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Abundance distribution, morphological variation and juvenile condition of robins, *Erithacus rubecula* (L.), in their Mediterranean range boundary

Javier Pérez-Tris, Roberto Carbonell and José Luis Tellería *Departamento de Biología Animal I (Zoología de Vertebrados), Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain*

Abstract

Aim It has been suggested that populations nearing the border of a species' range should be maladapted because they occupy progressively less suitable environments. In some instances, however, peripheral populations might acclimate or even be adapted to local conditions. We studied Iberian robins to evaluate whether southern, peripheral populations become more restrictive in selecting their habitats, are locally differentiated or show evidence of maladaptation.

Location We divided the Iberian Peninsula into three regions (the Eurosiberian and Supra-Mediterranean regions in northern Iberia, and the Mediterranean Lowlands in southern Iberia), which define a gradient of increasing dryness southwards. In each region, we selected one representative locality, where we captured individuals during three study years.

Methods We reviewed 72 community studies to test whether Iberian robins occupy fewer forests and decrease in abundance southwards. Because robins are sedentary in the southernmost region, but largely abandon both northern areas in winter, we analysed the variation in migration-related morphology to test for population differentiation in the range boundary. To examine how populations cope with environmental variation, we studied four indices of juvenile condition (fluctuating asymmetry, fledgling size, ptilochronology and size-corrected body mass), each related to nutritional conditions in a particular stage of growth, from early development to independence.

Results Although robins restricted their range southwards, there was no change in local abundance between regions. Southernmost robins, consistent with their sedentary behaviour, had shorter and more rounded wings than northern robins, although the populations did not differ in terms of body size. Fluctuating asymmetry and fledgling size did not evidence a higher developmental stress in peripheral populations, although southernmost robins had a lower juvenile condition during their independence (as shown by ptilochronology and residual body mass).

Main conclusions The distribution of abundance found in this study supports the idea that Iberian robins could select habitats above a somehow restrictive threshold of quality. In addition, morphological correlates of migratory behaviour provided evidence of population differentiation at the range edge. This introduces the possibility that among-region variations in juvenile condition actually reflect reproductive benefits for migrants, related to the occupation of seasonally productive habitats, rather than the maladaptation of sedentary, peripheral populations. From this perspective, and in view of the patterns of distribution and morphology that we found, southern Iberian robins might be independent populations locally adapted in the range boundary.

Keywords
Abundance, *Erithacus rubecula*, migratory behaviour, morphological differentiation, range boundary.

Correspondence: Javier Pérez-Tris. Tel.: 34-91-394-4949. Fax: 34-91-394-4947. E-mail: jperez@eucmax.sim.ucm.es

Resumen

Objetivos Se ha sugerido que las poblaciones de una determinada especie deberían estar peor adaptadas cerca del borde de su distribución, donde sus hábitats son cada vez menos adecuados. En ocasiones, sin embargo, las poblaciones periféricas podrían aclimatarse, o incluso adaptarse, a las condiciones locales. En este trabajo estudiamos petirrojos ibéricos para evaluar si las poblaciones periféricas meridionales son más restrictivas al seleccionar sus hábitats, están localmente diferenciadas o muestran alguna evidencia de inadaptación.

Localización Dividimos la Península Ibérica en tres regiones (Eurosiberiana y Supramediterránea en el norte, y tierras bajas mediterráneas en la mitad meridional), que definen un gradiente de xericidad creciente hacia el sur. En cada región, seleccionamos una localidad representativa donde capturamos petirrojos durante tres años de estudio.

Métodos Revisamos 72 estudios de comunidades para examinar si los petirrojos ocupan menos bosques y disminuyen su abundancia hacia el sur en Iberia. Dado que los petirrojos son sedentarios en la región meridional, pero abandonan en gran medida las regiones norteñas, estudiamos la variación interpoblacional en rasgos relacionados con la migración para examinar la diferenciación de las poblaciones periféricas. Para evaluar la respuesta de las poblaciones a las variaciones ambientales, estudiamos cuatro índices de condición física de los juveniles (asimetría fluctuante, tamaño corporal, ptilocronología y peso corregido por el tamaño), cada uno de ellos relacionado con el estado nutricional de los individuos en un momento concreto entre su desarrollo temprano y su emancipación.

Resultados Aunque los petirrojos restringieron su distribución hacia el sur, su abundancia local no varió entre regiones. Los petirrojos meridionales, de acuerdo con su comportamiento sedentario, presentaron alas más cortas y redondeadas que los norteños, aunque no encontramos diferencias de tamaño corporal. La asimetría fluctuante y el tamaño de los volanderos no reflejaron un mayor estrés durante el desarrollo de los petirrojos en las poblaciones meridionales, si bien éstos mostraron una peor condición física durante su emancipación (medida mediante la ptilocronología y el peso residual).

Principales conclusiones La distribución de abundancias observada apoya el que los petirrojos ibéricos podrían seleccionar los hábitats que superasen un cierto umbral de calidad. Además, las poblaciones meridionales parecen estar diferenciadas en el borde de la distribución, de acuerdo con la variación morfológica asociada al comportamiento migrador de cada población. Esto introduce la posibilidad de que las variaciones interpoblacionales de condición juvenil reflejen en realidad las ventajas reproductivas que los petirrojos migradores obtendrían ocupando hábitats estacionalmente productivos, en lugar de la inadaptación de las poblaciones sedentarias periféricas. Desde este punto de vista, y de acuerdo con los patrones de distribución y variación morfológica observados, los petirrojos del sur ibérico podrían constituir poblaciones independientes, localmente adaptadas en el borde de la distribución de la especie.

