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# SEASONAL CHANGES IN ABUNDANCE AND FLIGHT-RELATED MORPHOLOGY REVEAL DIFFERENT MIGRATION PATTERNS IN IBERIAN FOREST PASSERINES

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SUMMARY.—*Seasonal changes in abundance and flight-related morphology reveal different migration patterns in Iberian forest passerines*. Although the attenuation of seasonality southwards in the temperate region is known to be a major determinant of the latitudinal decline in the migratory behaviour of many passerines, the spread of altitudinal migrations in southern areas as a response to similar changes with elevation still remains obscure, principally because no extensive ringing programs have been conducted in these areas. Here we use spatio-temporal changes in abundance and variations in flight-related morphology to infer differences in the migratory behaviour of forest passerines in the Iberian Peninsula, where the environmental optimum for these species moves seasonally between northern highlands (very suitable for breeding but unproductive in winter) and southern lowlands (less suitable for reproduction but highly productive in winter). According to this pattern of environmental conditions, we predict that migratory behaviour should be more intense in the highlands while sedentary behaviour should be the rule in the lowlands. We studied abundance and morphology of several common passerines (Robin *Erithacus rubecula*, Blackbird *Turdus merula*, Blackcap *Sylvia atricapilla*, Firecrest *Regulus ignicapillus*, Blue Tit *Parus caeruleus* and Great Tit *P. major*). In all species but Blackbirds, winter abundance increased in lowlands but decreased in highlands, despite some European migrants arriving at this later area for wintering. A common pattern of variation in flight-related morphology was found, birds having longer and more pointed wings in highlands. In addition, a trans-Saharan migrant species that we used as a control (the Nightingale *Luscinia megarhynchos*) did not differ in these traits between regions. Both the seasonal changes in abundance distribution and the morphological variations between regions indicate a stronger migratory behaviour of birds in highlands as compared to lowlands. This kind of movements, which are probably widespread across the Mediterranean region, are likely to constitute small-scale, altitudinal migration patterns overlapping with the broader latitudinal migratory system in the Palaearctic.

*Key words*: ecomorphology, environmental seasonality, Iberian Peninsula, Mediterranean forests, migratory behaviour, spatio-temporal distribution.

RESUMEN.—*Los cambios estacionales de abundancia y la morfometría del ala y de la cola sugieren diferentes patrones migratorios en los paseriformes forestales ibéricos*. Un patrón biogeográfico sobradamente conocido es la acentuación del comportamiento migrador de las aves del Paleártico con la latitud como consecuencia del aumento de la estacionalidad. Sin embargo, no está tan claro si las aves responden de igual modo a las variaciones de estacionalidad en los sectores más meridionales, donde la existencia de montañas y mesetas da lugar a una elevada heterogeneidad ambiental (Fig. 1). Esta escasez de información puede deberse al limitado esfuerzo de anillamiento aplicado al estudio de los movimientos de estas poblaciones de aves, lo que obliga a utilizar aproximaciones alternativas que permitan inferir el alcance relativo de sus movimientos. En este trabajo integramos información procedente de (1) cambios estacionales en la abundancia de los paseriformes forestales entre la mitad norte (montañas y mesetas, adecuadas para la reproducción pero duras en invierno) y la mitad sur (menos elevada y muy adecuada para la invernada) de la península Ibérica (Fig. 1) y (2) datos procedentes del estudio de algunos rasgos morfométricos relacionados con el comportamiento migrador de las aves. Nuestro objetivo es ilustrar si el comportamiento migrador de estas especies es más acusado en las mesetas que en las llanuras de la mitad sur peninsular. Para ello estudiamos seis especies comunes de invernada presahariana (Petirrojo *Erithacus rubecula*, Mirlo Común *Turdus merula*, Curruca Capirotada *Sylvia atricapilla*, Reyezuelo Listado *Regulus ignicapillus*, Herrerillo Común *Parus caeruleus* y Carbonero Común *P. major*), más una especie trans-sahariana, el Ruiseñor Común *Luscinia megarhynchos*, que utilizamos como control dado su comportamiento migrador homogéneo en toda la Península. Revisamos 67 estudios de comunidades ampliamente distribuidos por la Península, en los que la abundancia de estas especies había sido medida en primavera e invierno. En todas las especies, con excepción del Mirlo Común, la abundancia invernal aumentó en la mitad sur peninsular y disminuyó en las mesetas (Fig. 2), aunque en al-

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gunos casos este patrón pudo verse afectado por la llegada de invernantes desde áreas más norteñas. Medimos individuos de cada una de estas especies en cinco localidades diferentes, tres en las mesetas y dos en las llanuras meridionales (Fig. 1 y Apéndice), lo que permitió establecer un patrón común en la morfología asociada con el comportamiento migrador. Controlando el tamaño estructural de las aves (Tabla 1 y Fig. 3), las poblaciones de las mesetas presentaron en general alas más largas y apuntadas (medido el apuntamiento alar mediante la primera componente principal extraída en un análisis de componentes principales con las distancias entre la punta de cada primaria y la punta del ala; Tabla 2), así como colas más cortas, que las de las llanuras. La única excepción fue el Ruiseñor Común, que mostró rasgos similares en ambos sectores de acuerdo con su patrón migratorio (Tablas 3 y 4; Fig. 4). Los cambios estacionales en abundancia y las variaciones morfológicas fueron consistentes, por lo tanto, con una mayor intensidad de los movimientos de las aves de las mesetas. Nuestros resultados confirman la variación intraespecífica descrita para muchas de estas especies en la península Ibérica (Tabla 5) y suponen un paso adelante en el conocimiento de dicha variación al darle un significado ecológico, en relación con el comportamiento migrador predominante en cada región peninsular. De acuerdo con la distribución de las áreas montañosas en el Paleártico, este tipo de movimientos – probablemente de corto alcance – podrían estar muy extendidos en la cuenca Mediterránea, solapándose con los movimientos latitudinales de más amplio rango de estas especies.

*Palabras clave:* bosques mediterráneos, comportamiento migrador, distribución espacio-temporal, ecomorfología, estacionalidad ambiental, península Ibérica.

## INTRODUCTION

Migration is a dynamic response of birds to changing environmental conditions through which many populations and species track seasonal productive outputs across environmental gradients (Baker, 1978; Berthold, 1996). Seasonal changes in productivity are considered to trigger large-scale migrations (Moreau, 1972; Greenberg, 1980; Alerstam & Högstedt, 1982), which have long been studied by research programs based on the analysis of ringing recoveries (Gauthreaux, 1996). Today we have a good knowledge of the migratory patterns of many bird species, including the changing intensity of migratory behaviour across latitudinal gradients (Alerstam, 1990; Berthold, 1993). Variation in the extent of migratory behaviour is considered to be the outcome of an increasing spring productivity and a decreasing winter suitability with latitude, a correlation which has been profusely studied in almost all latitudinal migratory systems in the world (MacArthur, 1959; Willson, 1976; Herrera, 1978; Newton & Dale, 1996a, b; Chesser, 1998). However, although elevation causes variations in seasonal productivity at mid and low latitudes that parallel those associated with latitude all across the temperate zone, little is known about the relevance of altitudinal migrations in this area (Mead, 1983). This gap in our understanding of avian migratory systems is undoubtedly due to the lack of extensive ringing programs applied to the relatively small bird populations breeding in montane areas (Gauthreaux, 1996). Because of these limitations in the study of altitudinal migrations, the scant evidence of such movements has been obtained in rather scattered work, which in many occasions dealt with other aspects of the biology of birds and only referred to altitudinal movements as a secondary topic in the study (e.g. Czajkowski & Dejonghe, 1981; Rabenold & Rabenold, 1985; Lo Valvo *et al.*, 1988).

In this paper we explore the movements of forest passerines in the Iberian Peninsula, where highlands and mountains are surrounded by mild Mediterranean lowlands making up a suitable scenario for the development of altitudinal migrations (Fig. 1). The northern half of Iberia is characterised by plateaux and mountains where forest passerines meet good conditions for reproduction, contrasting with southern Iberian environments where the summer drought prevents many of these species from breeding (Tellería & Santos, 1993; 1994; Tellería *et al.*, 1999). The opposite occurs in winter, which makes northern Iberian forests less productive, while the southern lowlands and the Mediterranean coasts experience a peak of primary production (Tellería, 1988; Tellería *et al.*, 1988). Accordingly, these lowlands receive a large number of migrant birds coming from other parts of Europe to exploit the sprouting vegetation and the ripening of fruiting shrubs in winter (Herrera, 1981; 1998; Tellería *et al.*, 1988; Fuentes, 1992; Blondel & Aronson, 1999). One can thus postulate that populations of forest birds breeding in lowlands will rely on these abundant winter resources, while highland populations will be forced to escape the impaired environmental conditions in northern Iberia during winter. However, ringing data are scarce for Iberian forest birds and do not provide conclusive information about seasonal movements (Tellería *et al.*, 1999). Because this traditional method for the study of bird migration does not allow us to disentangle the possible variations in migratory behaviour of Iberian forest birds, we have addressed the topic by relying on alternative methods based on correlates of that migratory behaviour. Thus, we have inferred the movements of these species in highlands and lowlands through two complementary approaches:

A) *Seasonal changes in abundance*. Migratory movements are of prime importance in determining the spatio-temporal changes in the structure of bird communities. In the southern Iberian forests, the arrival of Palaearctic migrants for wintering causes a huge increase in both abundance and richness of birds (Herrera, 1981; Tellería, 1988). Because of the problems outlined above, the possible contribution to this increase of the comparatively small northern Iberian populations remains unknown. However, seasonal changes in abundance can help us to unravel to what extent forest passerines leave the northern highlands in winter. According to the seasonal variation in environmental conditions in the Iberian Peninsula, we can predict a decrease in abundance in highlands parallel to the well-known increase in lowlands.

