

Feather traits and ptilochronology as indicators of stress in Iberian Blackcaps *Sylvia atricapilla*

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*This paper compares feather traits to explain differences in stress between three Blackcap *Sylvia atricapilla* populations distributed along a N–S gradient of increasing drought in the Iberian Peninsula. Indices based on the width of growth bars, length, mass and fluctuating asymmetry (FA) of rectrices were examined for age effects and variation between populations along the gradient. The growth bars of juveniles (but not adults), feather mass, mass/length ratio and FA varied between populations (narrower bars, lighter feathers and increasing FA in the southern populations), providing evidence of increasing stress of moult in Blackcaps of drier Iberian regions.*

Many Palearctic forest passerines are decreasing in abundance in the Mediterranean region as drought increases.^{1,2} Although knowledge of the environmental factors involved and of the way they might affect bird biology is incomplete, this pattern might be linked to restrictions on primary productivity. Blue Tits *Parus caeruleus* breeding in southern France, for instance, have lower body size and breeding success in Mediterranean sclerophyllous forests than in contiguous moister forests, where their breeding cycle matches better the seasonal distribution of food abundance (caterpillars).^{3,4} Blackcaps breeding in Spain also show increasing asymmetry of tarsus-length as drought increases in proximity to their southern range boundary.⁵ It has been suggested that Mediterranean forests might act as sink habitats for some forest birds.⁶

Moult involves a large amount of energy since feathers produced in a complete moult account for 20–30% of the total lean dry body mass of passerines.^{7,8} Moult duration and feather characteristics depend on several factors related to the requirements of birds and the availability of food (e.g. food quality, hours

available to feed, thermoregulation, body size, etc.⁹), the timing of feather replacement¹⁰ as well as the body condition of moulting individuals.^{11,12} Therefore, one would expect populations of a single species in a given region, subject to different regimes of food availability, to show differences in the mean moulting patterns and plumage quality.^{13,14} Length, mass and symmetry of feathers have been considered to be very sensitive to nutritional stress^{15,16} so that they could be used to assess body condition in birds.¹³

This paper analyses some features of the tail feathers of three Iberian populations of Blackcap distributed along a gradient of increasing xericity. This species is abundant in forests and farmlands in the northern Palearctic region, but in the south, and especially the Mediterranean region, it is restricted to some moist forest patches.¹ Like many other passerines, adult Blackcaps have a full moult after breeding, and juveniles develop their tail and wing feathers in the nest and during the first days after fledging.⁵ Iberian Blackcaps moult in summer, when the abundance of invertebrates decreases in xeric Mediterranean forests and scrub.¹⁷ Some features of the tail and wing feathers may reflect the effects of this food shortage, providing an index of the ability of different populations to cope with the

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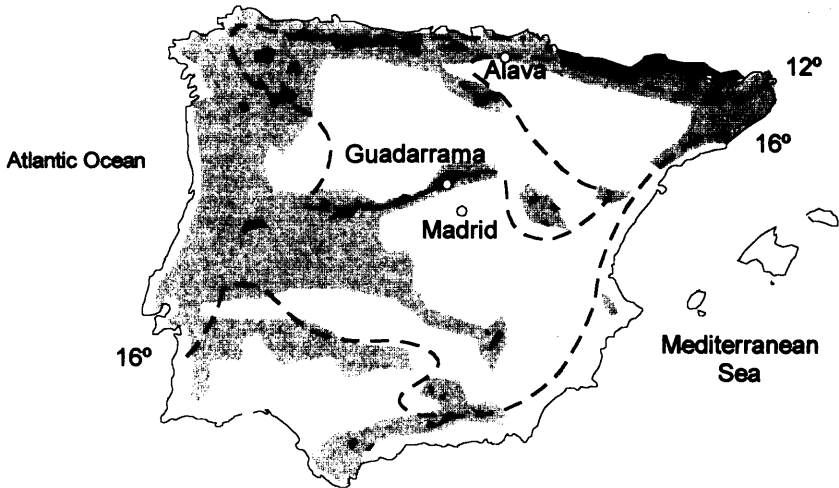


Figure 1. Location of the Blackcap study areas (white circles) in the Iberian Peninsula. Mean annual temperature isotherms for 12°C and 16°C and areas with mean annual precipitation over 600 mm (light shading) are shown. Black areas, mountains.

trophic restrictions in this critical period across the southern border of the species' range.