Palabras clave

Abundancia, borde de distribución, comportamiento migrador, diferenciación morfológica, *Erithacus rubecula*.

INTRODUCTION

Many studies have proposed that the well-being of populations should decrease towards the border of a species' range. The niche hypothesis, for example, suggests that habitat suitability decreases from the core areas causing a decrease in both the abundance and fitness of populations nearing the species border (Brown, 1984, 1995; Lawton, 1993). However, peripheral populations may either acclimate or adapt to local conditions, or even have an evolutionary history that is independent of the main population (Caughley *et al.*, 1988; Blondel *et al.*, 1993; Hoffmann & Blows, 1994). In any case, either phenotypic plasticity or population differentiation would allow peripheral populations to avoid maladaptation (Hoffmann & Blows, 1994).

European forest passerines seem to face a decreasing habitat suitability in the Mediterranean region. However, there is little empirical evidence illustrating how populations respond to changing environmental conditions in peripheral areas. In the Iberian Peninsula, for example, it is known that they have a more fragmented distribution southwards (Santos & Tellería, 1995; Tellería *et al.*, 1999), and several studies have found a lower body condition in populations occupying some marginal, dry environments (Carbonell & Tellería, 1998, 1999). However, this does not necessarily apply to all peripheral Iberian populations. In fact, there are moist forests in the southernmost point of Iberia whose avifauna is similar, both in richness and abundance, to that recorded in northern Iberia (Santos & Tellería, 1995). Moreover, some passerines are known to be sedentary in these forests and to be morphologically differentiated from their north-Iberian migratory counterparts (Tellería & Carbonell, 1999). The existence of these peculiar bird communities introduces the possibility that the Iberian peripheral populations of some bird species are locally adapted.

In this paper, we study the variation in some population traits of robins (*Erithacus rubecula* [L.]) distributed along a north-to-south gradient of increasing dryness in the Iberian Peninsula. The robin has a wide distribution in the Western Palearctic (Cramp, 1988), and is also widespread in northern Iberia, but its distribution becomes patchy from there southwards (Tellería & Santos, 1994; Tellería *et al.*, 1999). Therefore, it is a suitable model for studying the biology of a typical European forest passerine nearing the boundary of its Mediterranean range. We evaluate whether robin populations acclimate to their environments, are differentiated or show evidence of maladaptation in the southernmost Iberian breeding grounds from three complementary perspectives.

Patterns of abundance distribution

If robins actually occupied progressively worse environments across the Iberian gradient, the fragmentation of the species' range southwards should involve a parallel decrease in abundance in the occupied forests (Lawton, 1993; but see also Blackburn *et al.*, 1999). However, robins may occupy only suitable habitats regardless the distance to the species' border, thereby preventing their maladaptation in the range boundary. If robins actually selected habitats above some threshold of quality, we should find a similar density across the Iberian gradient.

Morphological differentiation

The adaptation of peripheral populations to local conditions may be prevented by gene flow from central, densely populated sectors (Holt & Gomulkiewicz, 1997; Kirkpatrick & Barton, 1997). In some instances, however, isolation in the range border may preclude this interchange and hence allow local differentiation (Hoffmann & Blows, 1994). It has been suggested that Iberian robins belong to the nominate subspecies *E. r. rubecula* (L.) but grade in the south into *E. r. witherbyi* Hartert (Cramp, 1988). However, the possible differentiation of southern populations has never been studied, although it is known that they are sedentary whereas northern populations are partially or totally migratory (Tellería *et al.*, 1999). In many bird species, migratory populations differ from their sedentary counterparts in that they have longer and more pointed wings, as well as a shorter tail (e.g. Leisler & Winkler, 1985; Norberg, 1995; Tellería & Carbonell, 1999). In contrast, the different use of habitats by migrant and sedentary populations may also involve variations in diet, and hence in its related morphology (Carrascal *et al.*, 1990; Tellería & Carbonell, 1999). The existence of these morphological correlates of migratory behaviour would be good evidence of population differentiation, as long as it has been demonstrated that these traits are controlled genetically in robins (Biebach, 1983; Berthold, 1991).

Juvenile condition

If robins were unable to acclimate or adapt to peripheral conditions (see above), they should achieve a lower fitness near the range boundary (Caughley *et al.*, 1988; Hoffmann & Blows, 1994; Brown, 1995). Juvenile survival is a major component of the variation in fitness among bird populations (Newton, 1989), and is determined largely by the body condition of juveniles between early development and independence (Lindén *et al.*, 1992; Møller, 1997; Lindström, 1999). Therefore, a lower juvenile condition in peripheral populations could be a fair surrogate of lower fitness in the range boundary.

