Biological Journal of the Linnean Society, 2003, **78**, 479–488. With 4 figures

Effects of habitat heterogeneity and local adaptation on the body condition of a forest passerine at the edge of its distributional range

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Received 19 July 2002; accepted for publication 29 October 2002

We studied fluctuating asymmetry and feather growth rates as indicators of fitness of blackcaps (*Sylvia atricapilla*) breeding at the border of their distribution range in the Iberian Peninsula. Iberian blackcaps increase their abundance with increasing rainfall and ground cover of brambles. In border habitats, they are sedentary and morphologically different from migrants, suggesting that they could be adapted to peripheral conditions. We tested whether juvenile body condition depends on (1) distance from the centre of the range, (2) mean precipitation or (3) bramble cover. Controlling for environmental variation, we tested for differences between migratory and sedentary populations. Body condition varied across the Iberian gradient in parallel with changes in precipitation. Controlling for this effect, sedentary populations were in better body condition than migratory populations. Our results support the idea that environmental heterogeneity causes fitness to fluctuate across species' ranges, and also that local adaptation may mean that peripheral populations are more than a 'tail end' of the species. *Biological Journal of the Linnean Society*, 2003, **78**, 479–488.

ADDITIONAL KEYWORDS: environmental gradients – fluctuating asymmetry – Iberian Peninsula – migratory behaviour – ptilochronology – species borders – *Sylvia atricapilla*.

INTRODUCTION

The border of a species' range usually represents a frontier beyond which their populations cannot persist. Species borders have long been thought to be caused by decreasing suitability of environments towards the periphery of the range, which reduces the probability that a species can fulfil all conditions necessary for the population to be maintained. This situation should involve a decline in density and a decline in the occurrence of populations before the eventual complete disappearance of the species (Brown, 1984, 1995; Brown, Stevens & Kaufman, 1996; Blackburn *et al.*, 1999); paralleled by an impairment of individuals' fitness, such as body condition, survival or breeding success (Caughley *et al.*, 1988; Hoffmann & Blows, 1994; Siikamaki & Lammi, 1998).

The theory of the configuration of species ranges was developed based on the idea that environmental quality progressively decreases from central to peripheral areas (Brown, 1984, 1995). However, the main components of environmental suitability usually show a patchy distribution, so that habitat quality does not decrease monotonically towards the border, but fluctuates across the species' range (Hanski, 1994; Levin, 1994; Brown, 1995). For example, variables of the greatest importance in the definition of biogeographical gradients, like precipitation and temperature, fluctuate across geographical gradients. On the other hand, structural elements necessary for the persistence of species, like food resources, refuges against predators or breeding sites, are not necessarily lost at constant rates towards the range boundary. As a con-

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sequence, situations of both high and low habitat suitability may be found anywhere, and although the former may be less frequent towards the border and the latter may be rarer in central areas, populations may find suitable habitats independently of their position in the species' range (Lawton, 1993). Fluctuating habitat quality is likely to result in a parallel variation in fitness rather than a progressive impairment towards the border (Brown *et al.*, 1996). Multimodal fitness distributions have, however, received little attention until very recently, and an even smaller effort has been made to understand which factors may determine such variation (Blondel *et al.*, 1993; González-Guzmán & Mehlman, 2001).

Fluctuation of habitat features is not the only possible factor causing multimodal variation in fitness across species ranges. For example, variation in fitness associated to differences in habitat quality might be affected by local adaptation of populations to conditions that are otherwise suboptimal in the rest of the species' range (Blondel *et al.*, 1993; Hoffman & Blows, 1994). The persistence of peripheral populations despite their assumed low fitness is usually attributed to immigration from central areas, which are inhabited by populations that can supply individuals at a rate that exceeds the rate of mortality in the suboptimal environments (Dias, 1996). This immigration precludes local adaptation in the range boundary by maintaining a high frequency of unadapted individuals in a demographic sink (Dias, 1996; Holt & Gomulkiewicz, 1997; Kirkpatrick & Barton, 1997). However, isolation from central areas and adaptation to peripheral environments could allow peripheral populations to overcome environmental constraints at the species' border, and hence represent more than a 'tail end' of the species (Hoffmann & Blows, 1994; García-Ramos & Kirkpatrick, 1997).