B) *Morphological variation*. A common pattern in passerines is that differences among populations or species in the extent of their migrations are related to differences in flight-related morphological traits (Leisler & Winkler, 1985; Winkler & Leisler, 1992). These differences have been interpreted as the outcome of migration-related selective pressures opposing manoeuvrability-related selective forces, which would shape different morphological traits depending on the extent of migratory journeys. Longer and more pointed wings improve endurance in long non-stop flights, while short and round wings improve efficacy in take-offs (Pennycuick, 1989). Thus, populations that undertake longer migrations usually show longer and more pointed wings than their sedentary counterparts (Rayner, 1988; Norberg, 1990; Winkler & Leisler, 1992). Also, it is known that a longer tail increases drag during flights, and migratory birds have been observed to have shorter tails than sedentary ones even at the expense of a somehow impaired manoeuvrability (Winkler & Leisler, 1992; Norberg, 1995). Therefore, when changes in migratory behaviour among populations of a species cannot be studied directly, the evaluation of changes in the morphological correlates of migratory behaviour may provide a formal way to test for such differences (Wainwright, 1994). According to our hypothesis, we predict that highland populations will have longer and more pointed wings, as well as a shorter tail, than conspecific populations breeding in lowlands.

## METHODS

### *The Iberian Peninsula as a study area*

The Iberian Peninsula is located at the southern edge of the Western Palaearctic, between 36° N and 43° N. Environmental variation due to the gradually decreasing oceanic influence towards south-east, together with elevation in plateaux and mountains, permits the differentiation of several bioclimatic sectors (see Font, 1983 for details; Fig. 1). The northern Atlantic belt is a rainy sector with mild winters, not included within the Mediterranean realm and hence excluded from our study. Further inland, the Iberian Central Plateau (the so-called highlands in this paper), emerges as a huge extension of more than 80000 km$^2$ with an elevation higher than 600 m a.s.l. This region has a seasonal pattern of primary production, showing a marked contrast between temperate summers and harsh winters (Aschmann, 1971; Font, 1983). In spring, forest passerines are widespread and abundant in these highlands, making up rich communities in nearly all forested areas in the region (Tellería & Santos, 1993; 1994). In the southern half of Iberia, the southern Mediterranean region (lowlands) is characterised by a strong summer drought, which constrains the distribution of forest birds throughout the region except in some rainy mountains and coastal sectors (Tellería & Santos, 1993; 1994). During winter, however, the temperate and relatively

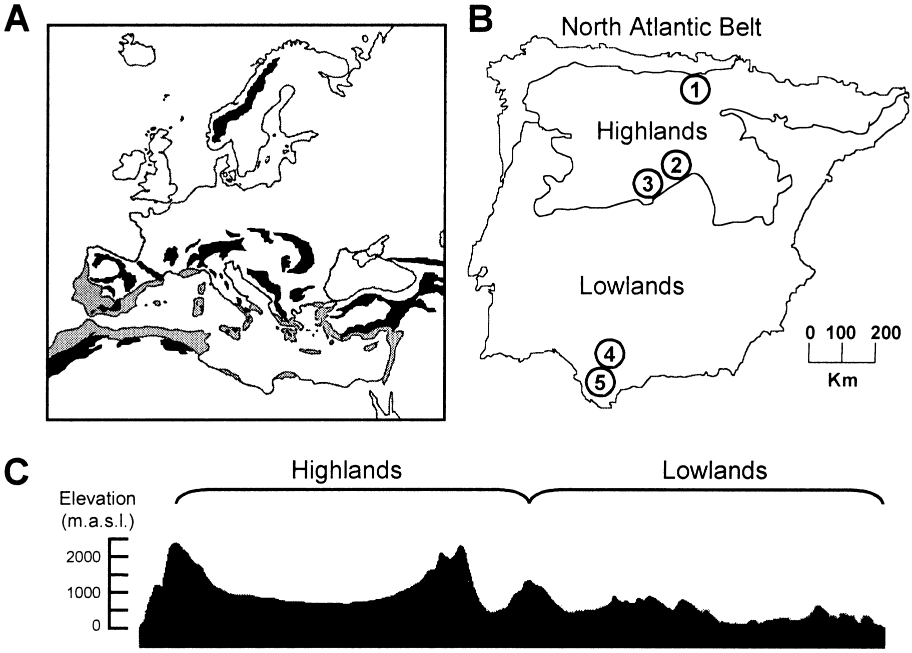

FIG. 1.—A) Distribution of the warm Mediterranean climate (in grey, according to Aschmann, 1971) and the most important mountains in the Western Palearctic (in black), indicating the potential for altitudinal movements of birds in the Mediterranean zone. B) Regional division of the Iberian Peninsula in this study. We have differentiated between the northern highlands (very productive in spring but unproductive in winter) and the southern lowlands (with the opposite trend of primary production). The northern, mild Eurosiberian area has been excluded. The localities where we trapped individuals are shown with numbers (1: Álava; 2: Guadarrama; 3: Madrid; 4: Ojén and 5: Tarifa). C) North-to-south altitudinal profile showing the contrast between highlands and lowlands.

*[A) Distribución del clima Mediterraneo térmico (en gris, según Aschmann, 1971) y de las montañas más importantes del Paleártico Occidental donde pudieran darse movimientos altitudinales (en negro). B) División de la península Ibérica seguida en este estudio. Hemos diferenciado entre mesetas norteñas (muy productivas en primavera pero improductivas en invierno;* Highlands) *y llanuras meridionales (con patrones opuestos de productividad primaria;* Lowlands). *Se ha excluido la atemperada Región Eurosiberiana del norte ibérico. Las localidades donde se capturaron aves se expresan con números (1: Álava; 2: Guadarrama; 3: Madrid; 4: Ojén y 5: Tarifa). C) Perfil Norte-Sur que muestra el contraste altitudinal entre las mesetas septentrionales y las llanuras meridionales.]*

moist environmental conditions allow for an intense production of fruits and the activity of many insects (Herrera, 1981; Mooney, 1981), which sustain huge populations of wintering birds (Tellería, 1988; Tellería *et al.*, 1988; 1999; Blondel & Aronson, 1999).

### *The study of bird abundance*

We used the comprehensive review by Tellería *et al.* (1999) on the distribution of bird abundances in the Iberian Peninsula. These authors gathered most of the work published so far on the composition and abundance of Iberian bird communities. From this general database, we selected those studies in which bird densities were estimated by line-transect counts over the same itineraries in both spring and winter. By using only the counts that were repeated by the same authors we were able to control for the within-site changes in abundance when testing for variation between regions. The final data-set was composed of 67 survey sites widely distributed across the Iberian Peninsula (42 in highlands and 25 in lowlands; see Tellería *et al.*, 1999 for details). The species studied were those for which we captured enough individuals to perform sound analyses of morphological variation (see below). For each species, we conducted a two-way ANOVA with the region (highlands *vs*. lowlands) as a between-subjects factor and the season (spring *vs*. winter) as a within-subjects factor. In this ANOVA, the interaction will test for the hypothesised seasonal change in the regional distribution of abundance of each species. Only those sites in which the corresponding species was found at least once were used in these analyses.

### *The localities where birds were trapped*

We trapped forest passerines from 1995 to 1999 during May-July in five localities of the Iberian Peninsula (Fig. 1), which were representative of highland and lowland environments (see Carbonell & Tellería, 1998a for a detailed description of the study sites):

*Highlands*: a) Álava (42°55′N 2°29′W, mean elevation 620 m; mean annual rainfall 1000-1500 mm; mean annual temperature 12°C). This site lies on the northern edge of the Iberian highlands, and it is covered by mixed oak and maple forests (*Quercus faginea*, *Q. robur* and *Acer campestre*). b) Sierra de Guadarrama (40°54′N 3°53′W; 1100 m; 700-1000 mm; 10°C), a mountain range covered by *Quercus pyrenaica* and *Pinus sylvestris* forests. Birds were caught in mixed *Fraxinus excelsior, Alnus glutinosa* and *Quercus pyrenaica* forests interspersed with meadows. c) Madrid (40°30′N 3°4′W; 600 m; 300-500 mm; 14°C), a set of riparian forests (*Populus nigra*, *Tamarix gallica*, *Salix* spp.) along the Guadarrama and Jarama Rivers, which flow through a cereal-farming landscape.