METHODS

Study area

The environmental variation that robins meet in the Iberian Peninsula can be summarized into three main regions (Fig. 1; Lautensach, 1964; Font, 1983; Tellería *et al.*, 1999). In each region, we selected one study site at which both precipitation and temperature were close to the regional average values (Lautensach, 1964; Font, 1983). The Eurosiberian Region constitutes the non-Mediterranean sector of the Iberian Peninsula, where robins are widespread and abundant. In this region, we captured robins in mixed oak forests (*Quercus faginea* Lam. and *Q. robur* L.) in Álava (42°55′N 2°29′W; 620-m elevation). The Supra-Mediterranean Region is a plateau above 800 m elevation where robins occupy mild areas in mountains and plains. This region is characterized by a marked contrast between a highly productive spring and a very harsh winter. There, we captured robins in Sierra de Guadarrama (40°54′N 3°53′W; 1100-m elevation), in mixed forests (*Q. pyrenaica* Willd., *Fraxinus excelsior* L. and *Alnus glutinosa* L.) interspersed with meadows. Finally, the Mediterranean Lowlands represent the typical dry Mediterranean climate, characterized by an intense summer drought. Well-developed forests are lacking across this region except in some moister mountain and coastal sectors, which are the

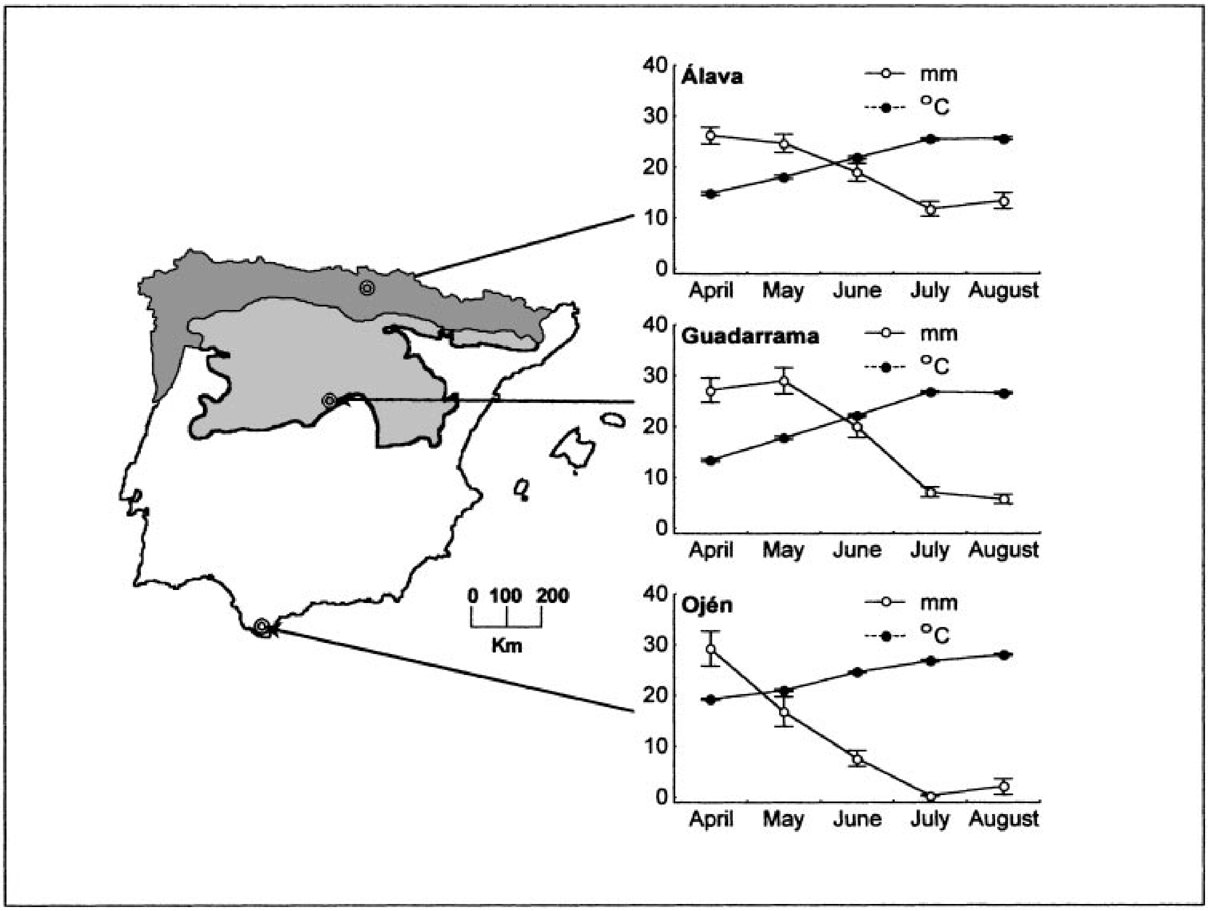

Figure 1 Regional division of the Iberian Peninsula: Eurosiberian Region (dark grey), Supra-Mediterranean Region (light grey) and Mediterranean Lowlands (white). The diagrams show the monthly variation in precipitation (mm) and maximum temperature (°C) for the period April–August (measured from 1986 to 1997) in the study localities selected in each region (means and standard errors are shown).

only sites where robins may be found. We sampled mixed oak forests (*Q. suber* L. and *Q. canariensis* Willd.) in Sierra de Ojén, in the southernmost point of Iberia (36°01′N 5°36′W, 250-m elevation).