We studied blackcaps (*Sylvia atricapilla* L.) near their Mediterranean range boundary in the Iberian Peninsula. The blackcap is a small (*c.* 15 g) passerine typical of European moist forests. Like many other forest passerines, blackcaps breed abundantly and are widely distributed in the north of the Iberian Peninsula, where environmental conditions are similar to those in central Europe (which represents an ecological optimum for these species; Mönkkönen, 1994). However, the abundance of blackcaps decreases in Mediterranean areas, where they become progressively restricted to remnant moist forest, up to the point where they eventually reach their range boundary in southern Iberia (Tellería & Santos, 1993). Nevertheless, in small forested areas located in the southernmost point of the Iberian Peninsula (near the Strait of Gibraltar) blackcaps and many other forest passerines reach a higher abundance than expected from the overall range distribution (Tellería & Santos, 1993). In addition, these peripheral populations are sedentary, and remain morphologically distinct from their northern migratory counterparts (they have short and rounded wings and long tails, consistent with their sedentary life style, as well as other differences in body size and bill morphology; Tellería & Carbonell, 1999; Tellería, Pérez-Tris & Carbonell, 2001). Given that migratory behaviour and its morphological correlates are genetically controlled in the blackcap (Berthold, 1996), morphological and behavioural differences support the differentiation of these peripheral populations. Indeed, their success in exploiting non-seasonal habitats in southern Iberia according to a sedentary strategy suggests that they have somehow been able to overcome the restrictions of southern Mediterranean environments (Pérez-Tris & Tellería, 2002a, 2002b).

Iberian blackcaps breed in a wide array of forested habitats, from mature woodlands to poorly developed river banks, although they avoid the driest Mediterranean environments (Carbonell & Tellería, 1998a; Tellería, Asensio & Díaz 1994). This occurrence in habitats of different quality may cause variation in the fitness of blackcaps across the Iberian Peninsula. Previous studies have found that body condition of blackcaps decreases at the transition from moist to dry environments in the northern half of the Iberian Peninsula (Carbonell & Tellería, 1998b, 1999), but nothing is known about the possible continuation of this pattern towards the range boundary in the south, nor about the possibility of enhanced body condition of the sedentary, morphologically distinct populations inhabiting the border. To shed light on this gap in our knowledge, we studied variation in body condition of juvenile blackcaps near their Mediterranean range boundary. Juvenile body condition is directly related to fitness because (1) it reflects the quality of the reproductive output of populations (Lindén *et al.*, 1992), (2) health at fledging determines survival early in life (a major component of variation in fitness of birds; Lindström, 1999), and (3) stress suffered during growth (for example in relation to a poor nutrition) may translate into negative effects on fitness later on in life by reducing life span or breeding success (Metcalfe & Monaghan, 2001). Moreover, the study of juveniles has the advantage that selection against low-quality phenotypes has not yet taken place, and hence it cannot hide between-population differences in body condition, as it could do if adults were considered. We specifically tested whether juvenile body condition of blackcaps decreased towards the range border or varies according to fluctuation in habitat quality. In addition, we evaluated whether juvenile body condition was enhanced at the species' border, as predicted if peripheral, sedentary populations show local adaptation.

METHODS

STUDY AREAS AND CAPTURE OF BLACKCAPS

We selected five localities in the Iberian Peninsula (Fig. 1), representing the different environments in which blackcaps can be found in this area (forests of different degrees of development, from moist mixed forests to dry river banks; Carbonell & Tellería, 1998a; Tellería *et al*., 1999). One of the five localities was a group of moist forests (*Quercus robur* mixed with *Quercus faginea*) located in the north of the Iberian Peninsula, and situated in the transitional zone between the Eurosiberian and the Mediterranean Iberian regions (Álava, 42°55′ N, 2°29′ W, mean altitude 620 m a.s.l., mean annual rainfall 1000–1500 mm, mean annual temperature 12°C). We selected two further localities in central Iberia, in developed moist forests (*Quercus pyrenaica* mixed with *Fraxinus excelsior* in Sierra de Guadarrama, 40°54′ N, 3°53′ W, 1100 m a.s.l., 700–1000 mm, 10°C), and a set of dry riparian forests (*Populus nigra* mixed with *Tamarix gallica* associated with rivers flowing through shrublands and agricultural landscapes in Madrid, 40°30′ N, 3°4′ W, 600 m a.s.l., 300–500 mm, 14°C). In southern Iberia, at the blackcaps' range boundary, we also selected well-developed forests (*Quercus suber* mixed with *Quercus canariensis* in Sierra de Ojén, 36°01′ N, 5°36′ W, 250 m a.s.l., 1000–1500 mm, 16°C) and dry river banks (*Nerium oleander*, *Olea europaea* and *Salix* spp. associated with streams flowing through grasslands and dry Mediterranean shrublands in Tarifa, 36°01′ N, 5°36′ W, 0–5 m a.s.l., 700–1000 mm, 18°C). Blackcaps were mist-netted in all five sites from mid June to late July 1997, coinciding with the peak of the fledging season. All individuals were measured by one of us (RC), ringed to avoid repetition, and released.