*Lowlands:* a) Sierra de Ojén (36°01′N 5°36′W; 250 m; 1000-1500 mm; 16°C). Birds were caught in rainy hills covered by mixed *Quercus suber* and *Q. canariensis* forests. b) Tarifa (36°01′N 5°36′W; 0-5 m; 700-1000 mm; 18°C). This sector lies at the foot of the Sierra de Ojén, near the Atlantic coast. Forest birds occupy riverside formations with *Alnus glutinosa*, *Populus nigra* and *Nerium oleander* in the Jara River, which flows through deforested grasslands.

### *Trapping and measurement of birds*

Mist-netting was conducted in each locality during a research program originally devoted to the study of morphology and body condition of Blackcaps *Sylvia atricapilla* (Carbonell & Tellería, 1998b; 1999; Tellería & Carbonell, 1999) and Robins *Erithacus rubecula* (Pérez-Tris *et al*., 2000a), so these two species were the most abundant in our data-set. Proper sample sizes for morphometric analyses were obtained for six species, beloging to three families of European forest passerines: thrushes (Robin and Blackbird *Turdus merula*; F. Turdidae), warblers (Blackcap and Firecrest *Regulus ignicapillus*; F. Sylviidae) and tits (Blue Tit *Parus caeruleus* and Great Tit *P. major*; F. Paridae). These species differ in most features of ecology and behaviour (diet and feeding strategies, nesting places, social systems, etc.), and may be considered as potential short-distance migrants as all of them have migratory populations in some part of their range that spend the winter in the Mediterranean Region (Cramp, 1988; 1992; Cramp & Perrins, 1993). We also gathered enough data for one long-distance migrant whose populations spend the winter in sub-Saharan Africa (the Nightingale *Luscinia megarhynchos*; F. Turdidae). This species was used as a control for the relationship between flight-related morphology and migratory behaviour. Thus, according to our hypothesis, no morphological change should be found between highland and lowland Nightingale populations, since all of them have the same trans-Saharan migratory pattern.

Body measurements included tarsus length (to the last scale before the toes), the length of the straightened tail, maximum wing chord and bill depth. Bill depth was chosen instead of bill length as a measure of bill size because the latter takes longer for growing, and hence most juveniles had not attained its final size at the moment of their capture. We also recorded the wing formula by measuring the distances from the tip of each primary (1 to 9, numbered descendantly) to the wing tip (the so-called primary distances). Measurement methods were those proposed by Svensson (1992) and are fully described in Tellería and Carbonell (1999). We did not measure wings or tails that were still growing, and some individuals could not be measured completely because of time restrictions. Due to these missing values, sample sizes were heterogeneous. A summary of biometrics of the species studied can be found in the Appendix.

We aged individuals according to plumage characters. In all the seven species studied, adults undertake a complete post-nuptial moult late in summer, whereas juveniles perform a partial moult which does not affect flight feathers (but Great Tits frequently moult the tail in the post-juvenile moult; Jenni & Winkler, 1994; *pers. obs.*). Thus, three age classes can be recognised in summer before the post-nuptial moult: more than one-year old birds (individuals with a single generation of feathers moulted completely in the previous year), one-year old birds (which moulted partially and retained juvenile flight feathers) and fledglings, which have a juvenile plumage in prime condition. Because one-year old individuals have the same flight-feathers they had as fledglings, these birds were classified as juveniles with regard to flight-related morphology. In our analyses, however, we only distinguished between juveniles (birds that were born in the ongoing study year) and adults (which included birds that were born in the preceding breeding season or before). The reason of this distinction is that the change in wing length and shape after the first complete post-nuptial moult (if the juvenile and the adult flight plumages of the same individual are compared when they are in prime condition) is negligible as compared to the decrease due to one-year feather abrasion in either second-year or older birds (*unpubl. data*; see Flegg & Cox, 1969; Francis & Wood, 1989 for similar results).

Sexing adults was difficult in the sexually-monomorphic species (Robins, Nightingales, and most Blue Tits) because many birds had already lost their reproductive characters (brood-patch or protruding cloaca) when we trapped them. In addition, no sexual dimorphism is apparent in the first-year birds of any of the species studied (notice that size-based methods cannot be used in this study). Therefore, we did not consider the sex of birds in our analyses. Although sexual size dimorphism is common among passerines (see Cramp, 1988, 1992; Cramp & Perrins, 1993 for reviews on the species considered in this paper), it should not have affected our results given that (1) sexual dimorphism concerns size but not shape (i.e. proportions), so that no effect of gender on shape remains after differences in body size among individuals were statistically controlled for in our analyses (see below), and (2) the sex-ratio was homogeneous among populations ($P > 0.1$ for all chi-square tests comparing sex-ratios among localities or between highlands and lowlands).

### *The analyses of morphology*

When studying the changes between bird populations in flight-related morphology, it is important to control for possible variations in body size that could confound actual variations in body shape between individuals (Norman, 1997). We discarded tarsus length for this purpose despite it having been shown to be a good correlate of avian body size (Senar & Pascual, 1997) because this trait could vary between populations independently of body size (Winkler & Leisler, 1985; 1992; Tellería & Carbonell, 1999). Therefore, our first step was to derive indices of body size for each of the seven species by means of a principal component analysis (PCA) of body measurements (tarsus length, bill depth, wing length and tail length). This method allows to extract an index of the structural size of individuals (Rising & Somers, 1989; Freeman & Jackson, 1990) effective for measuring the nutrient reserve-independent size of birds (Piersma & Davidson, 1991). Usually, every measurement had a high loading in the first component of body size (bsPC1), which sometimes was the only one extracted by the PCA. In these cases, bsPC1 was therefore interpretable as a proper index of structural size (Table 1). When the interpretation of principal components was not so straightforward, we chose the index of structural size by first relying on the factor loadings of skeletal measurements (tarsus and bill) in each component and, if still in doubt, by checking the efficiency of each component in predicting body mass (Rising & Somers, 1989; Senar & Pascual, 1997). Thus, the bsPC1 was considered to be the best index of structural size in all species but the Robin, for which we used the bsPC2

TABLE 1

Coefficients of correlation between each body measurement and the principal components of body size extracted by PCA. For species in which more than one component were extracted (bsPC1 or bsPC2), the asterisk indicates the one selected as an index of structural size.

*[Coeficientes de correlación entre cada medida corporal y la componente principal descriptora del tamaño obtenida mediante un ACP. En el caso de aquellas especies en las que se obtuvo más de una componente (bsPC1 o bsPC2), el asterisco indica la utilizada como medida de tamaño estructural.]*

| Species *[Especies]* | *n* | Tarsus *[Tarso]* | Bill depth *[Altura del pico]* | Wing *[Ala]* | Tail *[Cola]* | Eigenvalues *[Autovalores]* | Variance (%) *[Varianza (%)]* |
|---|---|---|---|---|---|---|---|
| *E. rubecula* | 218 | | | | | | |
| bsPC1 | | 0.11 | –0.36 | 0.87 | 0.88 | 1.68 | 42.08 |
| bsPC2* | | 0.89 | 0.46 | 0.10 | –0.02 | 1.02 | 25.43 |
| *T. merula* | 58 | | | | | | |
| bsPC1* | | 0.01 | 0.38 | 0.85 | 0.85 | 1.59 | 39.81 |
| bsPC2 | | –0.87 | 0.50 | –0.15 | –0.07 | 1.04 | 25.90 |
| *S. atricapilla* | 515 | | | | | | |
| bsPC1 | | 0.56 | 0.47 | 0.74 | 0.80 | 1.73 | 43.18 |
| *R. ignicapillus* | 20 | | | | | | |
| bsPC1* | | 0.62 | 0.02 | 0.94 | 0.85 | 1.99 | 49.68 |
| bsPC2 | | –0.54 | 0.89 | 0.02 | 0.35 | 1.21 | 30.31 |
| *P. caeruleus* | 45 | | | | | | |
| bsPC1 | | 0.67 | 0.81 | 0.91 | 0.79 | 2.55 | 63.65 |
| *P. major* | 58 | | | | | | |
| bsPC1 | | 0.77 | 0.44 | 0.86 | 0.83 | 2.21 | 55.28 |
| *L. megarhynchos* | 46 | | | | | | |
| bsPC1* | | 0.74 | –0.05 | 0.94 | 0.88 | 2.21 | 55.23 |
| bsPC2 | | 0.43 | –0.95 | –0.20 | –0.20 | 1.16 | 28.97 |

(Table 1). Differences in body size between populations were examined as a first step in the analysis of morphological variation.

