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THE USEFULNESS OF BIOMETRICS FOR THE STUDY OF AVIAN CONNECTIVITY WITHIN EUROPE. A CASE STUDY WITH BLACKCAPS *SYLVIA ATRICAPILLA* IN SPAIN

LA UTILIDAD DE LA BIOMETRÍA EN EL ESTUDIO DE LA CONECTIVIDAD MIGRATORIA EN EUROPA. UN CASO DE ESTUDIO CON CURRUCAS CAPIROTADAS *SYLVIA ATRICAPILLA* EN ESPAÑA

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SUMMARY.—The use of biometrics in studies of migratory connectivity is still relatively infrequent in Europe. This is partly due to the fact that biometrics is a less accurate tool when compared to ringing recovery data, or such techniques as stable isotope analyses, use of geolocators or satellite telemetry. Combination with one of these (recovery data) allows us to test the usefulness of biometrics in connectivity analyses, as well as to evaluate/quantify the influence of migratory behaviour on phenotypic traits such as flight morphology. We used historical recovery data, together with flight morphology data obtained from a consistent collection protocol during a three-year ringing programme carried out at seven sites in Spain (within the eastern half of Iberia), to test the usefulness of flight morphology for analysing spatio-temporal distribution patterns of migrants at a population scale. Blackcaps *Sylvia atricapilla* were used as our avian model. Two hypotheses were tested: (1) whether migrant blackcaps use the shortest

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flyways between their breeding and non-breeding areas, so that blackcaps entering Iberia through more eastern flyways come from breeding regions further east, and (2) whether the species is a leap-frogging migrant, in which populations from more northerly regions overwinter further south than those of more southerly origin. Blackcaps entering Spain through the western Pyrenean flyway (WF) had more westerly origins than those entering through the eastern Pyrenean flyway (EF). Blackcaps captured in the WF had more rounded and shorter wings as well as relatively longer tails than those from the EF, indicating a more marked long-distance migration morphology in the EF. However, blackcaps from the EF did not come from more distant regions, so flight morphology was not linked to distance travelled from the region of origin. The fact that both recovery data and biometrics differed between flyways suggests that here flight morphology is an adequate tool with which to study population-associated connectivity patterns. No evidence of leap-frog migration was detected in the study area where biometric data were obtained.

Key words: Biometry, blackcap *Sylvia atricapilla*, population connectivity, recovery data, ringing.

RESUMEN.—El empleo de la morfología en estudios de conectividad migratoria está muy poco extendido en Europa. Aunque esto es parcialmente debido al hecho de que la morfología es más imprecisa que otras metodologías tales como el análisis de recuperaciones, el análisis de isótopos estables o el uso de sistemas de posicionamiento, la combinación de la morfología con una de las técnicas anteriores puede ser una buena oportunidad para testar su utilidad en el análisis de la conectividad y para evaluar el impacto de la migración en rasgos como la morfología de vuelo. Empleamos recuperaciones históricas y medidas biométricas ligadas a la morfología de vuelo de siete zonas de muestreo en España con el fin de comprobar la utilidad de la morfología en el análisis de patrones de distribución geográfica y temporal. Para ello se utilizó la curruca capirotada *Sylvia atricapilla* como modelo. Se consideraron dos hipótesis: (1) si las currucas que migran usan las rutas más cortas entre sus área de cría y no cría, de tal modo que las currucas que entran en España por regiones más orientales tienen un origen más oriental y (2) si la especie realiza un patrón de migración en salto de rana, por el que las poblaciones que crían más al norte pasan el invierno en regiones más al sur que las que crían más al sur. Las currucas de la ruta oriental (la que entra por los Pirineos Orientales) proceden de regiones más orientales que las que se capturan en la ruta occidental (la que entra por los Pirineos Occidentales), y además tienen alas más largas, apuntadas y colas proporcionalmente más cortas que las currucas de la ruta occidental, lo cual indica la existencia de una morfología más marcadamente migratoria en la ruta oriental y está en concordancia con las recuperaciones. Así, la morfología de vuelo en este caso está asociada al origen, aunque no a la distancia a las regiones de origen, y se revela como una herramienta útil con la que estudiar los patrones de conectividad al nivel de población. No se halló evidencia de migración en salto de rana para el área en la que se obtuvieron las muestras biométricas.

Palabras clave: Biometría, curruca capirotada *Sylvia atricapilla*, conectividad, recuperaciones, anillamiento.

INTRODUCTION

Understanding population-associated spatio-temporal distribution patterns is of high interest for research into the biogeography and evolution of the migration patterns and dynamics of bird populations (Webster *et al.*, 2002; Newton, 2004). In this context it is crucial to identify specific populations during both their breeding and non-breeding periods.

Avian morphology –particularly flight morphology– is shaped by migration distance, with wings becoming longer and more pointed, and tails shorter, with increasing distance between breeding and non-breeding (wintering) sites, a finding that is manifested both interspecifically (Mönkkönen, 1995; Calmaestra and Moreno, 2001) and intraspecifically (Copete *et al.*, 1999; Fiedler, 2005; Arizaga *et al.*, 2006; Förschler and Bairlein, 2010). Accordingly, biometry can potentially be used as a tool with which to study connectivity patterns of migrants. In particular, if populations with different migration distances use different migration flyways, and/or are temporally segregated, their flight-associated morphology may be expected to differ either geographically and/or temporally. The use of biometrics in studies of connectivity is still relatively infrequent in Europe (e.g., Pilastro *et al.*, 1998). Biometrics is a less accurate tool than recovery data or such techniques as stable isotope analyses, the use of geolocators or satellite telemetry (Webster *et al.*, 2002; Pain *et al.*, 2004; Procházka *et al.*, 2008; Stutchbury *et al.*, 2009; Bachler *et al.*, 2010; Klaassen *et al.*, 2010). However, the combination of biometry and recovery data or one of the other techniques offers a good chance to test the usefulness of flight morphology in connectivity analyses, as well as to evaluate/quantify the role of migratory behaviour on phenotypic traits such as flight morphology.