METHODS

Study area

We studied Blackcaps in three areas representative of the Iberian climatic gradient (Fig. 1): Alava (42°55'N 2°29'W; 620 m altitude; mean rainfall 350 mm between April and August; mean April–August maximum temperature 21.2°C); Sierra de Guadarrama (40°54'N 3°53'W; 1100 m; 270 mm; 21.2°C); and Madrid (40°25'N 3°40'W; 600 m; 130 mm; 27°C). The Alava Blackcaps were studied in mixed forests of *Quercus faginea*, *Quercus robur* and *Acer campestre*, in a region where the species is very abundant.

The Sierra de Guadarrama population was located in a mountain valley covered by *Quercus pyrenaica*, *Fraxinus angustifolia*, *Populus nigra*, *Alnus glutinosa* and *Salix* spp., while the Madrid population was restricted to riparian forests containing *Ulmus minor*, *Tamarix gallica*, *Fraxinus angustifolia*, *Salix* spp. and *Populus nigra* plantations, of the southern, xeric piedmont of the Sierra de Guadarrama. These two last populations occupied the two habitats of the species that are typical in central Iberia,

where Blackcaps are restricted to certain patches of broadleaved forests in moist mountains and river banks.¹⁸

Field and laboratory methods

Between mid-May and the end of July 1996, we caught Blackcaps (47 males, 19 females and 41 juveniles) by using mist-nets and song playback. We measured their tarsus-length with a digital calliper to control for the effects of bird size on feather traits in the following analyses.⁸ The age and sex of birds were noted and, prior to release, the fifth left and right rectrices were removed. We selected these feathers to avoid loss of manoeuvrability caused by a reduction in the lifting surfaces of the tails.^{19,20} Juvenile feathers grew in the year of capture, whereas those of adults had grown the previous year.⁷ Some adults may have been second-year birds, however, which developed rectrices as nestlings or fledglings during the previous breeding period.

In the laboratory, we measured: (1) maximum feather length, using a Mytutoyo 500 digital calliper (resolution: 0.01 ± 0.02 mm); (2) mass, using a digital Mettler Toledo AG-245 balance (resolution of 0.01 mg and 0.02 mg instrumental repeatability); (3) total length of ten growth bars centred between the second

and distal third of the feather vane.²¹ Measurements were always taken by the same person (R.C.). These data were used to calculate the following three indices.

Total length of ten growth bars. Each growth bar corresponds to a growth period of 24 hours,²² and the better the quality and/or quantity of food ingested by the bird, the broader the bars.^{13,21} The aggregate width of the ten bars thus reveals the nutritional state of the birds during a ten-day period, being narrower in individuals with a deficient diet.¹³ As it may sometimes be difficult to count bars, we selected the better of the two feathers from each individual.

Length, mass and mass/length ratio of feathers. Under nutritional stress conditions, feathers are lighter and shorter than under normal conditions.¹⁶ Malnourished birds show reduced density of structural elements,¹⁶ so feathers of similar length, differing in mass, would reflect different densities of feathers. We evaluated feather density (mg/mm) by calculating the mass/length ratio and taking the mean scores of the two feathers from each bird.

Fluctuating asymmetry in length, mass and mass/length ratio of feathers. Fluctuating asymmetry (FA) reflects small, random deviations from perfect symmetry which may stem from the inability of individuals to undergo identical development of bilaterally symmetrical traits

on both sides of the body.²³ It is an epigenetic measure of the lack of homeostasis in growth due to environmental stress or lack of genetic variation.²⁴ It is usually scored by the absolute difference between left and right values of the bilateral traits under study (absolute FA).^{25–27} The levels of FA in the feathers of birds are sensitive to nutritional stress.¹⁵ FA may also result from differences in abrasion due to the uneven consistency of the feathers^{28,29} and hence it may be seen as an additional index of plumage quality.

In order to estimate the precision of measurement error (repeatability of measurements), we made two independent measurements of growth bar length, feather length and feather length asymmetries in ten birds. We performed an ANOVA in which these measurements were used as dependent variables and each individual as a class. High intra-class correlation coefficients r_i imply high repeatability.^{30,31} Our measurements were highly repeatable (right feather length, $r_i = 0.998$; left feather length, $r_i = 0.999$; FA of length, $r_i = 0.899$; length of ten growth bars, $r_i = 0.944$). We examined whether the asymmetry data conformed to the properties of fluctuating asymmetries (i.e. a normal distribution with a mean of zero) by test of normality and one-sample *t*-tests.³² The distribution of signed asymmetries closely approximated a normal distribution

Table 1. Mean values, standard error and sample size of variables measured in feathers for adults (A) and juveniles (Y) in the three study populations.