We used PCA of the primary distances to obtain wing-shape indices for each species (Chandler & Mulvihill, 1988; Lockwood *et al.*, 1998). These analyses were consistent among species in extracting a first component of wing shape (wsPC1) in which the innermost primaries had a high loading (Table 2). Therefore, we used the wsPC1 as a proper index of wing pointedness in all species.

Our statistical analyses were designed for testing specifically the hypothesis that highland populations have a morphology that is better suited to long-distance flights than that of lowland populations. In this study, the flight-related morphology is a non-measurable variable defined by the covariation of wing length, tail length and wing pointedness (in all species studied, these traits correlated to each other more than expected by chance, as shown by Bartlett's tests for sphericity with $P < 0.0001$ in all cases). In order to test for changes in flight-related morphology controlling for age and body size, we designed a multivariate general linear model in which locality and age were categorical predictors (factors), the structural size (bsPC1, or bsPC2 in the Robin) was a continuous predictor (covariate), and wing length, tail length, and wing pointedness (wsPC1) were the dependent variables. First of all, we tested for interactions between the factors and the covariate. Significant deviations from parallelism were only found in Blackcaps, in which the effect of body size changed between age classes. Therefore, in this species we estimated a generalisable effect of body size on flight-related morphology by nesting it within each age class. In the remaining species, the model included

TABLE 2

Coefficients of correlation between each primary distance (the distance from the tip of each primary feather to the wing tip) and the first principal component of wing shape extracted by PCA (wsPC1) used as an index of wing pointedness. Sample sizes are also shown (*n*). Primaries 6 and 7 showed no variance in Firecrests because they constituted the wing tip in all individuals.
*[Coeficientes de correlación entre la distancia de cada primaria (1 a 9) a la punta del ala y la primera componente de la forma del ala obtenida mediante un ACP (wsPC1), que hemos usado como índice de apuntamiento alar. También se indican los tamaños muestrales (*n*). Las primarias 6 y 7 no presentaron varianza en el Reyezuelo Listado, dado que constituyeron la punta del ala en todos los individuos estudiados.]*

| | *E. rubecula* | *T. merula* | *S. atricapilla* | *R. ignicapillus* | *P. caeruleus* | *P. major* | *L. megarhynchos* |
|---|---|---|---|---|---|---|---|
| *n* | 200 | 49 | 307 | 14 | 30 | 42 | 22 |
| Primary 9 | 0.10 | 0.18 | –0.28 | 0.36 | –0.09 | –0.32 | –0.02 |
| Primary 8 | –0.09 | –0.22 | –0.39 | 0.44 | –0.49 | –0.49 | 0.16 |
| Primary 7 | –0.18 | –0.22 | 0.31 | — | –0.26 | –0.34 | 0.25 |
| Primary 6 | 0.44 | 0.48 | 0.81 | — | 0.49 | 0.71 | 0.77 |
| Primary 5 | 0.67 | 0.89 | 0.93 | 0.72 | 0.76 | 0.77 | 0.95 |
| Primary 4 | 0.91 | 0.94 | 0.95 | 0.89 | 0.88 | 0.86 | 0.98 |
| Primary 3 | 0.93 | 0.95 | 0.95 | 0.94 | 0.93 | 0.89 | 0.96 |
| Primary 2 | 0.91 | 0.95 | 0.94 | 0.96 | 0.90 | 0.88 | 0.96 |
| Primary 1 | 0.91 | 0.91 | 0.90 | 0.99 | 0.87 | 0.74 | 0.90 |
| Eigenvalue *[Autovalores]* | 4.04 | 4.65 | 5.35 | 4.43 | 4.34 | 4.41 | 5.18 |
| Variance (%) *[Varianza (%)]* | 44.92 | 51.70 | 59.39 | 63.26 | 48.24 | 49.04 | 57.54 |

the usual terms in a two-way multivariate ANCOVA (the effect of both factors and their interaction, and the effect of the covariate). The corresponding model was then used to test for differences between regions by planning specific comparisons (Lindman, 1974) between highland localities (Álava, Guadarrama and Madrid) and lowland localities (Sierra de Ojén and Tarifa). Not all species occurred in all study sites, so different sets of localities were used to compare between highlands and lowlands in each case (Table 3). In some instances, however, we did not trap either adults or juveniles in some locality, which translated into incomplete designs for some of the species studied. In these cases, a Type IV sum of squares approach was adopted for testing our hypothesis (Table 3; see Goodnight, 1980). Once the differences in overall flight-related morphology were evaluated, we conducted univariate analyses (with the same terms as in the corresponding multivariate model designs) to evaluate which particular traits were responsible for the overall effect. To ease the interpretation of our results, we conducted these *post hoc* analyses in all species, regardless of whether overall differences in flight-related morphology were significant or not. All the analyses were done with the Visual GLM module implemented in STATISTICA 5.5 (StatSoft, 1999).

In all species except Blackcaps and Robins, the multivariate approach used to assess changes in flight-related morphology should have caused a dramatic decrease in power due to the reduction of an already small sample size. To check whether this affected our results, we repeated the univariate analyses for wing length and tail length considering all the birds with data for these measurements (wing pointedness was the missing value in all cases with incomplete data). We compared the size and the significance of these effects to see whether increasing sample sizes influenced our results.

## RESULTS

### *Seasonal changes in abundance*

Four species (Robins, Blackcaps and both tits) of the six passerines for which analyses of

Table 3

Models of planned comparisons used to test for differences between highlands and lowlands in flight-related morphology. For each species, the sample sizes of adults and juveniles in Álava (locality 1), Guadarrama (2), Madrid (3), Sierra de Ojén (4) and Tarifa (5) are shown (hyphens indicate the absence as breeder of the species from the corresponding locality). Below, the contrast vector that defines the comparison between highlands and lowlands in a multivariate general linear model with wing length, wing pointedness (wsPC1, see Table 2) and tail length as dependent variables (whose covariation defines flight-related morphology), population and age as categorical predictors, and body size (bsPC1 or bsPC2, see Table 1) as a covariate is shown.
*[Modelos de comparaciones planificadas utilizados para examinar las diferencias entre las aves de las mesetas y de la mitad sur peninsular en los rasgos morfológicos relacionados con el vuelo. Para cada especie se indica, en primer lugar, el tamaño muestral (*n*) para adultos y jóvenes de Álava (localidad 1), Guadarrama (2), Madrid (3), Sierra de Ojén (4) y Tarifa (5) (los guiones indican la ausencia de la especie como reproductora). Debajo, se presenta el vector de contraste (Contrast vector) que define la comparación entre los dos sectores en un modelo general lineal multivariante con la longitud y apuntamiento del ala (wsPC1, véase Tabla 2) y la longitud de la cola como variables dependientes (cuya covariación define la morfología relacionada con el vuelo), la población y la edad como variables categóricas, y el tamaño corporal (bsPC1 o bsPC2, véase Tabla 1) como covariante.]*

| | | Adults *[Adultos]* | | | | | Juveniles *[Jóvenes]* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Localities *[Localidades]* | | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| *E. rubecula* | *n* | 11 | 14 | — | 18 | — | 43 | 53 | — | 42 | — |
| | Contrast vector | 1 | 1 | | –2 | | 1 | 1 | | –2 | |
| *T. merula* | *n* | 6 | 15 | 0 | 5 | 1 | 6 | 10 | 1 | 1 | 2 |
| | Contrast vector | 4 | 4 | 0 | –5 | –5 | 4 | 4 | 4 | –5 | –5 |
| *S. atricapilla* | *n* | 27 | 41 | 7 | 47 | 10 | 62 | 28 | 11 | 48 | 20 |
| | Contrast vector | 2 | 2 | 2 | –3 | –3 | 2 | 2 | 2 | –3 | –3 |
| *R. ignicapillus* | *n* | 2 | 2 | — | 1 | — | 4 | 1 | — | 4 | — |
| | Contrast vector | 1 | 1 | | –2 | | 1 | 1 | | –2 | |
| *P. caeruleus* | *n* | 0 | 3 | — | 2 | 0 | 10 | 4 | — | 5 | 5 |
| | Contrast vector | 0 | 1 | | –1 | 0 | 1 | 1 | | –1 | –1 |
| *P. major* | *n* | 1 | 2 | 0 | 2 | 0 | 20 | 2 | 7 | 3 | 3 |
| | Contrast vector | 3 | 3 | 0 | –5 | 0 | 3 | 3 | 3 | –5 | –5 |
| *L. megarhynchos* | *n* | — | 10 | 4 | 1 | 3 | — | 1 | 1 | 0 | 1 |
| | Contrast vector | | 3 | 3 | –4 | –4 | | 3 | 3 | 0 | –4 |

seasonal changes in abundance distribution were done (the Nightingale, a summer visitor, was excluded) significantly decreased its abundance in highlands and increased their numbers in lowlands during winter (Fig. 2). Firecrests showed a similar but not so marked trend, increasing their winter abundance in lowlands but showing only a weak decrease in highlands. Blackbirds did not show any trend that could be interpreted as a seasonal rearrangement of their numbers in the Iberian Peninsula. Finally, the breeding abundances of Nightingales were similar in both Iberian regions (Fig. 2).