The blackcap *Sylvia atricapilla* is one of the commonest European passerines (Cramp, 1992). Its migratory behaviour varies markedly between different populations, a circumstance that also shapes its flight morphology (Fiedler, 2005). Thus blackcaps from Northern Europe are long-distance migrants whereas those nesting in Southern Europe, North Africa and Macaronesia are resident (Shirihai *et al.*, 2001). Iberia receives an autumn influx of blackcaps from elsewhere in Europe: mainly from France, south-western Scandinavia, the British Isles and Western Germany (Cantos, 1995). These either overwinter in Iberia or cross the region to winter in Africa (Tellería *et al.*, 1999). Thus, Iberia offers a good scenario and blackcaps a good avian model for testing whether flight morphology is a useful tool for the study of connectivity. Two hypotheses were considered here.

Hypothesis 1. Migrants commonly use the most direct routes linking their breeding and non-breeding areas (Bairlein, 2001; Newton, 2008). Thus, blackcap populations that enter Iberia through the eastern Pyrenees (hereafter, the Eastern Flyway, EF) may be expected to originate from more eastern regions than the populations that pass through the western Pyrenees (hereafter the Western Flyway, WF). If blackcaps coming to Iberia from further east also travel different distances from those that use the WF, they should also differ in flight morphology. A mismatch between recovery and biometry results would support the idea that biometric data are not sufficiently accurate for studying avian connectivity.

Hypothesis 2. Blackcaps have been suggested to be leap-frog migrants, with northern breeders overwintering south of birds that breed further south (Shirihai *et al.*, 2001). If the leap-frog migration hypothesis is applicable within an Iberian context (Cantos, 1995), we would expect that blackcaps captured in Iberia in winter are from more southerly breeding areas than those captured during migration, and that the former will thus exhibit less pronounced long-distance migration flight morphology than the through-migrants caught on passage. The presence of local resident birds, with their less-pronounced long-distance flight morphology (Pérez-Tris *et al.*, 1999; Tellería and Carbonell, 1999), should only add some statistical noise because their abundance is expected to remain fairly constant in autumn and winter and is probably negligible relative to that of the winter visitors.

We used historical recovery data together with flight morphology data obtained from a consistent collection protocol during a three-year ringing programme carried out at seven ornithological stations covering a wide region, mainly in the eastern half of Iberia, to

TABLE 1

Characteristics of the sampling localities. Location: Western Flyway, Eastern Flyway, southern Iberia (for further details see fig. 1). Period shows localities where blackcaps were caught only during migration (M) or during both migration and wintering (M+W). Sample size refers to the number of blackcaps for which all measurements (wing length, tail length, wing morphology) were recorded.
[Características de los puntos de muestreo. Localización: Ruta Occidental ("West"), Ruta Oriental ("East"), sur ("South") (para más detalles ver fig. 1). En periodo se muestra si las currucas son capturadas sólo en paso migratorio (M) o tanto en paso como en invierno (M+W). El tamaño de muestra se refiere al número de currucas para las que se midieron todas las variables de biometría (longitud del ala, cola y morfología alar).]

Site	Location	Period	Coord.	Altitude (m.a.s.l.)	Campaigns (from-to)	Sample size
1. Loza	West	M	42º 50' N 01º 43' W	500	04/05-06/07	947
2. Zarzalejo	West	M	40º 33' N 04º 10' W	1150	04/05-06/07	21
3. Castro Del Río	South	M+W	37º 41' N 04º 25' W	229	05/06-06/07	187
4. Gaibiel	East	M+W	39º 55' N 00º 30' W	524	04/05-06/07	189
5. Sagunto	East	M+W	39º 42' N 00º 15' W	30	04/05-06/07	190
6. Valencia	East	M+W	39º 28' N 00º 23' W	23	04/05-06/07	168
7. Alcoi	East	M+W	38º 41' N 00º 30' W	800	04/05-06/07	194

test the usefulness of flight morphology for the analyses of spatio-temporal distribution patterns of migrants at a population scale. Blackcaps were our avian model.

METHODS

Sampling sites

Blackcaps were mist-netted at nine Constant Effort Sites in Spain (see table 1 and fig. 1 for further details). Sampling took place from October 2004 to April 2007. Blackcaps from abroad occur in Iberia from September to April, either wintering or as through-migrants that cross the region to and from Africa (Cantos, 1995). September was excluded from the study since many short-distance migrants of local origin are captured then. Data collection was grouped into three periods: autumn (October-November), winter (December-February) and spring (March-April) (Cantos, 1995). Mist nets were opened at dawn for four hours once weekly (three days a week in Loza, as part of other parallel projects).

Captured blackcaps were individually ringed, sexed and aged as either first-years or adults: according to the presence or absence of any juvenile feathers in their wings and tails (Svensson, 1996). We also recorded wing length (± 0.5 mm; method III following Svensson, 1996), length of primary feathers P2 to P9 (± 0.5 mm; numbered from innermost to outermost), and tail length (± 0.5 mm). We also checked whether blackcaps were moulting (scored yes/no).

