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Article

Feather traits in four southern populations of the Eurasian blackcap *Sylvia atricapilla*: do altitudinal movements explain the differences?

Irene Hernández-Téllez, José I. Aguirre, Iván de la Hera, Alejandro Onrubia and José Luis Tellería

I. Hernández-Téllez (https://orcid.org/0000-0003-4496-0815) ✉ (ihtellez@ucm.es), J. I. Aguirre (https://orcid.org/0000-0002-0210-890X) and J. L. Tellería (https://orcid.org/0000-0001-6170-8860), Dept of Biodiversity, Ecology and Evolution, Univ. Complutense, Madrid, Spain. – I. de la Hera (https://orcid.org/0000-0003-0550-9562), Dept of Integrative Biology, Oklahoma State Univ., Stillwater, OK, USA. – A. Onrubia (https://orcid.org/0000-0001-8860-3524), Fundación Migres, Tarifa, Cádiz, Spain.

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Moult of birds is shaped by environmental and genetic drivers whose relative contribution to the structure of feathers may differ within and between populations. In this study, we compare some traits of tail feathers (growth bars, mass, rachis width and barb length) between four populations of the Eurasian blackcap *Sylvia atricapilla* breeding at different elevations within the southwestern Palaearctic. We tested if these traits were related to the primary productivity of habitats (a surrogate of food availability) or were better explained as an adaptation to altitudinal movements. The distribution of primary productivity was positively related to blackcap abundance suggesting that the species tracked the most productive areas to breed. In this environmental setting, wing morphology (wing length, concavity and pointedness) suggested that lowland blackcaps were sedentary while blackcaps from highland areas were involved in altitudinal movements. The feathers of blackcaps inhabiting the highlands showed wider growth bars and rachis than those of the most productive lowland areas but did not differ in feather mass and barb length. Fast feather growth has been related to time constraints to moult and wider rachis to improve flight efficiency in migratory birds. Our results therefore suggest that differences in feather characteristics between southern populations of the Eurasian blackcap are better interpreted as an adaptive response to altitudinal migration than as a consequence of regional food availability.

Keywords: altitudinal migrations, habitat suitability, morphometry, population differentiation, ptilochronology

Introduction

Plumage is composed almost entirely of protein (keratin) and represents a significant part of the birds' lean body mass, which makes feather production a very demanding physiological challenge for birds (Jenni and Winkler 2020). In addition, since feathers are metabolically inert structures once they are fully grown, the characteristics and quality achieved during their production can affect plumage performance with possible consequences for fitness (Harrison et al. 2011).

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As some feather characteristics have been considered flexible traits whose expression is primarily determined by environmental constraints, they have been often used as indicators of body condition in birds (Grubb 2006). However, increasing evidence suggests that genetic factors may contribute to phenotypic variation in feathers characteristics, raising the possibility that they have been partly shaped by selective pressures and subject to evolutionary change (Piersma et al. 2005, Gienapp and Merilä 2010, de la Hera et al. 2013, Saino et al. 2013). Thus, the expression of feather characteristics would be determined by both environmental and intrinsic factors, with the relative contribution of each factor differing within and between populations. When comparing populations, the intrinsic factors acting on plumage quality and production are diverse (body size and morphology, lifestyle or organization of the annual cycle, such as migratory requirements; Jenni and Winkler 2020) and may indicate different evolutionary strategies or constraints (van Noordwijk and de Jong 1986). In general terms, we know that there is a trade-off between feather growth rate and feather quality (Vágási 2013), and that feather structural properties may indicate adaptation to flight requirements and environmental conditions (Pap et al. 2015, 2019), but some patterns remain unclear. For instance, variation between Iberian populations in the mass and growth rate of tail feathers in Eurasian blackcap fledglings *Sylvia atricapilla* was related to local changes in precipitation, an environmental factor linked to productivity in Mediterranean habitats (Carbonell and Tellería 1999, Carbonell et al. 2003). However, a comparison between sedentary and North and central European migratory adults that winter in sympatry in southern Spain revealed lighter feathers and wider growth bars in migrants, including some differences in the mechanical properties of tail and wing feathers related to flight efficiency (de la Hera et al. 2009, 2010). It has been also shown that some traits (rachis width and barb length) seem to be related to flight efficiency in migrants (Pap et al. 2015, de la Hera et al. 2020). Thus, the question of whether the feather traits track the immediate environmental conditions or reflect an adaptation to migratory movements remains yet unresolved.