MEASURING BODY CONDITION

We used two measures of body condition, which allowed us to evaluate the effect of environmental constraints on development at two different times of fledgling growth (Brown, 1996; Pérez-Tris, Carbonell & Tellería, 2000).

First, we used fluctuating asymmetry of tarsus length as an index of the stress faced by blackcaps during early development (the tarsus of blackcaps reaches its final size well before fledging). Fluctuating asymmetry is a small, random deviation from perfect symmetry in bilateral characters attributed to developmental instability (Palmer & Strobeck, 1986). In large populations not subject to genetic stress, developmental instability is interpreted as the outcome of environmental constraints (Møller & Swaddle, 1997). Several studies have shown that fluctuating asymmetry increases in adverse environments, and that developmental instability is negatively correlated to direct measures of fitness (Møller & Swaddle, 1997; Siikamaki & Lammi, 1998). We measured the length of both tarsi to the last unbroken scale before the toes (using a 0.01-mm precision digital calliper, see Svensson, 1992), and computed asymmetry as the absolute value of the difference between right and left dimensions.

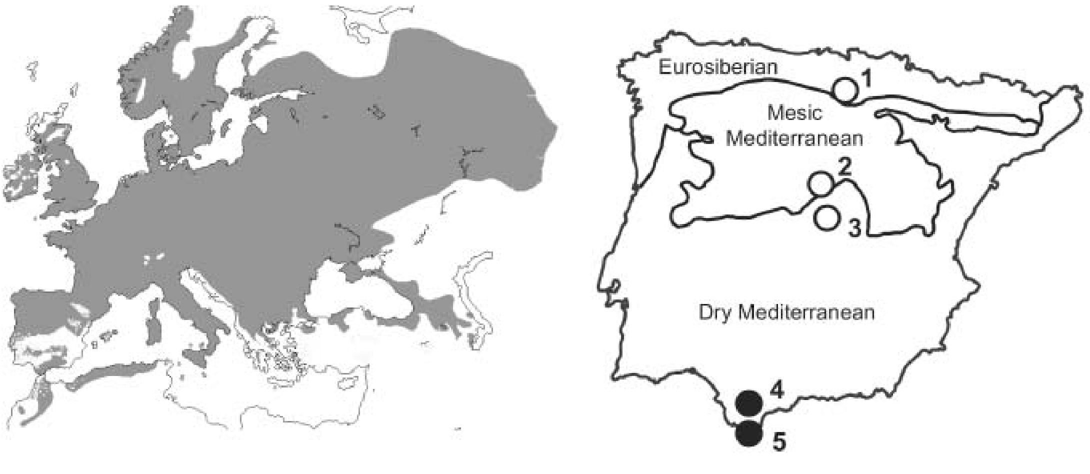

Figure 1. Left: distribution of Blackcaps in the western Palearctic. Right: the main environmental areas in the Iberian Peninsula, representing the gradient of increasing dryness from the moist northern areas (similar to Central European environments) to the dry southern environments where blackcaps reach the border of their range. The location of the five study sites (1, Álava; 2, Guadarrama; 3, Madrid; 4, Ojén; and 5, Tarifa) is indicated, with different symbols for migratory (circles) and sedentary (dots) populations.

Previous studies with recaptured birds (Carbonell & Tellería, 1998b) showed a high repeatability of asymmetry (intraclass correlation: $r_i = 0.91$). Signed differences between both tarsi closely fitted a normal distribution (Filliben's correlation in a normal probability plot, $r = 0.97$, $P < 0.001$, $N = 97$), whose mean did not significantly differ from zero ($t_{96} = 1.22$, $P = 0.11$). We normalized the distribution of asymmetry (which takes absolute values and hence adjusts a half-normal distribution) using the Box–Cox transformation $FA' = (FA + 0.03)^{0.009}$, where FA is the original value of fluctuating asymmetry, FA′ is the transformed value, and 0.03 and 0.009 are two coefficients obtained by iteration (for further details see Swaddle, Witter & Cuthill 1994). After transformation, fluctuating asymmetry closely fitted a normal distribution (Filliben's correlations: $r > 0.98$, $P < 0.0001$ in all five localities). Fluctuating asymmetry was not correlated with the mean tarsus length ($r = 0.08$, $F_{1,95} = 0.63$, $P = 0.43$), so we did not correct for tarsus length in our analyses of asymmetry.