### *Morphological variation*

Structural size showed different trends of regional variation in the species studied (Fig. 3). Robins showed a homogeneous body size in both regions. Blackcaps and Blackbirds were larger in lowlands, although this difference was significant only in Blackcaps. In the remaining

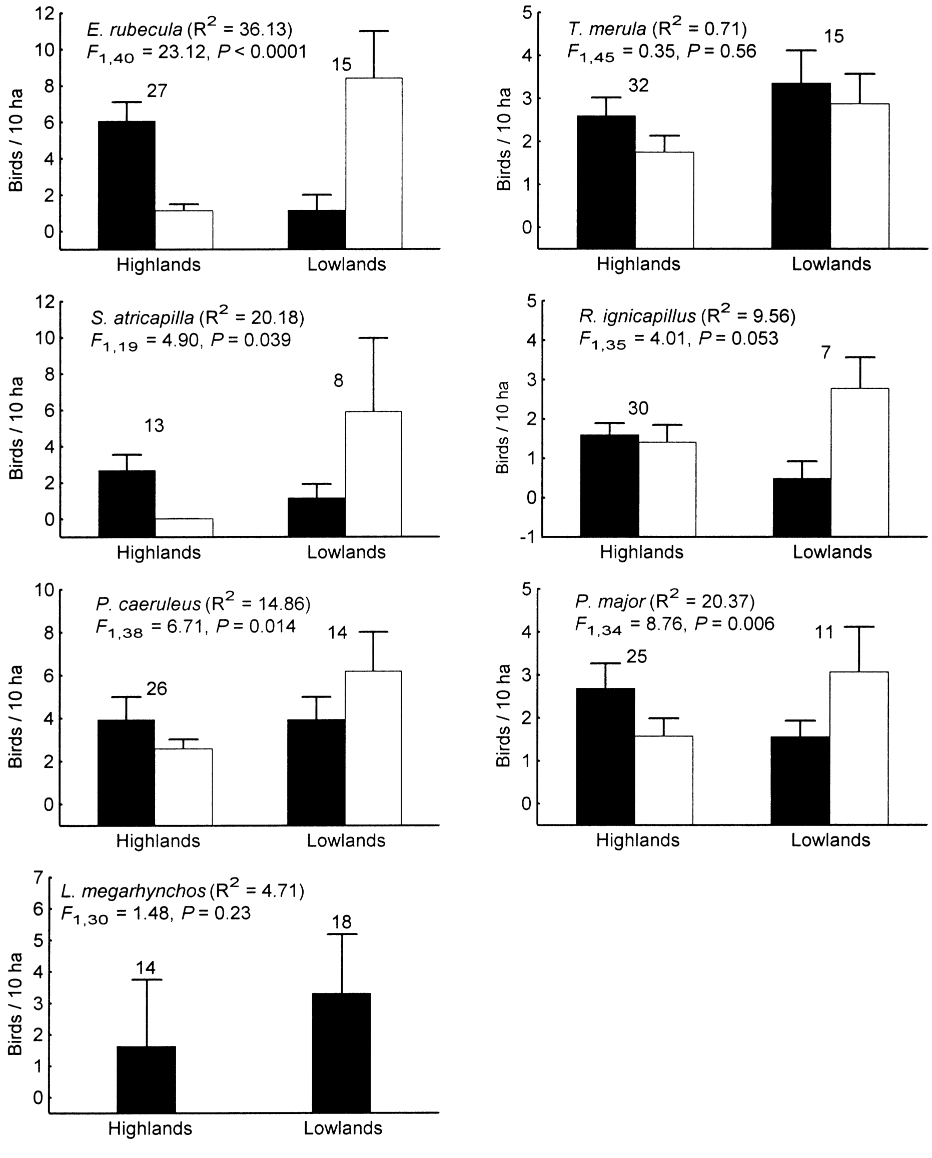

FIG. 2.—Seasonal rearrangements of abundance between highlands and lowlands. Mean abundances with standard errors in spring (black bars) and winter (white bars) of each species and the number of survey sites considered in each case are shown. The significance of the seasonal change in abundance distribution is measured by the interaction between region (between-sites effect) and season (within-sites effect), which is given in each plot together with the percentage of variance that it explains ($R^2$). For Nightingales (summer visitors) only the breeding abundances and the results of the corresponding one-way ANOVA are shown.

*[Cambios estacionales de abundancia (*Birds/10 ha*) entre las mesetas (*Highlands*) y las llanuras meridionales (*Lowlands*). Para cada especie se indican las abundancias medias (aves/10 ha) y los errores estándar durante la primavera (barras negras) y el invierno (barras blancas). Se indica el número de localidades consideradas en cada caso. El cambio estacional de la distribución de abundancias viene dado por la interacción entre la región (efecto entre sitios) y la estación (efecto dentro de sitios), cuya significación se expresa en cada caso junto con el porcentaje de la varianza explicada (*$R^2$*). En el caso del Ruiseñor Común, que es un visitante estival, solo se da el resultado del ANOVA de clasificación simple para las variaciones regionales en abundancia.]*

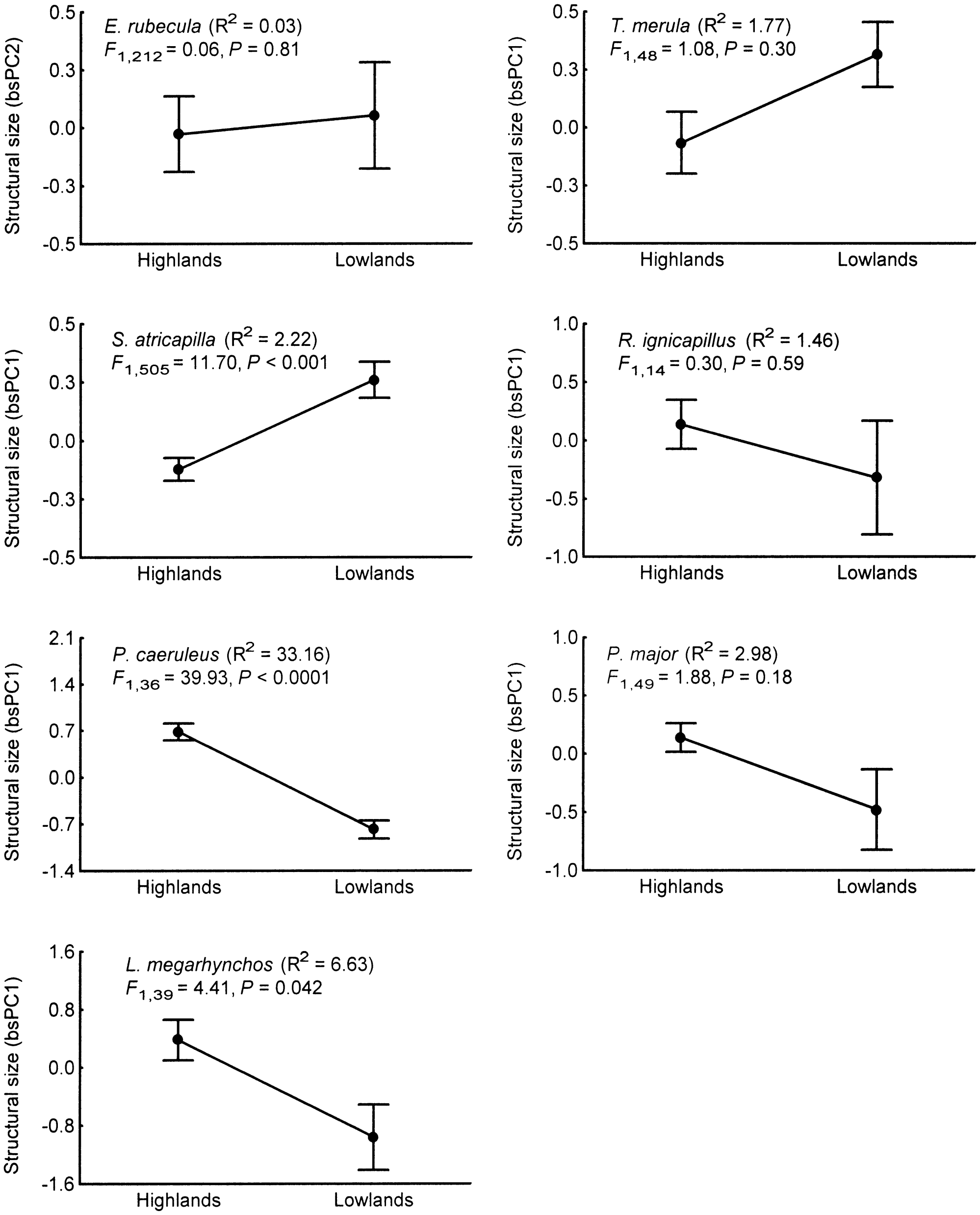

FIG. 3.—Variation between highlands and lowlands in the structural size of the seven species studied. Means and standard errors of the corresponding bsPC scores are shown. The results of the planned comparisons (highlands *vs.* lowlands) in a two-way ANOVA (population by age) are given, as well as the size of this effect measured as percentage of variance explained ($R^2$).