In this paper, we study the feathers in four Eurasian blackcap populations distributed along an elevation gradient within the southwestern Palaearctic (Fig. 1, 2A). Increasing evidence supports that the environmental heterogeneity caused by orography produces altitudinal displacements whose effects on bird biology have often been overlooked (Boyle et al. 2016, Boyle 2017, Sander and Chamberlain 2020). These movements could strongly affect the moult of the Eurasian blackcap populations, a partially migratory species in which migratory and sedentary individuals can coexist

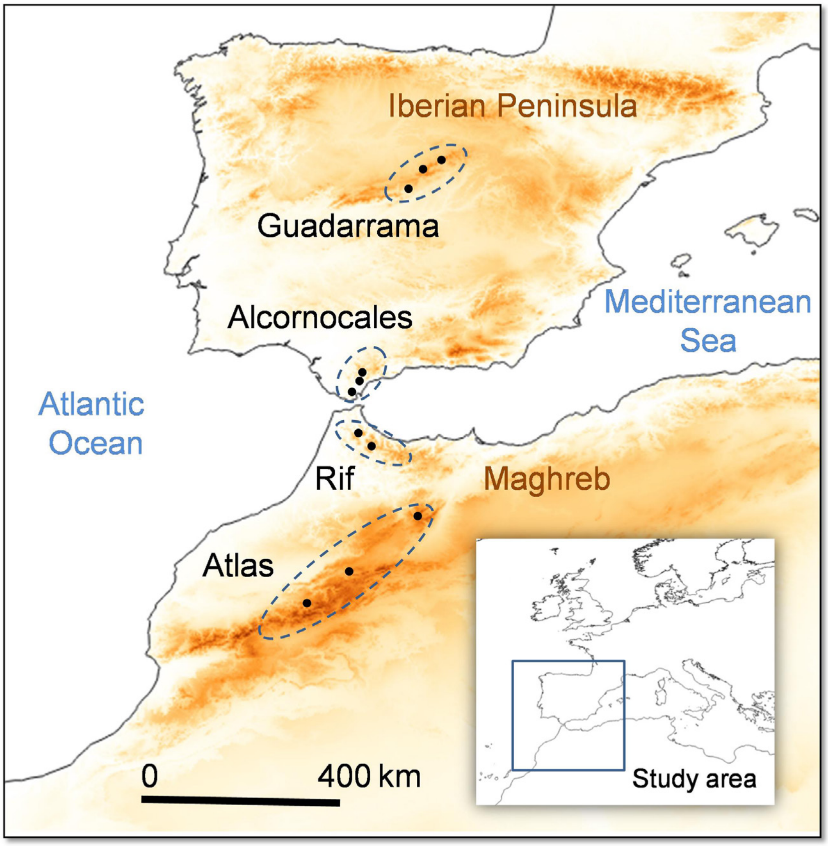

Figure 1. Location of the study areas where birds have been captured to study feather traits. The small spots show the sampling sites. The situation of the study area within the Western Palaearctic is also shown.

