
<td>3,231</td>
</tr>
<tr>
<td>Longitud del ala</td>
<td></td>
<td>21.94</td>
<td>&lt; 0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Wing convexity</td>
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</tr>
<tr>
<td>Convexidad alar</td>
<td></td>
<td>21.94</td>
<td>&lt; 0.001</td>
<td>0.56</td>
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<tr>
<td>Wing-tip roundness</td>
<td></td>
<td>8.93</td>
<td>0.003</td>
<td>1.06</td>
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<tr>
<td>Redondez de la punta</td>
<td></td>
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<td>0.368</td>
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</tbody>
</table>

Fig. 1.—Variation in wing length of Reed Warblers in relation to age and month. Mean, standard errors and sample sizes are shown. Solid circles, thin line: adults; open circles, pointed line: juveniles.

[Variación en la longitud del ala de Carriceros Comunes en relación a la edad y mes. Se muestra la media, error estándar y tamaños de muestra. Círculos rellenos, línea continua: adultos; círculos vacíos, línea dis-continua: jóvenes.]
de-off between costs of predation, which favour shorter and rounded wings with greater manoeuvrability in juveniles (Alatalo et al., 1984), and migratory costs which favour longer and pointed wings providing larger speed and less energetic waste in long flights in adults (Norberg, 1995). These effects, probably mediated by the inexperience of juveniles (Lind et al., 1999), could lead to an optimal wing shape different between ages (Alatalo et al., 1984).

However, results showed that the first component of wing shape (wing convexity) differed between ages in a way opposite than expected, juveniles having a more pointed wing at the leading edge than adults. These differences could be explained in terms of different amount of feather wear and moult patterns of this species. In the Reed Warbler, adults and juveniles undergo a complete primary moult in the African winter quarters (Cramp, 1992; Jenni & Winkler, 1994), arriving at the European breeding areas with a second generation of primary feathers, while juveniles only carry out a partial moult at the breeding areas having primaries not moulted and belonging to the first generation. Differential abrasion of the longest primaries could introduce variation in wing shape according to age, since the most affected feathers before moult are those forming the wing-tip. In adults, these feathers shorter than in juveniles, explaining a more rounded wing in adults, relative to first wing component. As this species has a migratory pattern which is highly homogeneous within populations (Bibby & Green, 1981), primary feather wear has to be taken into account as an important factor shaping the wings of this species, a fact that highlights the importance of distinguishing age groups in studies of wing shape variation (Alatalo et al., 1984; Swaddle et al., 1996; Nor- man, 1997; Merom et al., 1999).

In morphological terms, manoeuvrability involves less flight speed and less power at take-off (Norberg, 1995) which is in detrimental for long distant migrants, but it is in accordance with the particular phenology of this species at stop-over sites (Ormerod, 1990) due to the need of juveniles to arrive to the winter quarters later than adults (Dowsset-Lemair & Dowssett, 1987). Probably, a slight ontogenetic variation through an optimal wing shape, could explain the age-related differences in wing shape.
The use of the PCA analysis has proved useful to distinguish age-related differences in the wing shape of Bluethroats Luscinia svecica (Peiró, 1997b) and the residence status of Siskins Carduelis spinus (Senar et al., 1994), and works better intraspecifically than interspecifically (Senar et al., 2003). The seasonal breakdown of these components through a particular cycle could result in an interesting method to detect migratory waves, which could help to understand the phenology of many migratory species.

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REFERENCES


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