Secondly, we used ptilochronology as an index of body condition at fledging. Ptilochronology uses feather growth rates to estimate the capability of birds to mobilize energy and proteins (Grubb, 1995). Because each pair of one clear and one dark bar corresponds to one day of feather growth, the width of bars is a direct measure of the rate of feather production (Grub, 1995). Ptilochronology is one of the best measures of avian body condition (Brown, 1996), which has been proven to be effective in assessing limitations faced by birds in poor environments (Grub, 1995; Carbonell & Tellería, 1999). Given that juvenile blackcaps are still growing the tail after fledging (Cramp, 1992; pers. observ.), ptilochronology is a suitable index of body condition of blackcaps at fledging.

Before releasing blackcaps, we plucked their fifth rectrices to measure growth bars. We selected these feathers to minimize the loss of manoeuvrability due to reduction in tail surface (Thomas, 1993). We measured the width of ten growth bars in the centre of the feather vane, using a 0.01-mm precision digital calliper. We estimated repeatability of feather growth bars using measures of right and left feathers (intraclass correlation: $r_i = 0.94$, $F_{87,88} = 32.15$, $P < 0.0001$), and used the average of both feathers as the final value of feather growth rate (feather length produced per 10 days of growth).

MEASURING HABITAT QUALITY

Our goal in this paper was not only to test whether fitness progressively decreases or fluctuates towards the border, but also to identify which factors determine such fluctuations. Indeed, the interpretation of fluctuating fitness across the species range as the outcome of variations in environmental quality would be tautological if habitat quality were inferred from variation in fitness. Relevant components of habitat quality should be defined *a priori* and used to predict variations in fitness. Based on previous evidence, we studied two possible components of habitat quality for Iberian blackcap populations.

Climatic conditions

In the Mediterranean area, spatial variation in primary production is primarily determined by precipitation levels (Lautensach, 1967; Mooney, 1981). Consequently, the suitability of different Iberian areas for reproduction of blackcaps (measured by overall food abundance, shrub development, etc.) could depend on spring precipitation levels (Blondel & Aronson, 1999). In fact, the abundance of Iberian blackcaps is chiefly related to rainfall (Tellería & Santos, 1993, 1994). If breeding success of blackcaps depends on primary production, juveniles should show a better condition in the rainiest localities in the Iberian Peninsula.

Structural habitat features

Fitness of blackcaps could be determined by factors other than climate, such as the occurrence of structural features necessary for population maintenance (nesting places, foraging sites, refuges against predators, etc.). In fact, habitat selection constitutes an important mechanism for population limitation in birds (Newton, 1998). A study of habitat selection by breeding blackcaps in our study sites showed that the density of blackcaps was better predicted by the cover of brambles (*Rubus* spp.) than by any other structural variable (Carbonell & Tellería, 1998a). In addition, brambles were the main nesting substrate in a sample of 111 nest record cards of Iberian blackcaps available in the Spanish Ornithological Society. Among these records, 52.3% belonged to brambles, 16.2 to hawthorns (*Crataegus monogyna*), and the remaining 31.5% were distributed among 18 other shrub or tree species (own unpublished data). If these results for habitat and nest-site selection indicate that blackcaps encounter better conditions for breeding in habitats with a high cover of brambles, the distribution of this resource could proximately determine variations in juvenile condition across the Iberian Peninsula.

ENVIRONMENTAL FEATURES AND PREDICTIONS

We described each locality with respect to geographical, climatic and habitat variables (Table 1) and classified their populations as migratory or sedentary (Fig. 1).

Distance to the centre of the range was directly measured on a map, using the straight line between each

Table 1. Environmental features of the five localities studied, and contrast vectors used for planning comparisons of mean juvenile condition among localities according to the different hypotheses to be tested. We used Álava as a reference to measure distance from the centre of the range (which therefore had a distance of 0 km). Pairwise differences between localities were reduced to percentage differences (% dif.) using the largest difference from Álava as a reference. The coefficients of the contrast vectors define the strength and direction of changes between means, as predicted by differences in the corresponding variable. These coefficients are integers whose value is only constrained by the need of summing to zero in each comparison (see StatSoft, 1999). The number of fledgling blackcaps captured in each locality is also given (*N*)

	Distance				Precipitation			Cover of brambles (%)		
	N	km	% dif.	Vector	mm	% dif.	Vector	Cover	% dif.	Vector
Álava	36	0	0	53	247.1	0	21	22.48	0	29
Guadarrama	12	237	29.51	23	243.4	2.47	21	0.17	100	–21
Madrid	11	280	34.87	18	135.4	74.62	–14	4.88	78.89	–11
Ojén	27	790	98.38	–47	179.9	44.89	1	4.63	80.01	–11
Tarifa	11	803	100	–47	97.4	100	–29	16.1	28.60	14

site and Álava, the locality that is closest to the central European core areas in the species' range. Accordingly, Álava took the lowest value of distance to the centre of the range (which was arbitrarily set to 0 km). Precipitation in each locality was measured during the April–July period, which comprises the whole breeding season of blackcaps. Mean precipitation values were obtained from data recorded over more than 20 years by the meteorological stations neighbouring our study sites. Finally, the cover of brambles was measured during a study of habitat selection in blackcaps in the same localities (Carbonell & Tellería, 1998a). Apart from being the closest site to the centre of the species' range, Álava showed the highest values for precipitation and cover of brambles (Table 1), supporting the view that this locality has the highest quality in our set of study sites in relation to both geographical and environmental variables.