Previous studies have shown that robins are sedentary in southern Iberia, but largely abandon the northernmost regions during winter. Thus, despite the arrival of robins from central and northern Europe to winter in northern Iberia, there is a clear spring-to-winter decrease in robin abundance in both the Eurosiberian Region (where robin density decreases by 37%) and, most especially, in the Supra-Mediterranean Region (where abundance decreases by as much as 82%). Meanwhile, the species increases its abundance in the Mediterranean Lowlands during winter (696% higher), which is greatly influenced by the arrival of foreign robins (Tellería *et al.*, 1999; Pérez-Tris & Tellería submitted). In addition, ringing recoveries support the idea that robins are sedentary in southern Iberia, as shown by own recaptures of the same individuals in spring and winter, but also that they spend a shorter time in their northern breeding areas than in the southern ones (Pérez-Tris & Tellería submitted).

Abundance distribution

We reviewed 72 studies of Iberian forest bird communities, in which estimates of breeding abundance of all the species present in each community were obtained using line-transect counting (Tellería *et al.*, 1999 and references therein). Because none of these studies was specifically designed to assess robin abundance, they may be considered as a random sampling of the species distribution along the Iberian Peninsula. We used these censuses to evaluate: (i) the variation in density of robins among Iberian regions (mean densities in all sampled forests), (ii) the proportion of forests occupied, and (iii) the mean densities in the occupied forests in each region. We also evaluated the mean abundance of robins in our study localities to assess whether they deviate from the average values in each region, for which we censused robins in 1996 in several 500-m long by 50-m wide line transects.

Capture and measurement of robins

In 1996, we sampled our study localities early in the breeding season (in May). In 1997 and 1998, however, we captured robins after fledgling independence (June–July), in order to capture yearlings. In these 2 years, localities were visited successively from south to north, during the peak of the fledging season. Along the three study years, we trapped 61 adults and 134 juveniles mainly using mist-nets, but also with netted claptraps, which did not influence estimates of body condition based on body mass (ANOVA with body mass: locality $F_{1,113} = 13.22$, $P < 0.001$, capture method $F_{1,113} = 0.01$, $P = 0.92$, locality × method $F_{1,113} = 0.11$, $P = 0.74$). All robins were ringed before being released to avoid repetition. We took standard measurements of the length of both tarsi, bill length and bill height using a 0.01-mm precision digital calliper. We also recorded wing maximum chord and tail length, both to the nearest half millimetre. In 1997 and 1998, we measured the distances between the wing tip and the tip of the nine long primary feathers (primary distances, see Svensson, 1992 for details about all measurements). Robins were weighed using a 0.1-g precision digital balance. Finally, we pulled the right fifth rectrix feather to measure its length and the width of 10 growth bars in the centre of its vane (Grubb, 1995), for which we used a 0.01-mm precision digital calliper. Several missing values led to different sample sizes in our analyses.

Morphological variation among populations

We studied the variation in wing, tail, tarsus and bill measurements among robin populations (see an example with blackcaps *Sylvia atricapilla* [L.] in Tellería & Carbonell, 1999). In order to summarize the variation in morphological traits in robins, we first performed a PCA with all body traits except bill measurements, as juveniles did not have a full-grown bill when we captured them. Thus, we tested for overall among-population differences in morphology taking into account the possible differences between age classes, but we only studied bill morphology of adults. To analyse the variation in wing-shape among populations, we conducted a PCA with primary distances for deriving indices of wing shape (Chandler & Mulvihill, 1988; Lockwood *et al.,* 1998). We measured primary distances in very few adults (five, six and five in the northern, central and southernmost populations, respectively) because most of them were moulting the innermost primaries, so we only studied wing shape of juvenile robins. We did not consider the sex of the birds in these analyses because sexing robins is too difficult after females have lost their brooding patch. Nonetheless, sexual dimorphism of robins should not confound among-population variation unless sex-ratios were strongly and differentially biased in each population, which is unlikely.

Indices of juvenile condition

We studied four different indices of juvenile body condition, each related to the nutritional stress that robins experienced during a different stage of development. We used fluctuating asymmetry of tarsus length and juvenile size as two independent correlates of environmental stress early in life (Garnett, 1981; Møller, 1997; Sanz, 1997; Lindström, 1999). We also analysed ptilochronology (the width of growth bars in the tail feathers, which measure the amount of feather material that has been produced per day, Grubb, 1995) as an index of the nutritional conditions that juveniles experienced during the latest nesting period and soon after fledging, as they do not grow the tail completely until some days after leaving the nest. Finally, we utilized body mass relative to body size (Brown, 1996) as a measure of the body condition of juveniles at the moment of their capture, when most were already independent of their parents.

We compared juvenile condition among populations during 1997 and 1998, taking into account the different confounding variables that may affect our results. To make sure that juvenile robins had the same, very low age in all three localities, we checked the degree of completion of their postjuvenile moult (Bensch & Lindström, 1992). This was at the earliest stages in all individuals, and indeed had not started in most of them. When analysing ptilochronology, we included feather length as a covariate of the width of its growth bars (excluding individuals without a full-grown tail), thereby controlling for the effect of final feather size on feather growth rate (Grubb, 1995).

Finally, we evaluated the extent to which the particular environmental conditions in each study year could have influenced the juvenile condition of robins. To do so, we studied the variations in mean precipitation and maximum temperature in our study localities during both breeding seasons.