*[Variación entre las mesetas (*Highlands*) y las llanuras meridionales (*Lowlands*) en el tamaño estructural de las siete especies estudiadas. Se expresan las medias y los errores estándar de los valores de la componente principal (bsPC) correspondiente al tamaño de cada especie. También se dan los resultados de las comparaciones planificadas (mesetas* vs. *llanuras) en un ANOVA de clasificación doble (población y edad) así como la varianza explicada por este efecto (*$\mathrm{R}^2$*).]*

species, body size was larger in highlands, although differences were significant only in Blue Tits and Nightingales. The small sample size is likely to have reduced the power of these comparisons, although the generalised lack of differences in body size can be also attributable to the fact that these effects were really small (Fig. 3).

Once body size was statistically controlled for, we were able to detect significant variations in flight-related morphology between highlands and lowlands in five of the six species for which we predicted such a pattern (Table 3 and 4). It should be noted that the small sample size decreased the power of these comparisons, so the fact that differences were so significant in these conditions should be interpreted as a further support for the strength of the pattern. The Great Tit was the only species for which we failed to detect any significant trend in flight-related morphology. Actually, Great Tits showed little variation in these traits, which seemed to affect wing length only, so that the lack of differences was certainly attributable to a small regional difference in flight-related morphology in this species (Fig. 4). Finally, as predicted by the migratory behaviour of Nightingales, this species showed no difference between regions in flight-related morphology (Table 3 and 4, Fig. 4).

*A posteriori* evaluations of the contribution of each particular trait to the overall differences showed that wing length and wing pointedness were more consistent among species in their regional variation than tail length (Fig. 4). All the five species in which a significant variation in overall flight-related morphology was found showed longer and more pointed wings in highlands. Even Great Tits, for which the overall pattern was not significant, tended to vary in that way. However, the predicted increase in tail length in southern populations only held significance in two species (Blackcaps and Blackbirds), and even tail length varied in the opposite direction in other two (Robins and Blue Tits; Fig. 4).

We obtained very similar results when the analyses of wing length and tail length were done with all data available in our samples (Table 5). Although sample sizes experienced a two or three-fold increase in the species with the smallest initial sample sizes (Firecrests and Nightingales, for example), we did not find significant differences in effect sizes measured as the percentage of variance explained by regional differences (Wilcoxon matched pairs test with species as sample units: wing length: $Z$ = 0.51, $P$ = 0.61; tail length: $Z$ = 0.68, $P$ = 0.50), nor did we find an increase in the statistical significance reached by these differences in the second analyses (wing length: $Z$ = 0.52, $P$ = 0.60; tail length: $Z$ = 0.0001, $P$ = 0.99).

## DISCUSSION

### *Seasonal changes in abundance*

Overall, the seasonal abundance distribution of the species studied fitted the pattern predicted by our hypothesis on the migratory behaviour of Iberian forest passerines. Winter abundance decreased in highlands and increased in lowlands for all these species, with the only exception of Blackbirds. This species is known to have become sedentary in almost all the southern half of its range during the last century (Berthold, 1999), which could partially explain the lack of seasonal changes in its abundance in the Iberian Peninsula. In addition, such changes could have been masked by hunting pressure during autumn-winter, as the Blackbird is the only game species in our study. This could have caused an underestimation of Blackbird densities in Iberian lowlands, where hunting pressure is higher (Santos *et al.*, 1988). Despite this bias in our results, the pattern that we have found reflects the complementary role of highlands and lowlands as either breeding or wintering grounds, and supports the effects of different environmental pressures on the movements of Iberian forest passerines. However, such a pattern could be influenced by the arrival of European migrants. It is known, for instance, that the Iberian Peninsula receives during winter huge numbers of Robins, Blackcaps and Blackbirds from central and northern Europe which occupy mostly southern areas, thus explaining the increase in abundance of these species in lowlands (Santos, 1982; Cantos, 1995; Bueno, 1998). However, despite some foreign birds arriving to the northern plateau too (as shown by ringing recoveries; see Santos, 1982; Cantos, 1995; Bueno, 1998), the abundance of these species decreases in this area during winter. On the

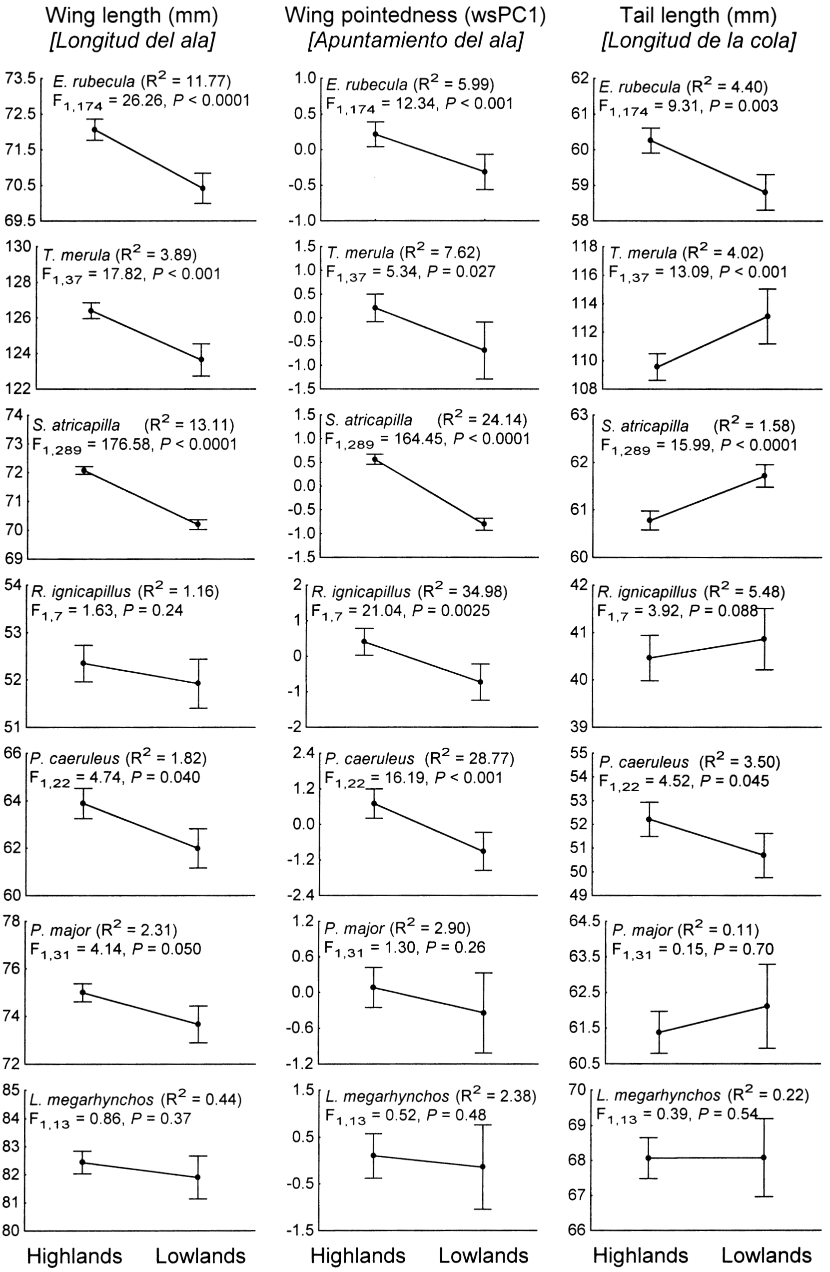

FIG. 4.—Variation between regions in the three traits that define flight-related morphology. Means adjusted by structural size with standard errors are shown, as well as the results of the planned comparisons between highlands and lowlands (with the same model as in the multivariate ANCOVA, see Tables 3 and 4) and the size of this effect (percentage of variance explained, $R^2$).