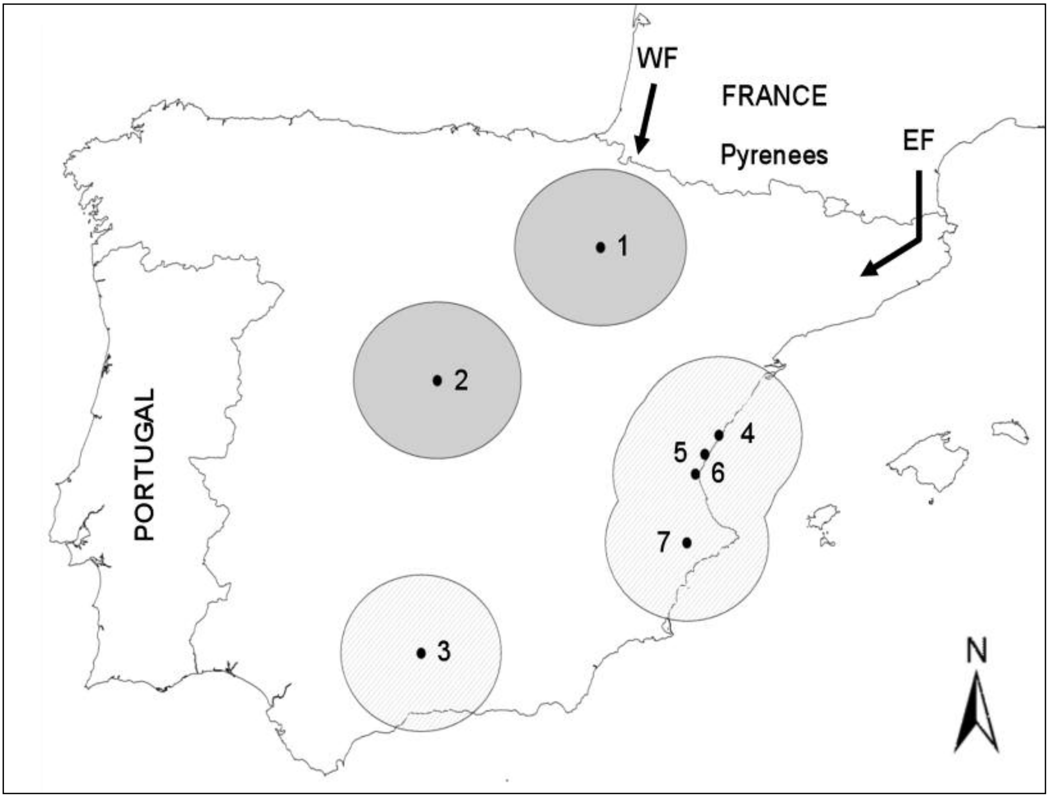

FIG. 1.—Sampling localities (dots numbered as in table 1) in Spain where the study was carried out; localities were assigned to the Western Flyway, WF (grey), the Eastern Flyway, EF (localities 4-7), or to the areas where both migrating and wintering blackcaps were captured (hatched). Arrows show the two routes along which migrants enter Iberia. The recovery data collected in the circular area (100-km radius) surrounding each sampling site were used to analyse the origins of blackcaps according to flyways and periods.

[Localidades de muestreo (numeración como en tabla 1) donde se llevó a cabo el estudio; las localidades han sido asignadas a la ruta Occidental, WF (gris), Oriental, EF (localidades 4-7) o a áreas donde se capturaron currucas tanto en paso como invernantes (barrado). Las flechas señalan las dos rutas por las que las currucas entran en la Península, a efectos del estudio. Las recuperaciones de aves anilladas empleadas para analizar el origen de las currucas según rutas y periodos se obtuvieron para un radio de 100 km alrededor de cada localidad.]

Recovery analyses

Historical data on blackcaps ringed in Spain and recaptured abroad, and ringed abroad and recaptured in Spain were obtained from the Euring databank (www.euring.org). Data on blackcaps both ringed and recaptured within Spain were not used.

In an initial approach, we used all the recoveries ($n = 1226$) to test with simple linear correlations for a possible relationship between the geographical locations of the capture and recovery sites in Spain and abroad, and between the capture sites in Spain and the distance to the ringing locations abroad. All analyses were repeated using recovery data for those birds whose recoveries abroad were during the breeding season (taken as May to August; Cramp, 1992); this was done to reduce possible biases due to blackcaps ringed at stopover locations and not their breeding sites. Since many tests were run for the same type of analysis (three correlations –autumn, winter and spring for each type of analysis), the Bonferroni correction for type 1 errors was employed. We next considered a subset of 417 recoveries, all of which were birds that were recaptured or ringed within a 100 km radius of each of the sampling sites where biometric data were collected (fig. 1). This was done to check for a possible direct relationship between biometrics and recoveries. In this case we did not repeat the analysis for the fraction of recoveries obtained abroad during breeding period, because of sample size constraints. ANOVAs were used to test separately whether (1) blackcaps passing through the WF and EF have a different origin (Hypothesis 1), and (2) whether blackcaps captured in winter originate from different areas to those captured during the autumn and spring migration periods (Hypothesis 2). With this goal, we conducted (1) an ANOVA on recaptures (coordinates), with flyway (WF/EF) and period (autumn/spring) as control factors, considering only data from the WF and EF (fig. 1); (2) an ANOVA on origin of migrants with period (autumn/winter/spring) as a factor, considering only data from those regions where both migrating and wintering blackcaps were captured (fig. 1).