RESULTS

Abundance distribution

The average density of robins decreased southwards in the Iberian Peninsula (Fig. 2; ANOVA: $F_{2,69} = 12.78$, $P < 0.001$), this being coupled with a decrease in the proportion of forests occupied in the southernmost region (chi-square test with frequencies given in Fig. 2; $x_2^2 = 24.97$, $P < 0.001$). However, we did not find significant differences between regions when comparing the densities in the occupied forests (Fig. 2; $F_{2,45} = 0.33$, $P = 0.72$). Although the scarcity of occupied sites in the Mediterranean Lowlands could have affected the power of this analysis, comparison of its significance value with that obtained previously (with not many more degrees of freedom) supports the interpretation that

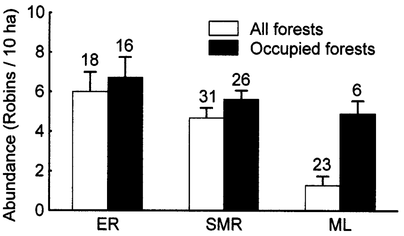

Figure 2 Abundance distribution of robins in the Iberian Peninsula. Mean densities, standard errors and sample sizes are shown (ER, Eurosiberian Region; SMR, Supra-Mediterranean Region; ML, Mediterranean Lowlands).

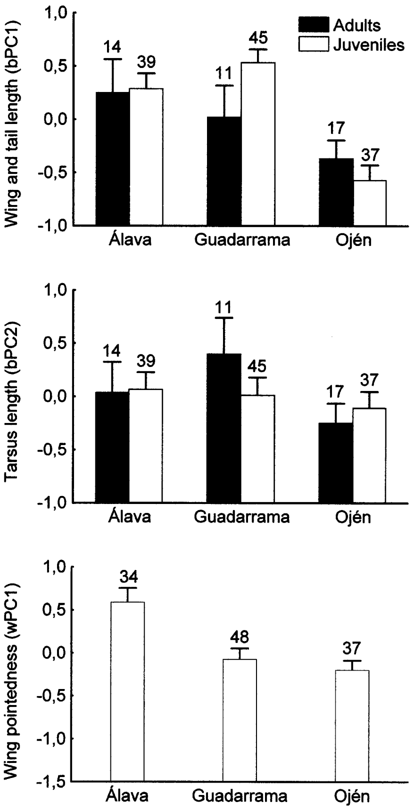

Figure 3 Variation among robin populations in wing and tail length (bPC1 scores), tarsus length (bPC2, a measure of body size) and wing pointedness (wPC1 scores, which were only analysed in juveniles). Means, standard errors and sample sizes are shown.

robins actually maintain similar local densities across regions. Moreover, differences between regions explained 27% of variation in robin abundance when all forests were considered, but <2% when only the occupied forests were analysed. The mean densities in our study sites did not differ from the regional means in the occupied forests (one-sample t-tests: Álava $t_{15} = 0.92$, $P = 0.37$; Guadarrama $t_{25} = 0.83$, $P = 0.82$; Ojén $t_5 = 0.37$, $P = 0.72$), supporting the idea that robin densities in our study sites were close to the regional averages.

Morphological variation among populations

The PCA with body measurements extracted two components of variation in body shape and size of robins (bPC1 and bPC2). Wing and tail length had a high loading in bPC1 (both 0.91, within-factor correlation $P < 0.001$), while tarsus length had a small loading in this component (–0.02, n.s.). However, tarsus length had a high loading in the bPC2 (0.99, $P < 0.001$), in which wing and tail length had a small loading (0.01 and –0.04, respectively, n.s.). A multivariate ANOVA analysing the variation among populations and between age classes in bPC1 and bPC2 together showed that, overall, the populations studied differed in morphology (Wilk's test, F-values obtained through Rao's approximation: population $F_{4,312} = 4.52$, $P = 0.0015$; age $F_{2,156} = 1.79$, $P = 0.17$; population × age $F_{4,312} = 1.23$, $P = 0.29$), between-population differences being significant for bPC1 (univariate population effect: $F_{2,157} = 7.55$, $P < 0.001$), but not for bPC2 ($F_{2,157} = 1.56$, $P = 0.21$). Therefore, this analysis shows that robins do not vary in body size as measured by bPC2, the component of morphological variation that is best related to a skeletal trait (tarsus length, see Rising & Somers, 1989; Senar & Pascual, 1997). Rather, the populations studied differ in body shape, southernmost robins having shorter wings and tails than their northern counterparts (Fig. 3).

Consistent with the variation in flight-related morphology described above, we also found between-population differences in the wing shape of juveniles. The PCA with primary distances extracted two components (wPC1 and wPC2, Table 1), which described wing pointedness as related to increasing inner (wPC1) or outer (wPC2) primary distances (Chandler & Mulvihill, 1988). Overall, robin populations differed in wing shape as described by these components (multivariate ANCOVA testing for between-population differences in wPC1 and wPC2 together: population $F_{4,260} = 3.89$, $P = 0.0043$; covariate wing length: $F_{2,130} = 26.76$, $P < 0.0001$; test of parallelism: $F_{4,256} = 0.86$, $P = 0.47$). This variation consisted of a decrease in wPC1 scores southwards (Fig. 3; univariate effects: population $F_{2,131} = 7.94$, $P < 0.001$, covariate wing length $F_{1,131} = 42.54$, $P < 0.0001$; test of parallelism: $F_{2,129} = 0.32$, $P = 0.73$), whereas wPC2 scores did not differ between populations (Table 2; population $F_{2,131} = 0.74$, $P = 0.79$, covariate wing length $F_{1,131} = 6.47$, $P = 0.012$; test of parallelism: $F_{2,129} = 1.55$, $P = 0.22$). This result shows that the variation in wing pointedness among Iberian robins consists of changes in length of the inner primaries, but does not affect the outer wing feathers.