Statistical analyses

In our study, the body condition of fledgling blackcaps is a non-measurable variable defined by the covariation between fluctuating asymmetry and feather growth rates: individuals in good condition show little asymmetry and wide feather growth bars. We conducted a multivariate ANOVA, including both components of body condition as dependent variables, to study differences in body condition between populations. Once the overall variation in body condition was thus evaluated, we assessed the particular contribution of each component of condition to between-population differences by means of univariate protected ANOVAs.

We specifically tested for geographical location, precipitation and habitat structure as determinants of the variation in body condition of blackcaps. To examine these hypotheses, we planned specific comparisons of means based on the variation between localities in distance to the centre of the range, rainfall or cover of brambles. These comparisons allowed us to test not only for the specific patterns of variation, but also for the specific magnitudes of between-mean change predicted by the corresponding hypotheses (StatSoft, 1999). Independent predictions were made for each hypothesis (distance, precipitation and cover of brambles) under the assumption that the percentage of change in body condition between two given localities should be similar to the percentage of change in the explanatory variable of interest between these two localities. Because the three explanatory variables show very different patterns of variation among localities (Table 1), unequivocal predictions were posed for each hypothesis (Fig. 2). To make our predictions, we first identified the locality for which the corresponding explanatory variable differed most from Álava (the reference site), and then we used this difference as a reference to reduce all other pairwise differences between localities to a percentage of the largest one (Table 1). To test each hypothesis, we implemented the contrast vectors derived from variation in distance, precipitation or cover of brambles (Table 1) in the Visual GLM module of the Statistica 5.5 computer program (StatSoft, 1999).

Once we had established which hypothesis best explains variation in body condition among populations, we examined the possible effect of local differentiation of sedentary populations on juvenile body

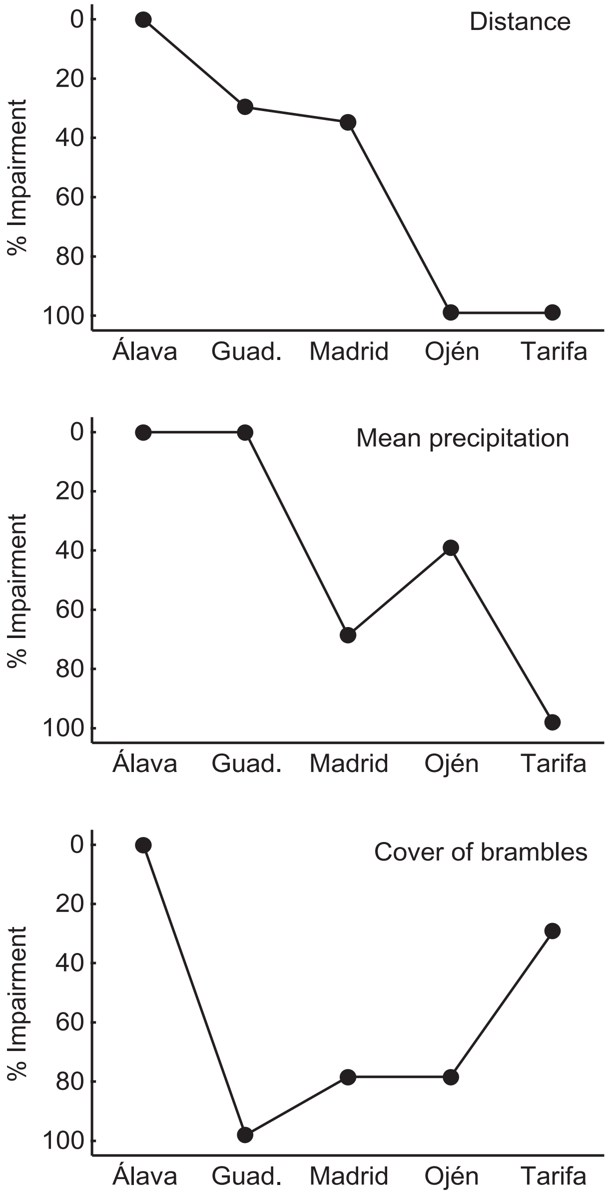

Figure 2. Predicted changes in body condition among localities according to the variation in distance from the centre of the range (top), mean precipitation in spring (middle) and cover of brambles (bottom). The plots show the expected percentage of impairment in body condition (i.e. increased asymmetry and decreased width of feather growth bars) with respect to the best predicted value, which has been assigned 0% impairment in body condition (100% impairment has been assigned to the lowest expected value in each case).

