

INTRASPECIFIC VARIATION IN THE WING SHAPE OF THE LONG-DISTANCE MIGRANT REED WARBLER *ACROCEPHALUS SCIRPACEUS*: EFFECTS OF AGE AND DISTANCE OF MIGRATION

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SUMMARY.—*Intraspecific variation in the wing shape of the long-distance migrant Reed Warbler Acrocephalus scirpaceus: effects of age and distance of migration.* The wing morphology of Reed Warblers *Acrocephalus scirpaceus* was studied during the breeding and non-breeding cycle in a western Mediterranean area. Wing morphology was first analysed by means of a principal component analysis (PCA) on primary lengths, which corrects for allometric effects on wing shape. Two-way ANOVAs were then used to test for differences in wing morphology according to age, month and their interaction. The PCA produced two components that were related to flight-related traits, namely wing convexity and wing-tip roundness. Primary feather wear was the factor that produced most differences between ages, since adults had a more convex and rounded wing than juveniles at the outermost edge of the wing. Monthly differences in wing shape appear to indicate that differential time of migration among morphologically distinct ages could have accounted for temporal variation in wing shape, pointing that adults increased the wing components during migratory passages while juveniles showed little variation. The existence of a morphological trade-off between costs of manoeuvrability and costs of migration is discussed in order to explain differences in wing shape between ages.

Key words: *Acrocephalus scirpaceus*, age classes, migratory waves, PCA analysis, wing shape.

RESUMEN.—*Variación intraespecífica en la forma alar del Carricero Común Acrocephalus scirpaceus: efectos de la edad y la distancia de migración.* La morfología alar del Carricero Común *Acrocephalus scirpaceus* fue estudiada durante el ciclo de permanencia de esta especie en un área del Mediterráneo occidental. La morfología alar fue primeramente analizada por medio de un Análisis de Componentes Principales (ACP) sobre las longitudes de las primarias, que fueron corregidas por efectos alométricos sobre la forma alar. Un ANOVA de clasificación doble fue usado para contrastar diferencias en la morfología del ala en relación con la edad, el mes y su interacción. El ACP produjo dos componentes relacionados con rasgos relevantes para el vuelo, uno relativo a la convexidad del ala y otro a su redondez. El desgaste de las primarias fue el factor que produjo mayores diferencias entre edades, ya que los adultos tuvieron alas más convexas y redondeadas que los jóvenes. Los resultados parecen indicar que el tiempo de migración diferencial entre edades morfológicamente distintas fue el factor que pudo explicar la variación temporal en la forma alar, indicando que los adultos incrementaron los componentes del ala durante el paso migratorio mientras que los jóvenes mostraron poca variación. La existencia de un balance entre los costos de maniobrabilidad y los costos de migración es discutida en relación con las diferencias en la forma alar entre edades.

Palabras clave: *Acrocephalus scirpaceus*, clases de edad, oleadas migratorias, análisis de componentes principales, forma alar.

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; Wiedenfeld, 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 atricapilla*

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lla; Lövey, 1983; Pérez-Tris & Tellería, 2001; Tellería *et al.*, 2001; Chiffchaffs *Phylloscopus collybita*; Tiainen & Hanski, 1985; Reed Buntings *Emberiza schoeniclus*; Copete *et al.*, 1999; Robins *Erithacus rubecula*; Pérez-Tris *et al.*, 2000), with large differences within populations in wing morphology which show intraspecific differences in migration patterns. In long-distance migrants, however, little intraspecific variation in wing morphology is expected, due to their very homogeneous migration patterns in all populations and age classes (Bibby & Green, 1981; Hedenström & Pettersson, 1986; Nowakosky, 1994; Norman, 1997).

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 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

Results of a PCA with the standardized primary lengths. The correlation between each primary and each component is shown (*: $P < 0.0001$).

[*Resultados del Análisis de Componentes Principales con las longitudes de las primarias estandarizadas. Se muestra la correlación entre cada primaria y cada componente (*: $P < 0.0001$).*]

	PC1	PC2
Primary 2 [2. ^a primaria]	0.045	-0.997*
Primary 4	0.776*	0.030
Primary 5	0.893*	0.026
Primary 6	0.938*	0.039
Primary 7	0.945*	0.018
Primary 8	0.935*	0.016
Primary 9	0.917*	-0.020
Primary 10	0.877*	-0.060
Eigenvalue	5.659	1.002
Variance explained (%)	70.73	12.53
[<i>Varianza explicada (%)</i>]		

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

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).