*[Variación inter-regional de tres rasgos morfológicos relacionados con el vuelo. Se dan las medias ajustadas por el tamaño estructural y los resultados de las comparaciones planificadas entre mesetas (*Highlands*) y llanuras (*Lowlands*), con el mismo modelo que en el ANCOVA multivariante de las Tablas 3 y 4, junto con el tamaño de cada efecto medido como porcentaje de la varianza explicado (*$R^2$*).]*

TABLE 4

Results of planned comparisons testing for differences between highlands and lowlands in flight-related morphology (see the models used to estimate these effects in Table 3, and see text for a more detailed description of the models tested in each case). The effects of the factor "region" and the covariate "body size" are shown.
*[Resultados de las comparaciones planificadas utilizadas para comparar la morfología de vuelo de las aves de las mesetas y del sur peninsular (véanse los modelos utilizados para estimar estos efectos en la Tabla 3, y más detalles acerca de los mismos en el texto). Se muestra el efecto del factor* "Región" *y el de la covariante "tamaño corporal"* (Body size).*]*

| | | *F* | d.f. | *P* |
|---|---|---|---|---|
| *E. rubecula* | Region | 9.27 | 3,172 | <0.0001 |
| | Body size | 6.52 | 3,172 | 0.0003 |
| *T. merula* | Region | 10.11 | 3,35 | <0.0001 |
| | Body size | 172.24 | 3,35 | <0.0001 |
| *S. atricapilla* | Region | 89.09 | 3,287 | <0.0001 |
| | Body size | 467.41 | 3,287 | <0.0001 |
| *R. ignicapillus* | Region | 7.51 | 3,5 | 0.027 |
| | Body size | 12.44 | 3,5 | 0.0093 |
| *P. caeruleus* | Region | 12.13 | 3,20 | <0.0001 |
| | Body size | 8.80 | 3,20 | 0.0006 |
| *P. major* | Region | 1.80 | 3,29 | 0.169 |
| | Body size | 70.28 | 3,29 | <0.0001 |
| *L. megarhynchos* | Region | 0.37 | 3,11 | 0.778 |
| | Body size | 123.31 | 3,11 | <0.0001 |

TABLE 5

Results of planned comparisons testing for differences between highlands and lowlands in wing length and tail length, considering all the data available for these traits. Comparisons are the same described in Table 3, although the contrast vectors (not shown) changed in some instances because the increase in sample size filled some cells that were empty in the multivariate design. Only the regional effect and the percentage of variance that it explains ($R^2$) are shown.
*[Resultados de un análisis de comparaciones planificadas realizado para ilustrar las diferencias entre las mesetas y el sur peninsular en la longitud de las alas y la cola, considerando todos los datos disponibles. Las comparaciones son las mismas que las descritas en la Tabla 3, aunque el vector de contraste (no presentado) cambió en algunos casos porque al aumentar el tamaño de muestra se completaron algunas celdas vacías en el diseño multivariante. Se exponen solo el efecto regional y el porcentaje de la varianza que éste explica (*$R^2$*).]*

| | Wing length *[Longitud alar]* | | | | Tail length *[Longitud de la cola]* | | | |
|---|---|---|---|---|---|---|---|---|
| | *F* | d.f. | *P* | $R^2$ (%) | *F* | d.f. | *P* | $R^2$ (%) |
| *E. rubecula* | 26.50 | 1,211 | <0.0001 | 10.30 | 12.80 | 1,211 | 0.0004 | 5.23 |
| *T. merula* | 13.89 | 1,47 | 0.0005 | 5.06 | 9.65 | 1,47 | 0.0032 | 3.49 |
| *S. atricapilla* | 401.33 | 1,503 | <0.0001 | 16.39 | 23.99 | 1,503 | <0.0001 | 1.37 |
| *R. ignicapillus* | 1.21 | 1,13 | 0.291 | 0.88 | 5.54 | 1,13 | 0.035 | 4.76 |
| *P. caeruleus* | 5.91 | 1,35 | 0.020 | 1.90 | 0.01 | 1,35 | 0.905 | 0.01 |
| *P. major* | 6.99 | 1,48 | 0.011 | 2.67 | 0.12 | 1,48 | 0.727 | 0.05 |
| *L. megarhynchos* | 0.64 | 1,38 | 0.429 | 0.15 | 1.86 | 1,38 | 0.181 | 0.93 |

other hand, the arrival of extra-Iberian birds would hardly explain the seasonal changes in abundance of Firecrests and tits: despite the well-known migratory movements of these species in northern and central Europe (Ulfstrand, 1962; van Balen & Hage, 1989), ringing recoveries do not evidence their regular arrival to Iberia (Tellería *et al*., 1999). Therefore, our results support that many forest birds leave the highlands thus contributing to the increase in their abundance in lowlands during winter. However, these results do not demonstrate the sedentariness of lowland populations, so that other clues that could corroborate this possibility are needed. Actually, evidence of year-round residence of southern populations has been gathered in some studies. For instance, it has been demonstrated that local birds make up an important fraction of the populations wintering in lowland forests, while their overwintering counterparts mainly occupy shrublands, orchards and open forests that are unsuitable for breeding (Pérez-Tris *et al*., 2000b; Tellería *et al*., 2001). In addition, recurrent winter recaptures of locals in their breeding forests of southern Spain provide evidence of sedentariness of lowland populations (Pérez-Tris *et al*., 1999; 2000b; *pers. obs.*). Finally, but not less importantly, we have found morphological differences that may be interpreted as correlates of the different migratory behaviour of forest passerines in highlands and lowlands.

### *Morphological differences*

An heterogeneous pattern was found among species when comparing body size between Iberian regions. Some species showed an increased body size in highlands, while others tended to be larger in lowlands or showed no change in body size between regions. Although variations in body size were generally small (Fig. 3), the mixed patterns found are difficult to interpret. Avian body size may be affected by many factors, such as climate, developmental conditions or migratory pattern (e.g. Geist, 1989; Baker, 1992; Holmgren & Lundberg, 1993; Tellería & Carbonell, 1999), which could have a different relative importance in determining changes between Iberian regions in each species and whose discussion goes beyond the scope of this study.

After controlling for body size, our results demonstrate the differentiation in flight-related morphological traits between highland and lowland forests passerines. Overall, wing length and wing shape showed a more consistent pattern of regional variation than tail length. Thus, all species showed longer and/or more pointed wings in highlands and such differences were significant or nearly significant in almost all cases. For all species differing in flight-related morphology except the Robin, the variation between regions in wing pointedness was stronger than the change in wing length (Fig. 4), which is consistent with the results obtained by Mönkkönen (1995) in a comparative study of the variation in wing shape between migratory and sedentary species. Changes in tail length, however, were less pronounced and even opposite to the trend predicted in two cases (Robins and Blue Tits). According to the overall pattern of variation in the traits studied, our interpretation is that tail morphology could be less affected by migration pressures than wing shape (see also Winkler & Leisler, 1992), and more dependent on other processes related to particular life styles that could impose different constraints on tail modification in each species (for example, feeding on the ground has different manoeuvrability requirements than leaf gleaning; see Leisler & Winkler, 1985). However, although these species-specific processes could have caused the observed deviations from the predicted patterns of variation in tail length, any *a posteriori* interpretation of these unexpected trends would be too premature. What really matters here is the fact that overall changes between regions in flight-related morphology support a more extensive migratory behaviour in highland populations of forest passerines compared to their lowland counterparts.

It has long been accepted that migrants have longer and more pointed wings, a trend which has been documented both in intraspecific and interspecific analyses (Mulvihill & Chandler, 1991; Winkler & Leisler, 1992; Mönkkönen, 1995). However, differences among populations in wing length and wing pointedness could also result from conflicting selective pressures caused by the requirements of manoeuvrability related to habitat structure or to particular foraging strategies (Leisler & Winkler, 1985; Winkler & Leisler, 1985; Rayner, 1988). We have found that highland populations of several species have longer and more pointed wings than their lowland counterparts, taking into account in our analysis the possible effect of changes in habitat structure among study sites (described by Carbonell & Tellería, 1998a). On the other hand, our multi-species study allowed us to control for possible species-specific effects (such as those apparently operating in the case of body size), thus making the proposed role of seasonal movements to be the most parsimonious explanation for the morphological differences described. Two facts emphasise the likelihood of this interpretation. First, despite the species studied showing noticeable differences in ecology and behaviour, they define an overall homogeneous trend of variation in wing length and wing shape between highlands and lowlands. We selected these species exclusively because they were the most frequently trapped in our study areas, which is unlikely to make them particularly prone to change between regions in the described way. Second, our interpretation is also supported by the lack of morphological variation in the trans-Saharan migrant Nightingales that we used as a control. As predicted by their homogeneous migratory behaviour, highland and lowland Nightingales showed no difference in flight-related morphology, despite their slight difference in structural size, and despite they being certainly similar in most aspects of their ecology and behaviour to some of the species studied like Robins or Blackbirds.

In summary, seasonal changes in abundance and differences in morphological traits support that highland and lowland Iberian forest passerines differ in migratory behaviour. We do not know, however, the proportion of highland populations that is involved in these displacements, which constitute without doubt a case of partial migration like those observed in the same species in other parts of their range (Cramp, 1988; 1992; Cramp & Perrins 1993).