		Alava	Guadarrama	Madrid
Tarsus-length (mm)	A	19.87 ± 0.10 (28)	20.10 ± 0.11 (17)	19.93 ± 0.17 (21)
	Y	19.80 ± 0.16 (19)	19.92 ± 0.21 (11)	20.09 ± 0.15 (11)
Width of 10 bars (mm)	A	29.45 ± 0.50 (23)	29.90 ± 0.71 (15)	30.08 ± 0.50 (19)
	Y	29.86 ± 0.54 (17)	28.14 ± 0.45 (11)	28.25 ± 0.40 (10)
Feather length (mm)	A	62.87 ± 0.40 (22)	63.31 ± 0.64 (15)	63.04 ± 0.50 (19)
	Y	64.21 ± 0.37 (17)	63.02 ± 0.39 (11)	64.34 ± 0.58 (11)
Feather mass (mg)	A	6.62 ± 0.10 (24)	6.37 ± 0.14 (15)	6.45 ± 0.09 (20)
	Y	6.92 ± 0.08 (17)	6.63 ± 0.10 (11)	6.73 ± 0.15 (11)
Feather mass/length (×100)	A	10.51 ± 0.14 (22)	10.05 ± 0.14 (15)	10.26 ± 0.08 (19)
	Y	10.78 ± 0.12 (17)	10.51 ± 0.13 (11)	10.45 ± 0.17 (11)
FA length (mm)	A	0.28 ± 0.05 (22)	0.27 ± 0.06 (15)	0.35 ± 0.08 (19)
	Y	0.29 ± 0.08 (17)	0.21 ± 0.04 (11)	0.24 ± 0.08 (11)
FA mass (mg)	A	0.09 ± 0.02 (24)	0.06 ± 0.02 (15)	0.12 ± 0.03 (20)
	Y	0.095 ± 0.02 (17)	0.08 ± 0.03 (11)	0.11 ± 0.02 (11)
FA mass/length (×100)	A	0.09 ± 0.01 (22)	0.09 ± 0.02 (15)	0.20 ± 0.04 (19)
	Y	0.12 ± 0.03 (17)	0.10 ± 0.04 (11)	0.15 ± 0.03 (11)

Values are given as mean ± se (*n*). FA, fluctuating asymmetry

Table 2. *F*-ratios of two-way ANCOVAs (df), with tarsus-length as the covariate, to test for the effects of age and population on several feather indices.

	Covariate	Factors		
	Tarsus length	Age	Population	Interaction
Width of 10 growth bars	1.44 (1,82)	5.56* (1,82)	0.29 (2,82)	2.11 (2,82)
Feather length	2.62 (1,88)	3.96* (1,88)	0.65 (2,88)	1.35 (2,88)
Feather mass	3.01 (1,91)	9.30** (1,91)	3.93* (2,91)	0.03 (2,91)
Mass/length	1.22 (1,88)	7.81** (1,88)	4.82* (2,88)	0.56 (2,88)
FA length	0.46 (1,88)	1.19 (1,88)	0.05 (2,88)	0.57 (2,88)
FA mass	0.27 (1,91)	0.13 (1,91)	1.55 (2,91)	0.20 (2,91)
FA mass/length	0.17 (1,88)	0.06 (1,88)	3.68* (2,88)	0.64 (2,88)

FA, fluctuating asymmetry: see text for details. Interactions between covariate and age/populations were not significant in any feather traits (test of parallelism). * $P < 0.05$; ** $P < 0.01$.

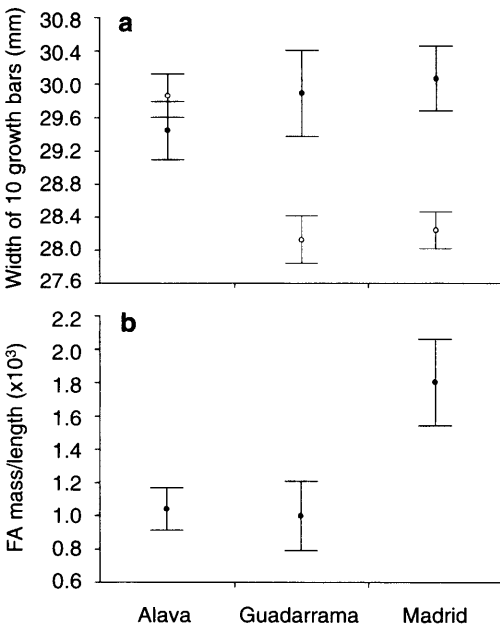


Figure 2. (a) Mean value (\pm se) of width of ten growth bars in rectrices of Blackcap juveniles (O) and adults (●) in the three study areas. (b) Absolute means (\pm se) of fluctuating asymmetry in rectrix mass/length ratio in each population (adults and juveniles).