[Resultados de los ANOVAs que analizaron las diferencias en longitud del ala, convexidad alar (valores de PC1) y redondez de la punta del ala (valores de PC2) en relación a la edad y mes. Las existencias de celdas vacías obligó a estimar los efectos de la edad y mes usando una suma de cuadrados de tipo IV (Goodnight, 1980). Las interacciones fueron estimadas usando los meses en los cuales se capturaron individuos de ambas clases de edad (junio a septiembre).]

	df	Wing length [Longitud del ala]		Wing convexity [Convexidad alar]		Wing-tip roundness [Redondez de la punta]	
		F	P	F	P	F	P
Age [Edad]	1,365	21.94	< 0.001	194.73	< 0.001	8.93	0.003
Month [Mes]	6,365	20.70	< 0.001	21.94	< 0.001	1.21	0.299
Age x Month [Edad x Mes]	3,231	7.12	0.001	0.56	0.639	1.06	0.368

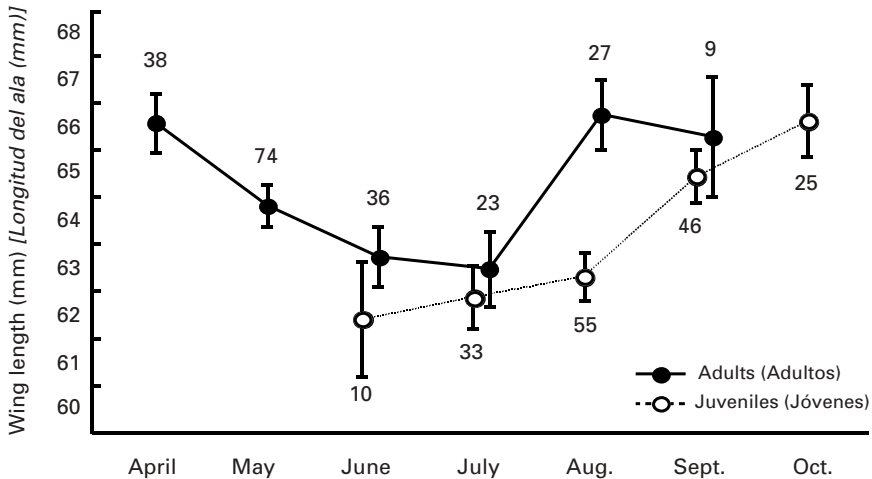


FIG. 1.—Variation in wing length of Reed Warblers in relation to age and month. Mean, standard errors and sample sizes are shown. Solid circles, thin line: adults; open circles, pointed line: juveniles.

[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 discontinua: jóvenes.]

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-

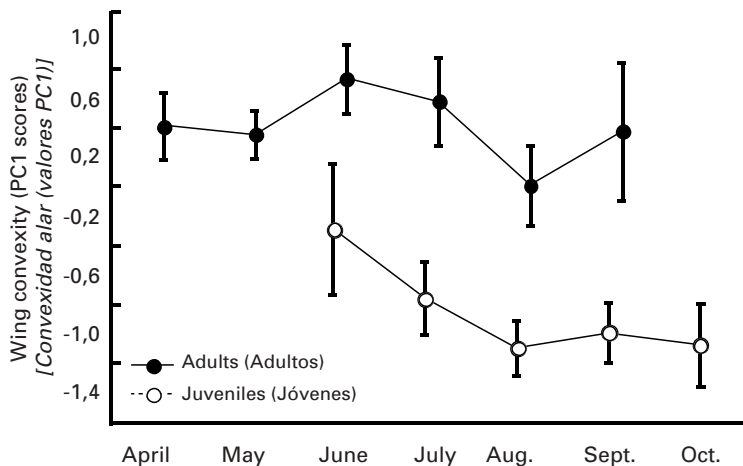


FIG. 2.—Variation in wing convexity and wing-tip roundness (as obtained by a PCA of standardized primary lengths) of reed warblers in relation to age and month. Mean and standard errors are shown. Sample sizes are as in Fig. 1. Solid circles, thin line: adults; open circles, pointed line: juveniles.

[Variación en la convexidad alar y redondez de la punta del ala (obtenidos a partir de una ACP de las longitudes estandarizadas de las primarias) de los Carriceros Comunes en relación a la edad y el mes. Se muestra la media y los errores estándar. Los tamaños de muestra son como en la Fig. 1. Círculos rellenos, línea continua: adultos; círculos vacíos, línea discontinua: 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 pri-

maries 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; Norman, 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 & Dowsset, 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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