TABLE 2

Principal Component Analyses (PCA) and PC scores that summarised flight-associated morphology.

[Análisis de Componentes Principales (PCA) y puntos PC utilizados como estimación de la morfología de vuelo.]

	PC1	**PC2**
Wing length	-0.777	0.074
Tail/Wing ratio	0.674	0.683
Wing morphology	0.707	-0.570
Eigenvalue	1.558	0.797
Variance (%)	51.9	26.6

Biometric analyses

Variables used to assess flight morphology were wing length and a tail/wing ratio (Fiedler, 2005), as well as wing morphology (wing roundness). This last variable was the index C_2, obtained from an equation provided by Lockwood *et al.* (1998):

$$e^{C2} = 3.332 \times P_9^{-3.490} \times P_8^{-1.816} \times P_7^{-0.893} \times P_6^{-0.003} \times \times P_5^{+0.829} \times P_4^{+1.351} \times P_3^{+1.661} \times P_2^{+2.363}$$

where P_2 to P_9 are the primary feathers. This equation is based on a body size-controlled Principal Component Analysis, PCA, on P2 to P9 primary lengths. Because of a slightly positive skewed distribution, not all of the biometric variables fitted a normal distribution (Kolmogorov test: $P < 0.001$), although they were symmetrically distributed and showed low standard deviations (SD/mean < 15%). Hence, we used parametric statistical procedures (General Linear Models, GLMs) that support small deviations from normal distribution. To obtain a single variable that summarised flight morphology, we conducted a PCA on flight-associated measurements: wing length, wing morphology and the tail/wing ratio. The first component (PC1) had negative factor loadings for wing length and positive loadings for the tail/wing ratio and wing morphology (table 2). Thus, positive values of this principal component were correlated with birds with short, more rounded wings and large tail/wing ratios (i.e. less marked long-distance migra-

TABLE 3

Simple linear correlations used to test the relationship between the geographical positions of capture locations of blackcaps in Spain and their areas of origin abroad. Correlations were carried out for all samples and for the fraction of blackcaps captured/recaptured abroad only during the breeding season (from May to August) (*). Sample sizes for each type of analysis and period are shown. Lat. = latitude, Lon. = longitude.

[Correlaciones lineales simples llevadas a cabo para comprobar la relación entre el punto de captura en España y en el área de origen. Las correlaciones se llevaron a cabo para el conjunto de muestras y para la fracción de currucas capturadas/recapturadas fuera sólo durante el periodo de cría (de mayo a agosto) (*). Se indica el tamaño muestral para cada análisis.]

	Lat. Spain		**Lon. Spain**	
	r	*P*	*r*	*P*
Autumn (n = 574/212)				
Lat. Abroad	–0.213	**<0.001**	–0.414	**<0.001**
Lon. Abroad	–0.060	0.152	+0.150	**<0.001**
(*)Lat. Abroad	+0.018	0.790	–0.148	0.031
(*)Lon. Abroad	–0.011	0.874	+0.214	**0.002**
Winter (n = 447/189)				
Lat. Abroad	–0.125	**0.008**	–0.219	**<0.001**
Lon. Abroad	+0.209	**<0.001**	+0.290	**<0.001**
(*)Lat. Abroad	–0.221	**0.002**	–0.232	**0.001**
(*)Lon. Abroad	+0.257	**<0.001**	+0.359	**<0.001**
Spring (n = 205/83)				
Lat. Abroad	–0.195	**0.005**	–0.400	**<0.001**
Lon. Abroad	+0.008	0.908	+0.211	**0.002**
(*)Lat. Abroad	–0.090	0.418	–0.252	0.022
(*)Lon. Abroad	+0.116	0.297	+0.261	**0.017**

Significance level after Bonferroni correction: $p < 0.02$

tion flight morphology), while negative values were correlated with long, more pointed wings and small tail/wing ratios.

Localities other than Castro del Río were classed as WF or EF; Castro del Río, in southern Iberia, was not assigned to either flyway due to its geographic location (see fig. 1; table 1). Thus, Castro del Río was not included in analyses comparing the WF and EF, but it figured in analyses comparing the migration and wintering periods. Only non-moulting birds of known age and sex were included. We considered each bird only once per season (autumn, winter and spring) and campaign (the time period from October of year *t* to April of year *t*+1).

Biometric analyses comprised (1) a GLM on PC1 that summarised flight morphology with flyway (WF/EF), period (autumn/spring), sex and age as control factors, and sampling locality as a factor nested into flyway ($n = 1347$) (Hypothesis 1); (2) a GLM on PC1 and period (autumn/winter/spring), with sex and age as control factors to test for differences in flight morphology ($n = 928$) between migration periods and winter in areas where both migrating and wintering blackcaps were present (Hypothesis 2).

SPSS 18.0 for Windows was used for statistical analyses and means are given ± SE. Statistical significance is considered to be achieved for *P*-values < 0.05 (Type I error).

TABLE 4

Simple linear correlations used to test the relationship between the geographical positions of capture locations of blackcaps in Spain and the distances to their areas of origin abroad. Correlations were carried out for all samples and for the fraction of blackcaps captured/recaptured abroad only during the breeding season (from May to August) (*). Sample sizes for each type of analysis and period are shown. Lat. = latitude, Lon. = longitude.