(Kolmogorov–Smirnov test: length asymmetry, $d = 0.11$, $P > 0.05$; mass asymmetry, $d = 0.125$, $P > 0.05$; mass/length ratio asymmetry, $d = 0.08$, $P > 0.2$), and did not differ significantly from a mean of zero (*t*-test against the null hypothesis that mean is equal to zero: mass asymmetry, $t_{97} = 0.78$, $P > 0.05$; mass/length ratio asymmetry, $t_{94} = 0.9$, $P > 0.05$), although

the length of rectrices showed significant directional asymmetry ($t_{94} = 2.52$, $P < 0.05$).

RESULTS

There were no differences between adult males and females (two-way ANCOVA, $P > 0.05$ for all the study features; covariate: tarsus-length) so that both sexes were pooled together in the following analyses (Table 1). Populations and ages did not differ in tarsus-length (two-way ANOVA of tarsus-length: populations: $F_{2,101} = 0.99$ ns; age class: $F_{1,101} = 0.05$ ns; population–age interaction: $F_{2,101} = 0.545$ ns) and feather indices were unrelated to tarsus length (see covariate in Table 2). There were no differences between populations in width of growth bars but juveniles had narrower bands than adults in the two southernmost populations (Tables 1 and 2; see Fig. 2a). The length of rectrices varied with age (juveniles had longer feathers than adults) but not between populations (Table 2). Feather mass and mass/length ratio varied between populations (lighter feathers in the southernmost population) and between age classes (juveniles had heavier feathers; Table 2). No significant differences were found in FA of the length or mass of rectrices between age classes or localities, but there were differences in asymmetry of mass/length ratio between populations (Table 2), with higher values in Madrid (Table 2, Fig. 2b).

DISCUSSION

Our results suggest higher levels of stress for

Blackcap populations in the dry, Mediterranean region of Iberia. However, the feather indices employed differed in their ability to reflect environmental constraints and in the extent of their variation with bird age. Differences between juveniles and adults in feather length and mass may reflect differences in wear, since juvenile feathers are new whereas those of adults were developed during the previous summer.⁷ Despite these inter-age differences, both the adult and juvenile feathers were lighter in the southern populations, reflecting the temporal constancy of this pattern between localities since adult and juvenile feathers were produced in two consecutive summers (1995 and 1996). A similar geographical pattern was found in juvenile growth bar widths, since bars were broader in Alava than in the southern populations. This suggests a greater inability of juveniles to develop their feathers as fast in southern localities. The lack of a difference between adults could reflect their greater capacity to overcome the environmental constraints of the southernmost areas. Forest birds in southern Spain experienced changes in their habitat selection patterns after the breeding period, usually moving to moister areas.¹⁷ Such a behavioural response may attenuate moult stress in adults, but not in juveniles, whose feathers develop in the nest and immediate surroundings while they are dependent upon food provided by the adults.³³

Asymmetry indices show inconclusive results since neither length asymmetry nor mass asymmetry described any significant patterns between populations and/or ages. Choosing appropriate characters for the study of FA is particularly important, because the degree of asymmetry of different characters may be uncorrelated so that some may be more reliable indicators of developmental stress than others.³⁴ For instance, the value of FA in a trait as a measure of stress decreases with increasing levels of directional asymmetry since a part of the observed asymmetry may be an inherited component of growth.^{34,35} Therefore, the usefulness of FA of feather length is probably low and the lack of inter-population variation might be the result of a misleading effect of the observed directional asymmetry.³⁴⁻³⁶ However, the values of FA for the mass/length ratio were largest in Madrid, supporting the view of a heavier moult stress on Blackcaps in the

Mediterranean region.

An alternative explanation for our results can be considered. The Blackcaps of the southern forest of Madrid may be of poor phenotypic quality primarily because birds of higher quality have left the area. It seems unlikely that the population of the Guadarrama mountains consists of individuals of lower quality coming from northern 'source' areas (separated by 150–200 km) or that populations of riparian forests consisted of individuals coming from the Guadarrama 'source' area located around 60 km distant. In summary, our results provide evidence of increasing stress of moult in Blackcaps in drier Iberian regions.

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