condition. To do so, we estimated the contribution of between-population differences to the variation in body condition that was not explained by environmental features, using localities as sample units in an ANCOVA with average asymmetry or feather growth rate in each locality as dependent variables, population (migratory vs. sedentary) as the factor, and a covariate (distance from the centre, precipitation or cover of brambles) selected according to the results of the former analyses. Because of the low power of an ANCOVA with only five data points, we gave more importance to the size of the effects estimated (measured as the percentage of variance explained) than to significance levels in this analysis.

RESULTS

JUVENILE CONDITION AND ENVIRONMENTAL FEATURES

Variation among localities in body condition of juvenile blackcaps (analysed by combining fluctuating asymmetry and feather growth rates together in a multivariate ANOVA) was not dependent on distance from the centre of the species' range (Wilks' Lambda = 0.96, Rao's approximated $F_{2,91} = 2.06$, $P = 0.134$), nor it was dependent on the cover of brambles measured in each locality (Wilks' lambda = 0.95, $F_{2,91} = 2.45, P = 0.092$). Precipitation was the only variable that significantly predicted body condition of juvenile blackcaps (Wilks' lambda = 0.89, $F_{2,91} = 5.68$, $P = 0.0047$; Fig. 3).

Once the pattern of variation in overall body condition was thus established, univariate analyses showed that both components of juvenile condition significantly contributed to variation in relation to precipitation (univariate ANOVA results using the contrast vectors corresponding to precipitation: fluctuating asymmetry $F_{1,92} = 4.73$, $P = 0.032$; feather growth rates $F_{1,92} = 7.41$, $P = 0.0077$). Therefore, these results show that, in rainy localities, juvenile blackcaps showed a higher developmental stability and less difficulty for growing their tail feathers at fledging (Fig. 3).

JUVENILE CONDITION AND POPULATION DIFFERENTIATION

Although a large amount of variation in body condition was accounted for by precipitation, differences between migratory populations and sedentary populations (living on the very edge of the range) contributed to further explain such variation. Nevertheless, this effect had a different importance depending on the component of body condition studied.

Compared to precipitation, population type (migratory vs. sedentary) had little effect on fluctuating asymmetry (Fig. 4). Thus, while precipitation (used as a covariate in an ANCOVA) explained 70% of variance in fluctuating asymmetry and was close to statistical significance ($F_{1,2} = 8.83$, $P = 0.097$), population type explained only 4% of variance ($F_{1,2} = 0.44$, $P = 0.575$), and hence could be considered not to be too relevant.

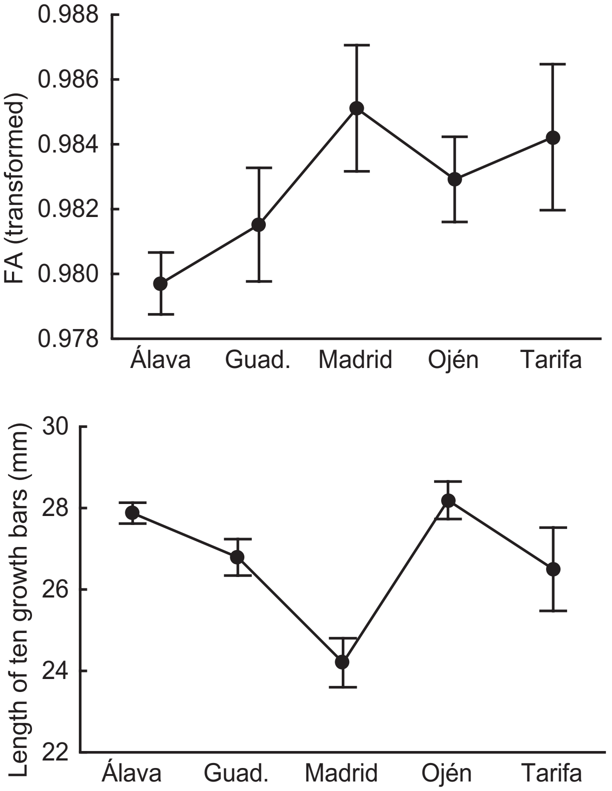

Figure 3. Variation among localities in two measures of body condition (fluctuating asymmetry of tarsus length and feather growth rates) of juvenile blackcaps. Means and standard errors are shown. The values of fluctuating asymmetry (FA) that are shown have been obtained by Box–Cox transformation of the original asymmetry values (see text for details).