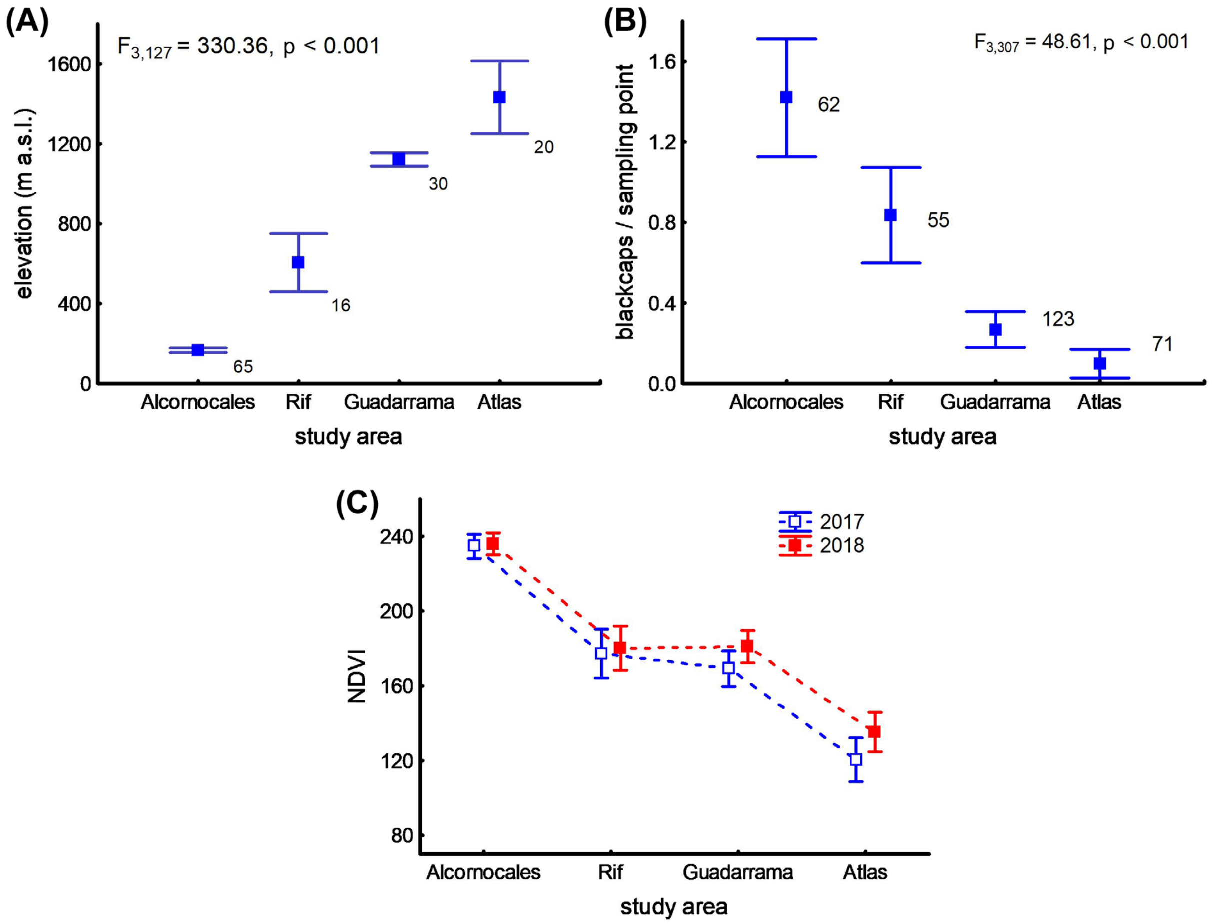

Figure 2. (A) Distribution of elevations at which the Eurasian blackcaps were captured. Figures show the numbers of birds considered in this study (age > 3). (B) Distribution of the Eurasian blackcap abundance between the study areas as reported by sampling points. Figures show the number of sampling points. (C) Between year distribution of primary productivity as reported by May–August NDVI scores. Panels A and B show the results of one-way ANOVA. In all cases the graphics show mean and standar error interval for the study areas.

in a small geographical area (Chapman et al. 2011). In our case, blackcap populations of the Iberian highlands and lowlands (Guadarrama and Alcornocales; Fig. 1) have been classified as migratory and sedentary, respectively (Tellería and Carbonell 1999, Pérez-Tris and Tellería 2002). Although the migratory behaviour of North African blackcaps remains yet unclear (Thévenot et al. 2003, Delmore et al. 2020), bird count data suggest that this species reduces its abundance at high elevation areas (Atlas mountains) during winter, suggesting the existence of seasonal altitudinal movements (Supporting information). Thus, the Eurasian blackcap and the heterogeneous configuration of the southwestern Palaearctic seems a suitable model to explore if the structure of feathers of different populations are shaped by immediate habitat suitability (e.g. food) or are better explained by adaptations to altitudinal movements. We will try to unravel this question by testing the following hypotheses:

Environmental effects: Primary productivity is a main driver of the abundance of primary consumers (Street and McNickle 2019, Fernández-Tizón et al. 2020), and the amount of this food resource (e.g. invertebrates) will affect moulting since birds depend on animal food to produce feather keratin (Gregg and Rogers 1986). Thus, if the study areas differ in primary productivity and blackcaps actively track the differences (e.g. through changes in abundance; Tellería and Pérez-Tris 2003), we predict that birds in the most productive areas will show faster growth rates and/or heavier feathers. Both traits have been positively related to food availability (Murphy 1996, Grubb 2006, Pap et al. 2008).