Finally, adult robins did not differ among populations in terms of bill length ($F_{2,56} = 0.11$, $P = 0.90$) or bill height ($F_{2,56} = 0.09$, $P = 0.92$; Table 2).

Table 1 Results of PCA with primary distances. The correlation of each variable with each component is shown.

	Factor loadings	
Primary distances	wPC1	wPC2
9th primary	0.21	0.75*
8th primary	−0.002	0.88*
7th primary	0.001	0.73*
6th primary	0.38*	0.05
5th primary	0.66*	−0.01
4th primary	0.92*	−0.10
3rd primary	0.94*	−0.06
2nd primary	0.92*	−0.02
1st primary	0.89*	−0.01
Eigenvalue	3.99	1.88
Variance explained (%)	44.30	20.86

* $P < 0.001$.

Table 2 Variation among robin populations in wPC2 scores of juveniles (means adjusted by wing length) and bill measurements of adults. Means, standard errors and sample sizes are shown.

	wPC2 (juveniles)		Bill measurements (adults)		
	Adjusted mean	*n*	Length (mm)	Height (mm)	*n*
Álava	−0.13 ± 0.15	34	14.92 ± 0.11	3.73 ± 0.03	21
Guadarrama	0.05 ± 0.14	48	14.99 ± 0.12	3.76 ± 0.03	12
Ojén	−0.12 ± 0.17	37	14.94 ± 0.09	3.75 ± 0.04	26

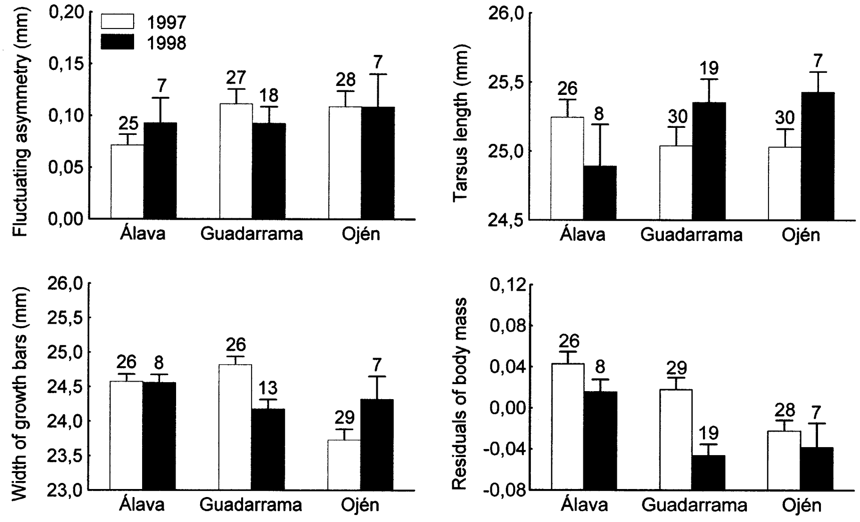

Figure 4 Variation in juvenile condition indices among robin populations in 1997 and 1998. Means, standard errors and sample sizes are shown. Residuals of body mass have been obtained by regressing fledgling mass on tarsus length (both log-transformed).

Indices of juvenile condition

Fluctuating asymmetry and body size

Both the tarsus length and its fluctuating asymmetry were highly repeatable (ANOVA: tarsus length $F_{9,17} = 540.80$, $P < 0.0001$, $r = 0.99$; fluctuating asymmetry $F_{9,17} = 44.05$, $P < 0.0001$, $r = 0.94$). Although these estimates were based on a small sample size (because of difficulties in recapturing many individuals), the high level of repeatability obtained suggests that measurement error should not have affected our results (Lessells & Boag, 1987). The signed differences between right and left measures fitted a normal distribution (Kolmogorov-Smirnov test: $d = 0.045$, $n = 112$, Lilliefors' $P = 0.2$) whose mean did not differ significantly from zero (one-sample *t*-test: $t_{111} = 1.81$, $P = 0.073$). We normalized the absolute value of these differences (fluctuating asymmetry, FA) via the Box-Cox transformation $FA' = [FA + 0.03]^{0.009}$ (Swaddle *et al.*, 1994). Fluctuating asymmetry was not correlated with mean tarsus length ($r = 0.02$, $t_{110} = 0.23$, $P = 0.83$), and did not differ significantly among populations or years (ANOVA: population $F_{2,106} = 0.41$, $P = 0.66$; year $F_{1,106} = 0.02$, $P = 0.89$; population × year $F_{2,106} = 0.50$, $P = 0.61$). This result was unlikely to be due to a low power in detecting a true difference among populations, because the variation of means showed no clear trend (Fig. 4). In contrast, and consistent with this lack of variation in the level of fluctuating asymmetry, juvenile size (measured by the tarsus length, as neither bPC1 nor bPC2 arose as a better index of body size) did not change among populations or study years (Fig. 4; ANOVA: population $F_{2,114} = 0.37$, $P = 0.69$; year $F_{1,114} = 0.60$, $P = 0.44$; population × year $F_{2,114} = 2.19$, $P = 0.12$).