[Correlaciones lineales simples llevadas a cabo para comprobar la relación entre el punto de captura en España y la distancia a los puntos de origen. Las correlaciones se llevaron a cabo para el conjunto de muestras y para la fracción de currucas capturadas/recapturadas fuera sólo durante el periodo de cría (de mayo a agosto) (*). Se indica el tamaño muestral para cada análisis.]

	Abroad: Entire year		**Abroad: Breeding season**	
Spain	*r*	*P*	*r*	*P*
Autumn ($n = 574/212$)				
Lat.	–0.600	<0.001	–0.728	<0.001
Lon.	–0.648	<0.001	–0.652	<0.001
Winter ($n = 447/189$)				
Lat.	-0.582	<0.001	–0.605	<0.001
Lon.	-0.587	<0.001	–0.581	<0.001
Spring ($n = 205/83$)				
Lat.	–0.588	<0.001	–0.687	<0.001
Lon.	–0.649	<0.001	–0.670	<0.001

Significance level after Bonferroni correction: $p < 0.02$

RESULTS

Recovery data

Blackcaps captured in northern Spain during migration had a more southerly origin when all recovery data compiled in Spain was considered, but this relationship was not significant when only recoveries obtained abroad during breeding season were considered (table 3). Therefore, the origins of the birds handled during migration were not related to latitude. However, blackcaps captured in the east had a more easterly origin than those caught further west, both in autumn and spring (table 3). Thus, their origin differed with longitude during migration in Spain. Blackcaps captured in the north and east of Spain travelled shorter distances (table 4).

Similar results were obtained in winter although, in addition, blackcaps captured in the north during this season had a more eastern origin (table 3). Again, distance from

TABLE 5

ANOVAs used to test whether the points of origin of blackcaps captured (or recaptured) in Iberia differed in relation to flyway (FW; Western Flyway, Eastern Flyway) and period (PE; autumn, spring). Sample size, *n* = 118. Sampling localities (*n* = 6; for details see table 1) were nested into flyways. Lat. = latitude, Lon. = longitude.

[ANOVAs utilizados para comprobar si el origen de las currucas que se capturaron (o recapturaron) en la Península varió entre rutas (PA, ruta Occidental y Oriental) y periodos (PE, paso pos- y pre-nupcial). Tamaño muestral, n = *118. Los puntos de muestreo (*n = *6; para más detalles véase tabla 1) se encuentran anidados en rutas (PA).]*

	SS	***df***	***F***	***P***
Lat. of origin				
PA	41.459	1	0.900	0.345
PE	102.050	1	2.216	0.139
PA × PE	23.475	1	0.510	0.477
Error	1375.949	114		
Lon. of origin				
PA	19.813	1	1.642	0.203
PE	87.990	1	7.290	0.008
PA × PE	94.496	1	7.829	0.006
Error	5250.018	114		
Distance				
PA	5062.879	1	0.021	0.886
PE	75541.100	1	0.311	0.578
PA × PE	92758.879	1	0.381	0.538
Error	2.773×10^7	114		

origin was negatively correlated with the latitude and longitude of recoveries in Spain (table 4).

Focusing on recovery data obtained in and around the sites where the biometric data were obtained in the WF and EF, we observed that blackcaps partly behave as broad-front migrants (fig. 2). We did not detect latitudinal differences in origins of blackcaps ringed (or recaptured) between the WF and EF, but

FIG. 2.—Origins of blackcaps captured on the Western Flyway (black dots) and on the Eastern Flyway (white dots) during both autumn and spring migration periods in Iberia. National borders are shown. *[Origen de las currucas que se capturaron en la Ruta Occidental (puntos negros) y en la Oriental (puntos huecos) durante el periodo de paso migratorio posnupcial y prenupcial. Las líneas señalan los límites entre países.]*

we did detect longitudinal differences (table 5), although these were only significant in autumn (fig. 3): probably due to the very low sample size in spring. It is notable that when all the recovery data obtained in Spain were analysed, significant longitudinal differences were also detected in spring (table 3). Longitude of captures (or recaptures) in Spain was positively correlated with that of recaptures abroad in autumn but not in spring (autumn: $r = 0.385$, $P < 0.001$, $n = 94$; spring: $r = 0.048$, $P = 0.825$, $n = 24$), and not with latitude abroad (autumn: $r = 0.188$, $P = 0.069$, $n = 94$; spring: $r = -0.102$, $P = 0.635$, $n = 24$). This indicates that blackcaps passing along the EF came from further east than those using the WF in autumn (once again interpretation of the spring data is constrained by the low sample size). In addition, the longitude of each sampling site was positively correlated with the mean longitude of recaptures abroad ($r = 0.962$, $P = 0.002$, $n = 6$). The origin distances of recoveries did not differ between periods or flyway (table 5).

In those areas where both migrating and wintering blackcaps were captured, no significant latitudinal ($F_{2,306} = 1.518$, $P = 0.221$) or longitudinal ($F_{2,306} = 0.569$, $P = 0.567$) differences of origin were detected between periods. The origin distance of recoveries did not differ between periods ($F_{2,306} = 0.681$, $P = 0.507$).