Migratory behaviour: Alternatively, we predict that changes in feather structure will result from evolutionary processes operating on populations but not from immediate environmental effects. In this context, as the Eurasian blackcap populations inhabiting the southwestern Palaearctic may be divided into migratory and sedentary populations, we predict that feather structure will be shaped by their migratory behaviour. More explicitly, we will test if migratory populations show faster feather growth rates than sedentary conspecifics to cope with the putative effect of time constraints to moult described for migrants (Kiat et al. 2019) and/or show wider rachis and shorter barbs to improve flight efficiency (Tubaro 2003, Weber et al. 2005, de la Hera et al. 2010, 2020).

Methods

Study area

The four study areas are located in the Iberian Peninsula (Guadarrama Mountains and Los Alcornocales Natural Park) and the Maghreb (Rif and Atlas Mountains), covering different elevation ranges within the typical Mediterranean climatic conditions (Fig. 1). In these mountains, the Eurasian blackcap occurs in the moistest forest sectors (e.g. patches of *Rubus* sp.), particularly in broadleaved woodlands of *Quercus pyrenaica*, *Q. canariensis* and *Q. suber* (Carbonell 2003). The species is increasingly scarcer in the southern border of the study area (Fig. 2B), where it tends to be constrained to some suitable localities within mountain ranges (Thévenot et al. 2003; Supporting information). In this way, the mountain ranges selected in this study are located within a gradient of decreasing suitability that could strongly affect moult in the Eurasian blackcap.

Capture and measurements of blackcaps

We mist-netted Eurasian blackcaps from the end of April to the end of June during two consecutive years (2018 and 2019). This period encompasses the breeding time of the species (Supporting information) and reduces the probability of capturing migratory individuals (the main passage period occurs between late March and late April; Gargallo et al. 2011). In Spain, the *Guadarrama* sampling sites were located around Rascafría (40.9050, −3.8795), whereas bird trapping in *Alcornocales* took place near Los Barrios (36.1851, −5.4926). In Morocco, the *Rif* samples were taken around Chauen (35.1704, −5.2690) and Moulay Abdeslam (35.3174, −5.5066), whereas the *Atlas* sampling occurred in areas of Taza (34.1487, −4.1265), Azrou (33.4388, −5.2222) and Ouirgane (31.1757, −8.080; Fig. 1). Mist-netted blackcaps were aged according to the EURING code system (age 3: hatched in the current spring; age 5: young individuals hatched during last spring, still with flight feathers that developed in the nest; age 6: adult individuals, with flight feathers that come from a complete moult), sexed (males and females) and measured (maximum wing chord, tail length, minimum tarsus length and bill length from skull front to bill tip) following Svensson (1992) and Jenni and Winkler (1994). Pectoral muscle was scored from 0 to 3 (by considering intermediate cases using 0.5 scores) following Bairlein (1995). We studied wing shape by considering the primary distances of the nine longest primaries (excluding the vestigial outermost primary: P10). Primary distance was defined as the distance from the tip of each primary to the tip of the longest primary with the wing folded, assigning a value of zero to the primary (or primaries) constituting the wingtip. All body and feather measurements were performed by official expert ringers of the Spanish Ringing Scheme (IHT, JAM and AO) who had their measuring procedures standardized. Finally, the second outermost tail feathers (rectrix number 5 from left and right side) were collected and stored in individual envelopes to be studied in the laboratory. We discarded those individuals of age 3 because they were not fully grown in some cases. Captures and collection of biological samples were performed under permission of the Moroccan and Spanish authorities.