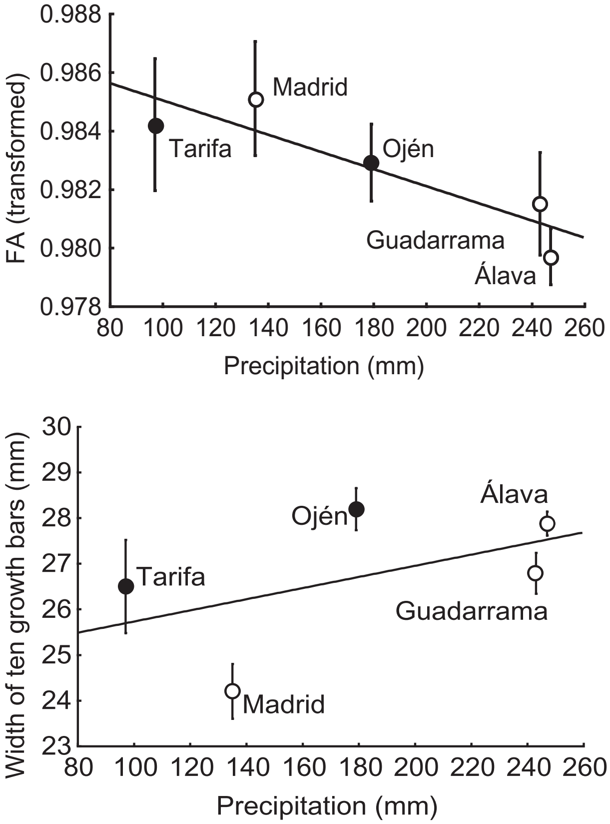

Figure 4. Relationships between mean precipitation at each locality and average values of fluctuating asymmetry and feather growth rates in blackcaps. Standard errors are also shown. ○, migratory populations; ●, sedentary populations (which live on the range edge).

However, population type accounted for a high and significant amount of variance in feather growth rates. After controlling for the precipitation at each locality ($F_{1,2} = 24.69$, $P = 0.038$, $r^2 = 0.80$), sedentary blackcaps showed significantly higher feather growth rates than expected, while migratory blackcaps showed the opposite trend ($F_{1,2} = 20.74$, $P = 0.045$, $r^2 = 0.67$; Fig. 4).

DISCUSSION

Our results show that juvenile condition of blackcaps, an important component of fitness, fluctuates towards the southern edge of the species' range, instead of showing a continuous decrease. This supports the view that monotonically decreasing habitat suitability from the centre towards the periphery of the range may be an unrealistic simplification of a more complex and dynamic process. Indeed, models based on true distributions of the components of habitat quality across the species range predict that abundance and fitness of species should follow a multimodal pattern near the range boundary (Lawton, 1993; Brown *et al.*, 1996). Since the last decade, the study of variation in fitness across species ranges has supported multimodal distributions instead of monotonic changes (Blondel *et al.*, 1993; Hoffman & Blows, 1994; González-Guzmán & Mehlman, 2001). Some cases in which a progressive decrease in fitness towards the border has been observed can be explained because only part of the relevant gradient was considered (as was the case with blackcaps in the northern half of the Iberian Peninsula; Carbonell & Tellería, 1998b, 1999).

Our study not only shows a pattern of multimodal variation in fitness of blackcaps, but also contributes to identifying the components of habitat quality involved in defining this pattern. The multimodal distribution of juvenile condition in Iberian blackcaps was better explained by variations in precipitation than by availability of structural elements selected by the species within its habitat. This is consistent with the fact that precipitation is the major determinant of the abundance of forest passerines across the Iberian Peninsula, including blackcaps (Tellería & Santos, 1994). Thus, habitat heterogeneity may be important in shaping variations in body condition at local scales, but factors operating at the regional scale would be more important in determining variation between localities across the species range. In the Mediterranean region, precipitation is the principal determinant of forest development, and hence of availability of food, refuges and nesting places for forest passerines. Because precipitation follows a multimodal pattern in the Iberian Peninsula, Iberian blackcaps did not decrease their fitness towards the southern Mediterranean border; rather, our results showed that blackcaps may find suitable environments even at the border of the species' range.