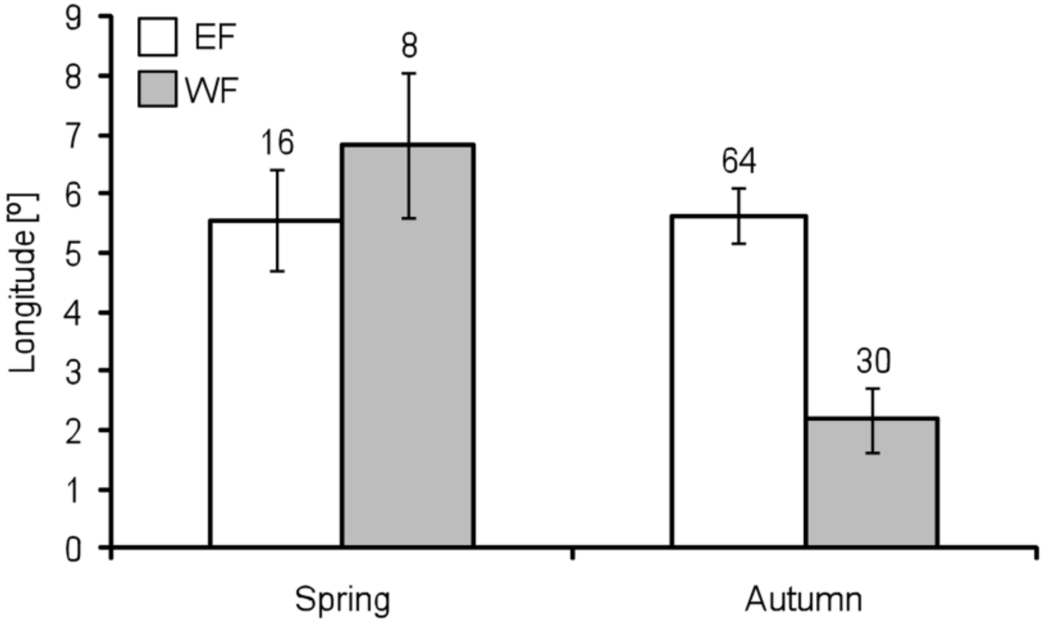

FIG. 3.—Mean longitude (± SE, sample size: positive values indicate east longitude) of origins of blackcaps captured (or recaptured) in Iberia (WF, Western Flyway; EF, Eastern Flyway). An *a posteriori* Tukey-B test detected significant differences in autumn, but not in spring.

[Longitud promedio (± SE, tamaño muestral) de origen de las currucas que se capturan (o recapturan) en la Península (WF, ruta Occidental; EF, ruta Oriental). Un análisis a posteriori de Tukey-B detectó diferencias significativas en el paso posnupcial, pero no en el prenupcial.]

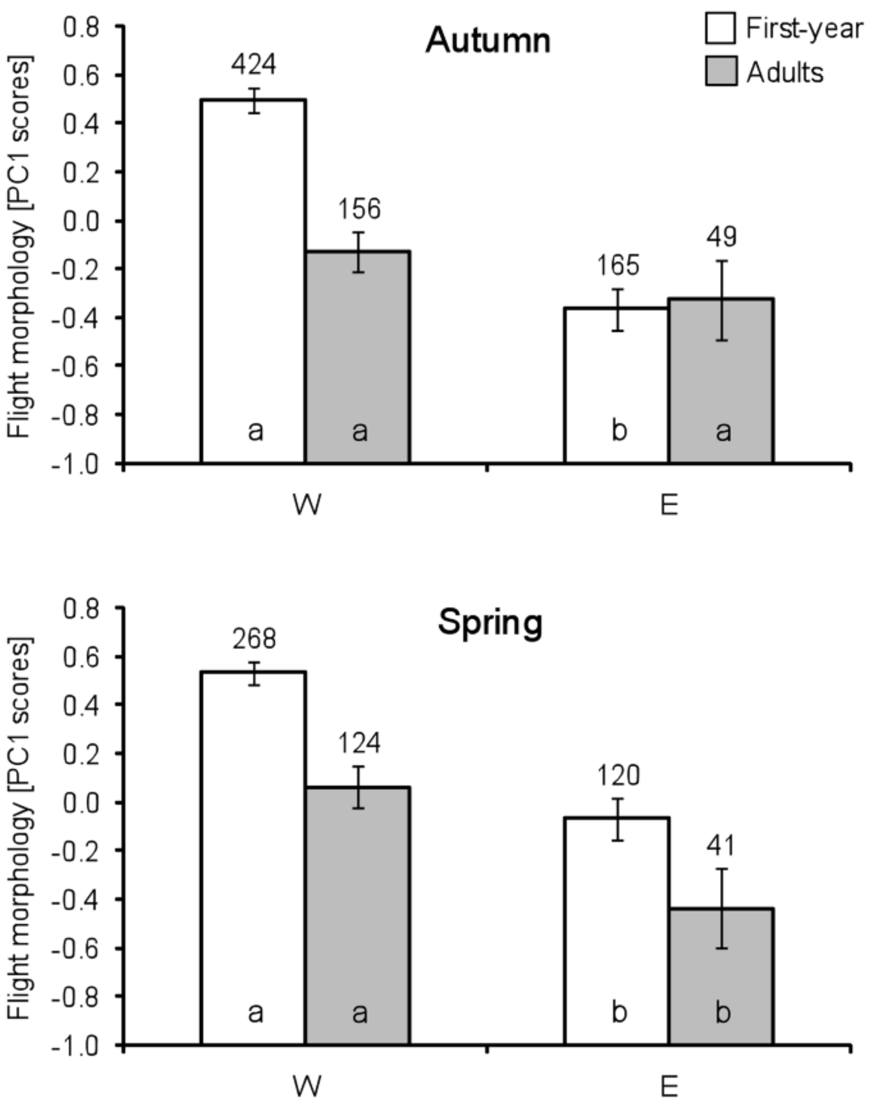

FIG. 4.—Variation in flight-associated morphology (mean ± SE, sample size above bars) in relation to flyways (W, Western; E, Eastern), period and age. The PC1 scores summarize flight morphology: positive scores are linked with short, rounded, wings and large tail-wing ratios, while negative scores are associated with long, more pointed wings and small tail-wing ratios. For each period and age class, means with the same letters are those for which there were not significant differences according to *an a posteriori* test.