Productivity and blackcap abundance

The suitability of the study areas for blackcaps was assessed from three complementary approaches. First, we used remotely sensed normalized difference vegetation index (NDVI) to assess primary productivity and forest health (Wang et al. 2004, Aubard et al. 2019). For this purpose, we downloaded the monthly distribution of NDVI scores from the NASA Earth Observations (NEO) program (<https://neo.sci.gsfc.nasa.gov/about/>). We selected the data from May to August for the years 2017 and 2018 to have a view of the productivity of the study areas during the breeding and moulting period of the captured blackcaps (2018 and 2019). These data were managed with QGIS 3.4.15 (QGIS Development Team 2020), and the productivity of those sites where each blackcap was mist netted (see below) was extracted by means of the Point Sampling Tool Plugin (<https://plugins.qgis.org/plugins/pointsamplingtool/>). Second, we explored whether blackcaps were more abundant in the most productive areas. To do this, we assessed the abundance of the Eurasian blackcap in the four study areas around the sampling points in May–June of 2019. This assessment was carried out by counting blackcaps in sampling points randomly distributed across different woodlands within each of the four areas (see Tellería et al. 2020 for further details on the sampling protocol). At each sampling point, the abundance of blackcaps was recorded during a 10-min period within a 100-m-wide radius (Johnson 2008). Finally, as density can be a misleading indicator of habitat quality by the effect of competition (Van Horne 1983), we used the pectoral muscle score of the Eurasian blackcaps as an index of body condition (Cooper et al. 2015; below). In this way, we tried to test if individuals of the most densely populated areas displayed a depleted condition during breeding. Although body mass controlled by bird size could also be a good indicator of body condition, we decided not to use it in this case due to the large allometry in body size-related morphological traits among the study populations (paper in preparation).

Wing morphology

We used wing morphology to infer the strength of seasonal movements of the Eurasian blackcap populations, since migratory populations are expected to have a more developed flight morphology (i.e. longer and more pointed wings) than sedentary ones (Tellería and Carbonell 1999, Fiedler 2005). We performed a principal component analysis (PCA) with the primary lengths to describe wing shape. For this purpose, we transformed primary distances into distances from the carpal joint by subtracting their primary distance from the wing length. These transformed distances (cP1–cP9) were then standardized according to the method suggested by Senar et al. (1994) that correct for the among-individual variation in wing size. The PCA provided two principal components. PC1 was interpreted as an index of wing concavity (eigenvalue = 4.47; explained variance = 0.50; factor loadings: P9 = 0.37, P8 = 0.27, P7 = −0.07, P6 = −0.63, P5 = −0.83, P4 = −0.90, P3 = −0.93, P2 = −0.89, P1 = −0.84) and PC2 as an index of wingtip pointedness (eigenvalue = 1.59; explained variance = 0.18; factor loadings: P9 = 0.78, P8 = 0.82, P7 = −0.29, P6 = −0.15, P5 = −0.09, P4 = 0.07, P3 = 0.18, P2 = 0.26, P1 = 0.29). Thus, higher scores in PC1 and PC2 were related to more concave wings and more pointed wingtips respectively, which are typical of the most migratory individuals.

Feather traits

Flight feathers have a natural pattern of light and dark bands perpendicular to the rachis that corresponds to different pulses of feather growth (Brodin 1993). One light plus one dark band is called a growth bar, and its width can be used to estimate feather growth rate (Grubb 2006). We studied the growth rate of each tail feather (with traits correlated with wing feather traits in blackcaps, Supporting information) by measuring the width occupied by ten growth bars centred at around two-thirds of feather length from the base (Grubb 2006). To do this, each feather was placed on a black cardboard and the width of the ten growth bars (hereafter, ‘feather growth rate’) was marked with two entomological pins on the edge of the internal vane. The distance between pins was measured with a Mitutoyo 500 digital calliper (resolution 0.01 mm). This measurement showed a repeatability index (R) of 0.94 (SE = 0.016; CI = [0.90, 0.97]), calculated through the rptR package (R = 0.95 for age 5 and 0.92 for age 6). The feathers replaced after accidental losses or with growth bars difficult to see as well as those individuals born during the study year were discarded from analyses (age 3 according to EURING codes), because most of them had not a fully grown plumage. In total, the feathers of 36 individuals were discarded (19 from Alcornocales, 2 from Rif, 10 from Guadarrama and 5 from Atlas). Feathers were weighed using a digital precision balance (Mettler Toledo ® AG-245 model; instrumental repeatability 0.01 ± 0.02 mg) in order to estimate the overall quantity of material invested in feathers. We used a binocular magnifier (×10) to measure the total length of the barbs located in the middle point of the feather, which were stretched using an entomological pin and its maximum length calculated using chart paper as background (resolution 0.5 mm) following de la Hera et al. (2020). We also measured the dorsoventral width of the rachis at the position of the superior umbilicus with a digital calliper (0.01 mm resolution). Finally, since all abovementioned feather metrics are expected to be larger in long feathers compared to short ones, we measured their overall length (resolution 0.01 mm) to control for this potential variation. To avoid interpersonal bias, all feather traits were measured by the same person (IHT).