Ptilochronology

Feather growth bars were narrower in the southernmost population in 1997 but not in 1998 (Fig. 4), when robins showed even narrower growth bars in the central population than in the southernmost (ANCOVA: population $F_{2,106} = 2.41$, $P = 0.095$; year $F_{1,106} = 0.02$, $P = 0.88$; population × year $F_{2,106} = 3.86$, $P < 0.05$; covariate rectrix length: $F_{1,106} = 6.96$, $P < 0.01$; tests of parallelism: all $P > 0.38$).

Size-corrected body mass

The residuals of body mass on body size (both log-transformed; $r = 0.21$, $F_{1,115} = 5.46$, $P < 0.05$) decreased southwards in both study years (Fig. 4) and were larger in 1997 than in 1998 (ANOVA: population $F_{2,111} = 7.34$, $P < 0.01$; year $F_{1,111} = 8.55$, $P < 0.01$; population × year $F_{2,111} = 1.76$, $P = 0.18$).

The relationship between weather and juvenile condition

Monthly precipitation changed notably between localities and study years, allowing us to detect a significant month by year interaction in a three-way ANOVA (locality $F_{2,60} = 10.79$, $P < 0.0001$; month $F_{4,60} = 7.26$, $P < 0.0001$; locality × month $F_{4,60} = 2.21$, $P < 0.05$; month × year $F_{4,60} = 3.70$, $P < 0.01$; the remaining effects and interactions with $P > 0.20$), even though we had only three precipitation values per month in

	Álava		Guadarrama		Ojén	
	1997	1998	1997	1998	1997	1998
April	5.9/18.6	29.9/14.3	14.3/18.2	58.6/11.4	16.9/20.1	10.4/18.4
May	22.2/22.2	25.0/18.6	54.7/17.5	48.4/17.0	7.4/22.1	12.7/20.7
June	26.7/21.6	11.6/22.6	15.9/20.5	10.2/22.3	9.2/24.7	1.3/24.3
July	32.0/22.8	3.3/23.9	18.7/24.6	4.6/27.8	0.9/25.6	0.0/28.0
August	15.9/27.7	3.3/25.0	8.0/26.6	3.3/28.2	0.2/27.4	0.0/28.2

Table 3 Precipitation (mm, left) and maximum temperature (°C, right) by months in the three study localities during the years in which we measured juvenile condition of robins. Data are means by periods of 10 days, so $n = 3$ in all cases.

each locality (one every 10 days). Accordingly, maximum temperature increased in the months of lower precipitation, which led to the same pattern and strength of interactions (locality $F_{2,60} = 15.09$, $P < 0.0001$; month $F_{4,60} = 83.14$, $P < 0.0001$; locality × month $F_{4,60} = 2.21$, $P < 0.05$; month × year $F_{4,60} = 7.35$, $P < 0.0001$; the remaining effects and interactions with $P > 0.14$). Because of the nature of the data analysed here, these ANOVA results should be considered as being for guidance only. However, they clearly illustrate that both northern localities suffered a stronger drought in 1998, when they received much less precipitation during June and July, whereas the southernmost locality supported its habitual hot and dry summer in both years (cf. Fig. 1 and Table 3).

DISCUSSION

Our study of robin distribution showed that the restriction of the species' range southwards does not relate a parallel decrease in density in the occupied habitats. It has been suggested that a decrease in abundance of birds towards the edge of the range is most likely to be detected when studying either the whole species' range or a narrow area immediately adjacent to the border (Blackburn *et al.*, 1999). The progressive fragmentation of the range of robins southwards in Iberia shows that we are in the latter situation. However, we still failed to detect a lower local abundance in the southernmost region. This supports the idea that Iberian robins could select sectors above a somehow restrictive threshold of habitat quality, which means that the species' border would be defined by a steep loss of suitable habitats rather than a gradual increase in environmental restrictions in the occupied sites (Lawton, 1993; Blackburn *et al.*, 1999 and references therein). It could be argued that an asymmetric flow of individuals from the most populated northern sectors to the unsuitable southern ones may also explain a similar abundance across the gradient. However, such a strong gene flow would swamp any differentiation of southern populations (Holt & Gomulkiewicz, 1997; Kirkpatrick & Barton, 1997), so that we should not have found morphological correlates of migratory behaviour of robins if directional flow were the factor maintaining similar densities across the Iberian gradient (as the geographical variation in migratory behaviour and its related morphology is unlikely to be the outcome of phenotypic plasticity, Berthold, 1999). In the Iberian Peninsula, the frequency of forest occupation by robins is related chiefly to the level of precipitation (Tellería & Santos, 1993, 1994), which suggests that environmental moisture could determine a threshold of habitat quality for robins. In fact, the ground runs dry in Mediterranean environments as the summer progresses (Joffre & Rambal, 1993), causing a decrease in the primary production of pastures that limits the availability of invertebrates in both soil and grass (Herrera, 1981; Mooney, 1981). Because robins feed principally upon ground invertebrates (Cramp, 1988), the need for a high soil moisture throughout the breeding season could constrain their distribution in a gradient of increasing dryness.