## *Conclusions and perspectives*

The existence of movements of birds in the Iberian Peninsula can offer a valuable insight into the diversity of migratory strategies in the Western Palaearctic. Iberian movements could illustrate that altitudinal migration is a widespread phenomenon, which has probably evolved independently in many species and in many different montane populations around the Mediterranean (Fig. 1). It has been postulated that migratory patterns of European birds could have evolved in parallel to the expansion of the breeding ranges of these species in the late Pleistocene (Safriel, 1995; Blondel & Mourer-Chauviré 1998; Taberlet *et al.*, 1998) by first developing short-distance, partial migratory movements that would have later derived towards total migrations (Berthold, 1999). Very likely, the colonisation of highlands had a similar effect at southern latitudes, where regional-scale movements could have evolved increasing the diversity of migratory patterns in the Palearctic migratory system. Nevertheless, phylogeographic studies would be needed to further disentangle the relationships between highland and lowland populations, as well as between Mediterranean and central-European birds.

According to our results, altitudinal migrations are relevant in affecting not only the spatio-temporal structuring of bird communities, but also the morphological traits of the birds involved in these displacements. The morphological differentiation that we have found among Iberian populations of forest passerines partially agrees with the taxonomic classifications proposed for these species by early studies carried out in Spain and Portugal (Table 6). These studies have described the Iberian populations as intermediate between the central-European ones and those present in northern Africa or in some Mediterranean islands. However, these classifications are imprecise in assessing the morphological differentiation of each species within the Iberian peninsula, and neither have they attempted to explain the origin of the observed variations (e.g. the role of seasonality in shaping more or less migratory-like morphs). Furthermore, it has long been accepted that the southern-like morphs of these species occupy almost all the Iberian Peninsula, an incorrect prejudice rooted in the wrong tendency to view the Iberian highlands as a Mediterranean region equivalent to the warm lowlands and coastal areas. Our results go a step further by providing an ecological significance to the differentiation of Iberian populations, which could be determined to a large extent by migration pressures.

TABLE 6

A summary of the taxonomic status of the seven studied species in south-western Europe and north-western Africa, according to different bibliographic sources (1: Vaurie, 1959; 2: Cramp, 1988; 3: Cramp, 1992; 4: Cramp & Perrins, 1993). The taxonomic adscription (according to these sources) of northern and southern Iberian populations studied in this paper is also indicated.
*[Resumen del estatus taxonómico de las especies estudiadas en Europa suroccidental y el noroeste de África según diferentes fuentes bibliográficas (1: Vaurie, 1959; 2: Cramp, 1988; 3: Cramp, 1992; 4: Cramp & Perrins, 1993). Se indica, además, la adscripción taxonómica de las poblaciones asentadas en las mitades norte y sur de la península Ibérica.]*

| Species *[Especie]* | Ref. | France *[Francia]* | Northern Iberia *[Norte de Iberia]* | Southern Iberia *[Sur de Iberia]* | Northern Africa *[Norte de África]* |
|---|---|---|---|---|---|
| *E. rubecula* | 1, 2 | *E. r. rubecula / E. r. melophilus* | *E. r. rubecula / E. r. melophilus* | *E. r. rubecula / E. r. witherbyi* | *E. r. rubecula / E. r. witherbyi* |
| *T. merula* | 1 | *T. m. merula* | *T. m. merula* | *T. m. merula / T. m. mauritanicus* | *T. m. mauritanicus* |
| | 2 | *T. m. merula* | *T. m. merula* | *T. m. merula* | *T. m. mauritanicus* |
| *S. atricapilla* | 1 | *S. a. atricapilla* | *S. a. atricapilla* | *S. a. atricapilla* | *S. a. atricapilla* |
| | 3 | *S. a. atricapilla* | *S. a. atricapilla* | *S. a. heineken* | *S. a. heineken* |
| *R. ignicapillus* | 1, 3 | *R. i. ignicapillus* | *R. i. ignicapillus* | *R. i. ignicapillus* | *R. i. balearicus* |
| *P. caeruleus* | 1 | *P. c. caeruleus* | *P. c. caeruleus/ P. c. ogliastrae* | *P. c. ogliastrae* | *P. c. ultramarinus* |
| | 4 | *P. c. caeruleus* | *P. c. caeruleus* | *P. c. ogliastrae* | *P. c. ultramarinus* |
| *P. major* | 1 | *P. m. major* | *P. m. major/ P. m. excelsus* | *P. m. major/ P. m. excelsus* | *P. m. excelsus* |
| | 4 | *P. m. major* | *P. m. major* | *P. m. corsus* | *P. m. excelsus* |
| *L. megarhynchos* | 1, 2 | *L. m. megarhynchos* | *L. m. megarhynchos* | *L. m. megarhynchos* | *L. m. megarhynchos* |

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shown.
*[Resumen de los rasgos morfométricos medidos en las siete especies estudiadas distribuidos según su ubicación en las mesetas o llanuras meridionales ibéricas. Se dan las medias, los errores estándar y el tamaño de la muestra.]*

| | Tarsus length (mm) *[Longitud del tarso]* | | | Wing length (mm) *[Longitud del ala]* | | | Bill height (mm) *[Altura del pico]* | | | Tail length (mm) *[Longitud de la cola]* | | | Body mass (g) *[Peso]* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | s.e. | *n* | Mean | s.e. | *n* | Mean | s.e. | *n* | Mean | s.e. | *n* | Mean | s.e. | *n* |
| *Erithacus rubecula* | | | | | | | | | | | | | | | |
| Highlands *[Mesetas]* | 25.20 | 0.06 | 175 | 71.97 | 0.13 | 171 | 3.63 | 0.02 | 173 | 60.20 | 0.19 | 148 | 15.77 | 0.12 | 176 |
| Lowlands *[Llanuras]* | 25.10 | 0.07 | 91 | 70.32 | 0.18 | 87 | 3.75 | 0.02 | 88 | 58.81 | 0.19 | 75 | 15.17 | 0.11 | 87 |
| *Turdus merula* | | | | | | | | | | | | | | | |
| Highlands *[Mesetas]* | 32.40 | 0.12 | 60 | 125.47 | 0.52 | 61 | 7.46 | 0.07 | 59 | 107.90 | 1.09 | 50 | 83.22 | 0.86 | 58 |
| Lowlands *[Llanuras]* | 33.32 | 0.24 | 17 | 122.94 | 0.85 | 18 | 7.79 | 0.11 | 18 | 114.09 | 0.74 | 11 | 86.36 | 2.33 | 17 |
| *Sylvia atricapilla* | | | | | | | | | | | | | | | |
| Highlands *[Mesetas]* | 20.14 | 0.03 | 383 | 71.64 | 0.09 | 385 | 3.87 | 0.01 | 360 | 60.45 | 0.12 | 356 | 16.46 | 0.06 | 379 |
| Lowlands *[Llanuras]* | 20.80 | 0.05 | 175 | 70.24 | 0.14 | 169 | 3.96 | 0.02 | 172 | 61.95 | 0.17 | 168 | 17.32 | 0.10 | 174 |
| *Regulus ignicapillus* | | | | | | | | | | | | | | | |
| Highlands *[Mesetas]* | 16.81 | 0.17 | 16 | 52.62 | 0.40 | 17 | 2.40 | 0.04 | 15 | 40.40 | 0.29 | 15 | 5.46 | 0.12 | 16 |
| Lowlands *[Llanuras]* | 16.41 | 0.26 | 7 | 51.07 | 0.80 | 7 | 2.60 | 0.05 | 7 | 40.42 | 0.58 | 6 | 5.71 | 0.23 | 7 |
| *Parus caeruleus* | | | | | | | | | | | | | | | |
| Highlands *[Mesetas]* | 16.40 | 0.12 | 29 | 65.17 | 0.32 | 30 | 4.34 | 0.05 | 27 | 52.74 | 0.31 | 25 | 10.44 | 0.16 | 29 |
| Lowlands *[Llanuras]* | 15.76 | 0.15 | 24 | 59.46 | 0.51 | 24 | 4.03 | 0.05 | 22 | 49.02 | 0.86 | 25 | 9.27 | 0.11 | 25 |
| *Parus major* | | | | | | | | | | | | | | | |
| Highlands *[Mesetas]* | 19.70 | 0.08 | 50 | 75.02 | 0.30 | 50 | 4.55 | 0.04 | 50 | 61.94 | 0.42 | 45 | 16.91 | 0.38 | 49 |
| Lowlands *[Llanuras]* | 19.35 | 0.25 | 14 | 72.60 | 0.77 | 13 | 4.68 | 0.07 | 14 | 60.75 | 0.90 | 14 | 16.94 | 0.25 | 14 |
| *Luscinia megarhynchos* | | | | | | | | | | | | | | | |
| Highlands *[Mesetas]* | 26.85 | 0.13 | 34 | 82.38 | 0.38 | 38 | 4.30 | 0.05 | 35 | 68.91 | 0.39 | 37 | 20.40 | 0.24 | 37 |
| Lowlands *[Llanuras]* | 25.98 | 0.59 | 15 | 78.87 | 0.67 | 13 | 4.17 | 0.06 | 15 | 64.88 | 0.63 | 13 | 20.83 | 0.54 | 15 |