Analyses

We used general linear models (Zuur et al. 2007) to test for differences in productivity, bird abundance, wing morphology, body condition and feather traits between the four study blackcap populations. All models met the assumptions of parametric tests except the analysis of pectoral muscle for which we alternatively used a set of Kruskal–Wallis tests. In the case of wing morphology and feather traits, all models included year (2018, 2019), sex (female, male) and age (age 5, age 6) as fixed effects, and in no case was there any correlation between the variables; whereas feather trait analyses additionally included feather length as a covariate. In addition, the parameter setting of ‘sum-to-zero contrast’ was used for the 4 factors (i.e. year, age, sex and study area) in the models. For the case of habitat productivity, we assessed differences between years and areas by using repeated measures ANOVA . All analyses were carried out with Rcmdr 3.5.3 (Fox and Bouchet-Valat 2020).

Results

Productivity, abundance and body condition

The mean monthly distribution of NDVI at the sites where blackcaps were captured showed significant differences between areas and years (repeated measures ANOVA, study area: $F_{3,127} = 111.72$, $p < 0.001$; year: $F_{1,127} = 268.73$, $p < 0.001$; study area × year interaction: $F_{3,127} = 62.27$, $p < 0.001$, Fig. 2C), with 2018 being more productive than 2019 and lowland forests displaying a higher productivity than mountain forests. Within this environmental setting, blackcap abundance displayed a significant decrease from lowlands to highlands (Fig. 2B; Supporting information). This pattern was not followed by the pectoral muscle scores. There are no significant differences between years, sex and age categories, but there is a significant difference between areas (Kruskal–Wallis $H_{3,132} = 8.33$, $p = 0040$) with the highest scores in the most and less elevated areas (Atlas and Alcornocales; Supporting information).

Wing morphology

We studied 132 Eurasian blackcaps (age 5 and 6) distributed at different elevations in the four study areas (Fig. 2A). Wing length differed between areas but not between years, with highland blackcaps having the longest wings (Fig. 3A). There was also a significant effect of sex and age on the patterns, with males and older individuals (age 6) showing the longest wings (Table 1). Wing concavity differed between areas similarly to wing length but did not show any effect of year, age and sex (Table 1). Wing pointedness showed an effect of sex and showed opposite patterns between lowland and highland Iberian localities (Fig. 3C, Table 1).