Together with this seemingly restrictive habitat selection towards the border, southern Iberian robins could avoid maladaptation in the range boundary by local differentiation. The morphological variation that we found is consistent with the different migration patterns of Iberian robins, and supports the differentiation of populations near the Mediterranean range boundary. That migratory robins do not have a shorter tail, in contrast with the predictions of aerodynamics (Norberg, 1995), and the morphological variation observed in other passerine species in the same ecological context (Tellería & Carbonell, 1999), could be related to selective forces other than migration. For example, a shorter tail could be constrained by practical requirements for flying in dense vegetation (Norberg, 1995). However, we did not find different feeding-related traits among robin populations, which suggests that feeding behaviour remains similar across Iberia (an example of variation in blackcaps is given in Tellería & Carbonell, 1999). Because feeding behaviour is likely to be a major determinant of habitat selection in robins (see above), this result is consistent with the existence of a threshold of environmental moisture below which robins would rarely occur.

The role of precipitation in the life history of robins was illustrated by the variation among populations and years in juvenile condition. The southernmost population begins to face a precipitation deficit from May, while the two northernmost populations will not suffer this stress until June (Fig. 1, Table 3). Accordingly, we did not find evidence of increased stress during the early development of southernmost robins, as shown by the homogeneous level of fluctuating asymmetry and body size both among populations and years. However, consistent with a differential accentuation of drought southwards during the postfledging period, juvenile condition decreased in the southernmost population during fledgling independence. Moreover, these differences intensified with increasing differences in environmental conditions among localities. Thus, southern robins faced more difficulties than their northern counterparts for growing the tail feathers in the rainiest year, but this trend disappeared when the northernmost localities received less precipitation. Later in the post-fledging period, juveniles evidenced the stronger environmental stress in the southern breeding grounds through a lower body mass. It should be noted that morphological changes could also influence this variation in body mass, as wing load depends on mass and wing shape (Norberg, 1995). Consistent with the results of ptilochronology, juveniles were heavier relative to body size in the rainiest year, which supports the idea that environmental conditions played a relevant role in shaping among-population differences in fledgling mass.

In summary, our results suggest that the hardness of the summer drought, probably due to its effect on food availability (Herrera, 1981; Mooney, 1981), could actually be a major proximate determinant of changes in juvenile condition in robins. Thus, the decrease in environmental moisture throughout the breeding season in southern Iberia could lead to a higher summer mortality of juveniles in these areas (as a consequence of their lower body condition, Brown, 1996). However, this does not necessarily mean that the southernmost populations are maladapted. Body condition must be interpreted in the context defined by the abundance distribution and morphological variation found. By means of both restrictive habitat selection and population differentiation, Iberian robins are likely to be adjusted to environmental heterogeneity and, in turn, enjoy similar developmental conditions along the Mediterranean gradient. After independence, juvenile robins benefit from a milder summer in northern Iberia, which translates into enhanced body condition compared with that of southern, more stressed populations. However, this may well resemble the differing reproductive benefits associated with either migratory or sedentary behaviours, in which case differences in body condition would have no net fitness consequence. Indeed, a higher level of survival in migratory robins late in the breeding season might be balanced by increased mortality due to the costs of migration (Alerstam & Högstedt, 1982; Alerstam, 1990). In contrast, and given that owner robins have advantages against intruders when defending winter territories (Tobias, 1997), sedentary populations could improve recruitment by acquiring the best territories before the arrival of northern conspecifics (Sherry & Holmes, 1996). In fact, we found that sedentary populations of robins have a smaller clutch size but a longer life expectancy than their migratory counterparts in the Iberian Peninsula (Pérez-Tris & Tellería submitted). From this perspective, one should be prudent when interpreting the lower juvenile condition of southern robins late in the breeding season as evidence of decreased fitness in the species' border. Southernmost Iberian robins are likely to be differentiated in the range boundary, a pattern that could be extensible to other forest passerines (Tellería & Carbonell, 1999; Tellería *et al.*, unpublished data). It is possible that, in some instances, both migratory and sedentary populations of robins occur in stressing environments, where they may attain a lower fitness than that achieved in their usual habitats (see some examples in Carbonell & Tellería, 1998, 1999), but this will not be the outcome of occupying peripheral areas in the species' range. Rather, our results suggest that environmental heterogeneity may result in either maladaptation or local adaptation depending on the geographical configuration of the habitats and the evolutionary history of the populations inhabiting them.

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BIOSKETCHES

Javier Pérez-Tris is studying for a PhD on the role of migration in determining variation in morphology and ecology of Iberian birds.

Roberto Carbonell has expertise in the morphology and body condition of Iberian forest passerines. He teaches Zoology at the SEK University, Spain.

José Luis Tellería is Head of the Vertebrate Zoology Section at Complutense University, where he teaches Applied Zoology of Terrestrial Vertebrates and Vertebrate Zoology.

The research group, lead by José Luis Tellería, has long been interested in biogeography, having conducted studies on the distribution of Iberian birds and the ecology of vertebrate communities in fragmented landscapes. Their current research is on the biology of marginal populations of forest birds and the patterns of distribution of Palaearctic vertebrates.