In a recent review, Blackburn *et al*. (1999) discussed which circumstances may explain why some studies have failed to illustrate the negative correlation between distance to the centre of a species' range and abundance or fitness of populations. An incorrect scale of analysis, the measurement of distance using wrong references for the centre of the range, the consideration of heterogeneous data obtained over many years (common to broad-scale studies) or the inclusion of non-breeding floaters in the study could all hide a true relationship between distance from the centre and population abundance (Blackburn *et al*., 1999). However, none of these caveats can apply to our study. We studied blackcaps in a relatively narrow region directly adjacent to the range edge, where the effect of impoverished conditions on habitat quality should be more manifest (García & Arroyo, 2001). In addition, we used data from one breeding season, using homogeneous methods and under very controlled conditions, so they cannot be affected by year-to-year variation that could account for our results. Finally, the use of juveniles born in the ongoing season, which are the product of reproduction in each population, prevents any effect of non-breeding floaters as potential sources of bias.

The idea that habitat quality should monotonically decrease across species ranges is rooted in the existence of geographical gradients of environmental conditions. Important components of environmental quality manifest geographical gradients, as in the case of precipitation in the Iberian Peninsula (Lautensach, 1967). These gradients may involve parallel variation in abundance and fitness of birds (Tellería & Santos, 1993; Carbonell & Tellería, 1998b, 1999). However, our results support the idea that habitat quality, as a consequence of environmental heterogeneity independent of geographical location, is what best explains whether or not populations perform well in a given environment. This would explain why discontinuous distributions of species within their geographical ranges are the rule rather than the exception. Several studies suggest that it is not environmental quality, but the probability of finding a suitable habitat, what decreases towards the border of a species' range (Lawton, 1993; Pérez-Tris *et al*., 2000). Under these circumstances, the range of a species may become increasingly fragmented from the centre to the periphery without peripheral populations necessarily facing worse conditions than central ones (Lawton, 1993).

The increased fragmentation of the species' range towards the border may further contribute to a multimodal distribution of fitness, because isolation may favour local adaptation to peripheral environments (Hoffmann & Blows, 1994). Among the populations that we studied, blackcaps living on the southern edge of the Iberian Peninsula are sedentary, and consistent with this they have a morphology that differs from that of migratory populations living further to the north, which supports the idea that they undergo differentiation in the range boundary (Tellería & Carbonell, 1999). In addition, this study shows that fledglings produced by these blackcaps are not in a poor body condition. In fact, sedentary blackcaps have a better condition than expected on the basis of precipitation (which is similar to that found in Álava, an Eurosiberian locality), while migratory populations occupying Mediterranean environments (Guadarrama and Madrid) have a comparatively worse condition (Fig. 4). The idea that sedentary blackcaps are independent populations locally adapted to the particular conditions of peripheral environments was also supported by previous studies. For example, migratory behaviour affects life-history traits of Iberian blackcaps, with sedentary populations having a lower clutch size and a higher survival than their migratory counterparts (Pérez-Tris & Tellería, 2002a). In addition, the morphological differentiation of sedentary blackcaps (which have a larger body size than migrants arriving to their range for wintering) apparently contributes to them having a higher social status in non-breeding grounds, allowing them to monopolize the best habitat types in winter (Pérez-Tris & Tellería, 2002b).

Isolation by distance and breeding-site fidelity may cause the effective allopatry of sedentary and migratory Iberian blackcaps, which would have favoured the persistence of differences between both population types. In addition, selection against migrant or resident blackcaps depending on environmental seasonality in each Iberian region could counteract possible gene flow (Berthold, 1996; García-Ramos & Kirkpatrick, 1997). According to this view, sedentary populations living on the edge would be self-sufficient entities, which successfully exploit their environments through a strategy better adjusted to the seasonal availability of resources in southern Mediterranean environments, and whose persistence does not require a continuous supply of individuals from central areas (Hoffmann & Blows, 1994). Recent studies have found a high frequency of subsistence of peripheral populations after episodes of range contraction in many species (Channell & Lomolino, 2000), which supports the idea of their potential to persist on the edge of the range regardless of the fate of their central counterparts.

ACKNOWLEDGEMENTS

The comments by Beatriz Arroyo, Pepa Casas, Manu Cleuvenot, Juan A. Delgado and Sergi Herrando improved an early version of this paper. The Agencias de Medio Ambiente (Diputación Foral de Álava, Comunidad Autónoma de Madrid and Junta de Andalucía) kindly authorized us to capture blackcaps. SEO/Birdlife provided access to nest record cards. This paper was funded by the projects PB92-0238 (Ministerio de Educación y Ciencia), PB97-0325 (Ministerio de Educación y Cultura), BOS2000-0556 (Ministerio de Ciencia y Tecnología), and by a FPI grant from the Universidad Complutense de Madrid (to JP-T).

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