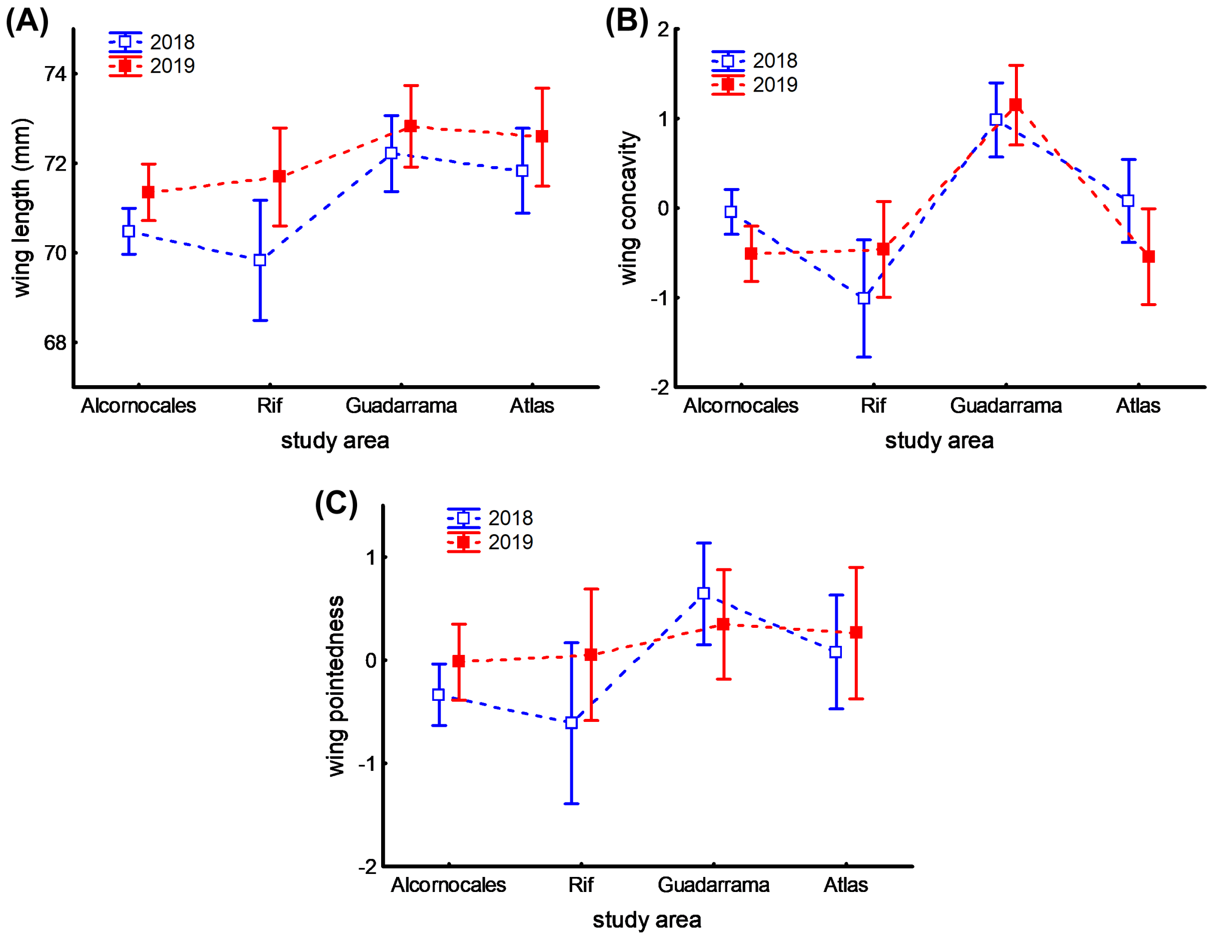

Figure 3. (A) Distribution wing length between study areas. (B) Distribution of wing concavity. (C) Distribution of wing pointedness index. In all cases, the results show mean and standar error for the absolute values of the study areas.

Feather traits

After accounting for variation in feather length, blackcaps exhibited significant differences in feather growth rate in relation to year, age and sex. In addition, the results suggest a pattern between the study areas in which highland individuals showed the widest growth bars (Fig. 4A, Table 2). In contrast, feather mass did not vary in relation to year, age, sex and neither showed any association with sites at different elevations (Fig. 4B, Table 2). Barb length was longer in adults and males and displayed the lowest scores in Guadarrama Mountains. Finally, rachis width was not affected by year, age and sex but was narrower in Alcornocales than in the highland populations (Fig. 4D, Table 2). These results do not support the prediction that blackcaps in the most productive areas would show wider feather bars and/or produce heavier feathers. More likely, they support the prediction that wider growth bars and rachis could be related to some adaptive traits related to migration.

Discussion

General comments

Our results suggest that the strength of differences in the feather metrics of the Eurasian blackcap populations within the southwestern Palaearctic will vary according to the scale of approach (within versus between population comparisons) and the idiosyncratic requirements of the studied traits. This means that the results in this paper are influenced by at least two experimental conditions to be considered when extending our conclusions to other experimental designs. First, potential links between feather traits and local environmental drivers are probably blurred by adaptations to migration that could not operate in sedentary or fully migratory populations. Second, we have studied different feather traits (growth bars, mass, barbs and rachis) that are probably shaped by different environmental or evolutionary processes. This can explain why the study traits show idiosyncratic thresholds of

Table 1. Results of the linear models in which the differences between areas in wing length and shape have been analysed after controlling for the effect of year, age and sex.