[Variaciones en la morfología de vuelo (media ± SE, tamaño muestral) en relación a la ruta (W, Occidental; E, Oriental), el periodo y la edad. La variable PC1 resume la morfología de vuelo: los valores positivos indican alas cortas, redondeadas y una cola más larga, mientras que los valores negativos indican alas largas, apuntadas y una cola más corta. Para cada periodo y edad se agrupan con una misma letra las medias para las que no se detectaron diferencias significativas de acuerdo a un test a posteriori.*]*

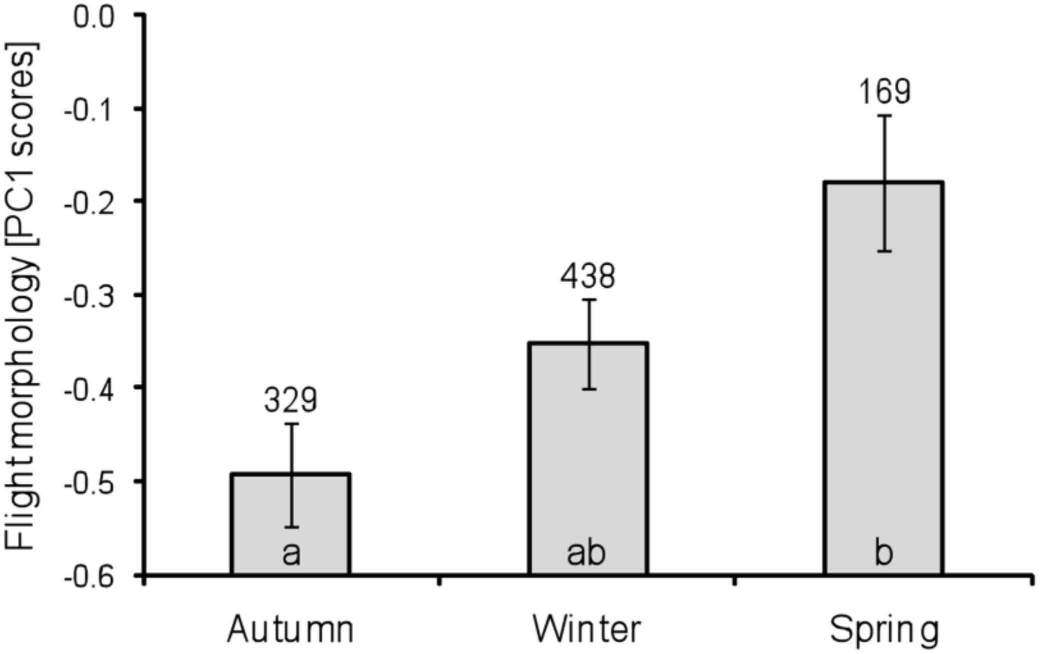

FIG. 5.—Flight-associated morphological variation (mean ± SE, sample size above error bars) during the non-breeding period in areas where both migrating and wintering blackcaps were detected. The letters group periods that did not show significant differences according to an *a posteriori* test.
[Variación en la morfología de vuelo (media ± SE, tamaño muestral) en periodo no reproductor en las zonas donde las currucas se capturaron tanto en paso como en invierno. Se agrupan con una misma letra las medias para las que no se detectaron diferencias significativas de acuerdo a un test a posteriori.*]*

Biometrics

Overall, flight morphology differed in relation to flyways, periods and age classes (table 6). In general, blackcaps captured in the WF and first-year birds had higher PC1 scores (and so relatively more rounded wings) than those from the EF and adults (fig. 4). Adults captured during the autumn migration period were an exception since in this case there were no significant differences between the WF and EF (fig. 4). The effect of sex on flight morphology in this GLM was negligible.

The flight morphology did not vary between periods in areas where both migrating and wintering birds were handled (table 7) but it did so in relation to age and sex. Overall, first-year birds and females had a less marked long-distance migration flight morphology (PC1 scores; age: first-year birds, –0.32 ± 0.04, *n* = 720; adults, –0.55 ± 0.07, *n* = 208; sex: males, –0.44 ± 0.04, *n* = 529; females, –0.28 ± 0.05, *n* = 399). However, the effect of period on flight morphology was almost significant and indeed, an *a posterior* analysis revealed significant differences between periods, with blackcaps having a less marked long-distance migration flight morphology in spring than in autumn (fig. 5).

TABLE 6

General Linear Models used to test the effects of flyways, FW (Western/Eastern), period, PE (autumn/spring), age, AG (sub-adults/adults) and sex, SX, on flight-associated morphology (summarised in a PC1) of blackcaps during migration period in Iberia. Sites were nested into flyways.
[Modelos Lineales Generalizados utilizados para comprobar el efecto de la ruta, PA (Occidental/Oriental), periodo, PE (posnupcial/prenupcial), edad, AG (sub-adultos/adultos) y sexo, SX, en la morfología de vuelo (resumida en el componente PC1 de un ACP) de las currucas que son capturadas en la Península en paso migratorio. Los puntos de muestreo se encuentran anidados en rutas.]

Source of variance	χ^2 Wald	*P*
PA	0.374	0.541
PE	0.004	0.948
AG	350.930	**<0.001**
SX	20.164	0.141
PA × PE	40.233	**0.040**
PA × AG	70.720	**0.005**
PA × SX	0.001	0.981
PE × AG	0.006	0.939
PE × SX	0.078	0.781
AG × SX	0.675	0.411
PA × PE × AG	40.102	**0.043**
PA × PE × SX	0.154	0.695
PA × AG × SX	10.164	0.281
PE × AG × SX	0.017	0.895
PA × PE × AG × SX	0.121	0.728
Site (PA)	218.301	**<0.001**

TABLE 7

General Linear Models used to test the effect of period, PE (autumn/winter/spring), age, AG (sub-adults/adults) and sex, SX, on flight-associated morphology of blackcaps during the non-breeding period within Iberia. Degrees of freedom (df) = 2, except for AG, SX and their interactions (df = 1).
[Modelos Lineales Generalizados utilizados para comprobar el efecto del periodo, PE (posnupcial/invierno/prenupcial), edad, AG (sub-adultos/adultos) y sexo, SX, en la morfología de vuelo (resumida en el componente PC1 de un ACP) de las currucas que son capturadas en la Península tanto en paso migratorio como en invierno. Los grados de libertad son dos salvo para AG, SX y sus interacciones (df = 1).]

Source of variance	χ^2 Wald	*P*
PE	5.387	0.068
AG	11.009	**0.001**
SX	4.766	**0.029**
PE × AG	1.815	0.404
PE × SX	4.956	0.084
AG × SX	0.011	0.916
PE × AG × SX	4.301	0.116

DISCUSSION

Population-associated pathways

Blackcaps ringed everywhere in Europe (excluding Iberia) were recaptured in both the EF and WF in Spain, confirming the idea that the blackcap is a broad-front migrant (Cramp, 1992), with no strong connectivity between capture regions in Europe and Spain. However, birds using the WF had on average more westerly origins than those using the EF: hence some birds apparently use the shortest paths between the breeding and non-breeding quarters (Bairlein, 2001). This strategy is also reported in several species of Afro-tropical European migrants (Zwarts *et al.*, 2009) and thus our results accord with the finding that the non-breeding geographical distribution of many European passerines is a mirror image of their breeding distribution.

As well as between adults in autumn, flight-associated morphology differed between flyways, thus suggesting a geographical segregation of populations. In particular, blackcaps captured on the WF had more rounded and shorter wings as well as relatively longer tails than those from the EF. This morphological difference accords with the finding that blackcaps captured in the EF came from regions further east. It was not, however, associated with distance to capture locations outside Spain. Indeed, blackcaps captured in eastern Spain travelled shorter distances than blackcaps captured further west in Spain. Our results hence support the hypothesis that blackcaps from eastern Europe show a more marked long-distance migration flight morphology, and that these birds tend to arrive in Spain chiefly through the EF. Since more marked long-distance migration flight morphology is associated with longer migration distances, we suggest that blackcaps passing through the EF may overwinter in more distant regions than blackcaps travelling along the WF. We cannot explain, however, why flight morphology did not differ between flyways only in adults in autumn.

Differences between migration periods and winter

Blackcaps captured during the winter in the sites where the biometric data were collected did not come from regions further south than birds captured during the migration period, and they did not differ morphologically. This result does not support the leap-frog migration hypothesis, and contradicts a previous study in which all Iberia was considered (Cantos, 1995), and is also at odds with our own findings on recovery data when all Spain was considered. Such a difference may be due to the fact that the relatively small geographical scale of the present study, relative to the whole of Spain, may have hampered our ability to detect significant differences in both recoveries and biometrics. It may otherwise simply show that blackcaps within our study area in the south and east of Spain originated from a relatively limited geographical area. Flight morphology also differed between age and sex classes. In particular, first-year birds and females had a less marked long-distance flight morphology. This accords with previous research on blackcaps (Pérez-Tris and Tellería, 2001) and other passerines (Alonso and Arizaga, 2005; Arizaga *et al.*, 2007). Selection for relatively shorter and more rounded wings in first-year birds, as compared to adults is considered to be promoted to minimise predation risk (Perez-Tris and Tellería, 2001), since this morphology is reported to increase manoeuverability during flight and, particularly, the ability to take off at a steep angle (Swaddle and Lockwood, 2003). By having relatively longer, more pointed wings, males could arrive at their breeding areas in spring sooner, and this has advantages in terms of breeding success and fitness (Kokko, 1999).

Conclusions

Flight morphology analyses revealed variations between flyways as did analyses using recovery data. In particular blackcaps captured on the EF had more easterly origins: at least in autumn, when the sample size was large enough to be reliable, and they had a more pronounced long-distance migration flight morphology. Because blackcaps captured on the EF did not come from more distant regions than use using the WF, we suggest that the former continue travelling to overwinter in more distant wintering areas than those from the WF. In this case, we consider that flight morphology is an adequate tool to obtain insights into migrant origins at a population level and that it could be used as a complementary method for studying connectivity patterns.

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