	Wing length (estimate ± SE)	Wing pointedness (estimate ± SE)	Wing concavity (estimate ± SE)
Intercept[1]	71.669 ± 0.174***	0.100 ± 0.104	0.023 ± 0.090
Year (2018)	−0.287 ± 0.152	−0.131 ± 0.091	0.135 ± 0.079
Age (5)	−0.451 ± 0.161**	0.078 ± 0.097	−0.046 ± 0.083
Sex (male)	0.296 ± 0.145*	−0.178 ± 0.087*	−0.078 ± 0.075
Alcornocales	−0.746 ± 0.214***	−0.259 ± 0.128*	−0.250 ± 0.111*
Rif	−0.905 ± 0.338**	−0.275 ± 0.202	−0.653 ± 0.175***
Guadarrama	0.928 ± 0.267***	0.437 ± 0.160**	1.067 ± 0.139***
$R^2 \times 100$	28.49	12.89	34.78
$F_{6,125}$	8.301	3.083	11.11
p	<0.001	0.008	<0.001

[1] Averaged intercept value according to sum to zero contrasts for study areas, sex categories, age classes and years. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

change between blackcap populations and differences in flexibility to environmental changes. Having into account these particularities and constraints, our results not only support some predictions but also suggest several uncertainties that we discuss below.

Environmental effects

The Eurasian blackcap is a forest passerine widely distributed across the Western Palearctic that, in the Mediterranean, tracks moist forest patches (Tellería and Pérez-Tris 2003). This can be explained because summer drought, a main restriction of Mediterranean productivity, constrains tree growth and, hence, forest occurrence and its associated avifauna distribution (Tellería and Santos 1993). Such habitat preferences fit well with the observed distribution of the Eurasian blackcap in our study area, where it reaches the highest abundances in the most productive woodlands of southern Spain (Alcornocales; Fig. 2B), an outstanding southern forest refuge of this and other forest passerines (Pérez-Tris and Tellería 2002). As body condition of the Eurasian blackcap did not deplete as its abundance increased, the observed pattern of primary productivity (Fig. 2C) seems a suitable surrogate of habitat suitability for the species. In this environmental setting, the altitudinal decrease in productivity and abundance underlines the increasing constraints that Eurasian blackcaps experience in mountain areas despite their ability to breed above 2000 m a.s.l. in the southernmost edge of this range (Thévenot et al. 2003). The low productivity of highlands has been often highlighted as a main constraint of species distribution in mountains (McCain 2009) that does not prevent the seasonal occupation of these high-altitude habitats by some birds for breeding (Boyle 2017).

Despite the observed patterns of abundance and productivity, the growth rate and mass of feathers did not increase in the more productive lowlands. This pattern is particularly odd in the case of feather growth rate that displayed a significant change between the two years (the wider growth bars occurred in the most productive year; Fig. 4A, Table 2). Although this supports the flexibility of growth bars to this temporal change, they did not track at all the between-area differences in productivity (Fig. 2C). This suggests a causal link between productivity and growth bars within populations (Gienapp and Merilä 2010), but not between them (Jenni and Winkler 2020), which could be related to different constraints or evolutionary strategies of populations that end up affecting growth bars (e.g. the migratory behaviour, see below). However, this explanation is in trouble when comparing these patterns with the feather growth rate of blackcap fledglings (age 3) studied in summer 1997 in Guadarrama and Alcornocales (Carbonell et al. 2003). In both cases, the growth bars decreased as drought increased within areas but did not show the between-area differences observed in this study. This was mainly related to a shortening of bars in the Guadarrama mountains (around 29 mm) if compared to the results in this study (Fig. 4A). These differences suggest the need for further research on the actual constraints of growing bars and the potential effect of some ongoing environmental changes in the resulting patterns (e.g. climate change and increasing tree cover etc.) in studies separated by 20 years. In fact, the Guadarrama mountains are under the strong effect of woodland encroachment that has enlarged the distribution of this species (Tellería 2020). In any case, results in this paper do not support any causal link between the distribution of primary productivity between areas and the growth rate or mass of feathers.

Migratory behaviour

Longer and sharper wings, a set of traits related to flight efficiency in migratory birds (Leisler and Winkler 2003), suggest that populations of the Eurasian blackcap inhabiting the highlands make seasonal movements along the elevation gradient (Fig. 3A–C). These morphological trends had been formerly detected in Iberian blackcaps and other passerines involved in seasonal movements between mountains and lowlands (Tellería and Carbonell 1999, Tellería et al. 2001). Our study with African blackcaps enlarges the scope but also shows some idiosyncratic patterns of the Atlas mountain birds as they do not show a sharp increase of wing concavity (Fig. 3B). This suggests

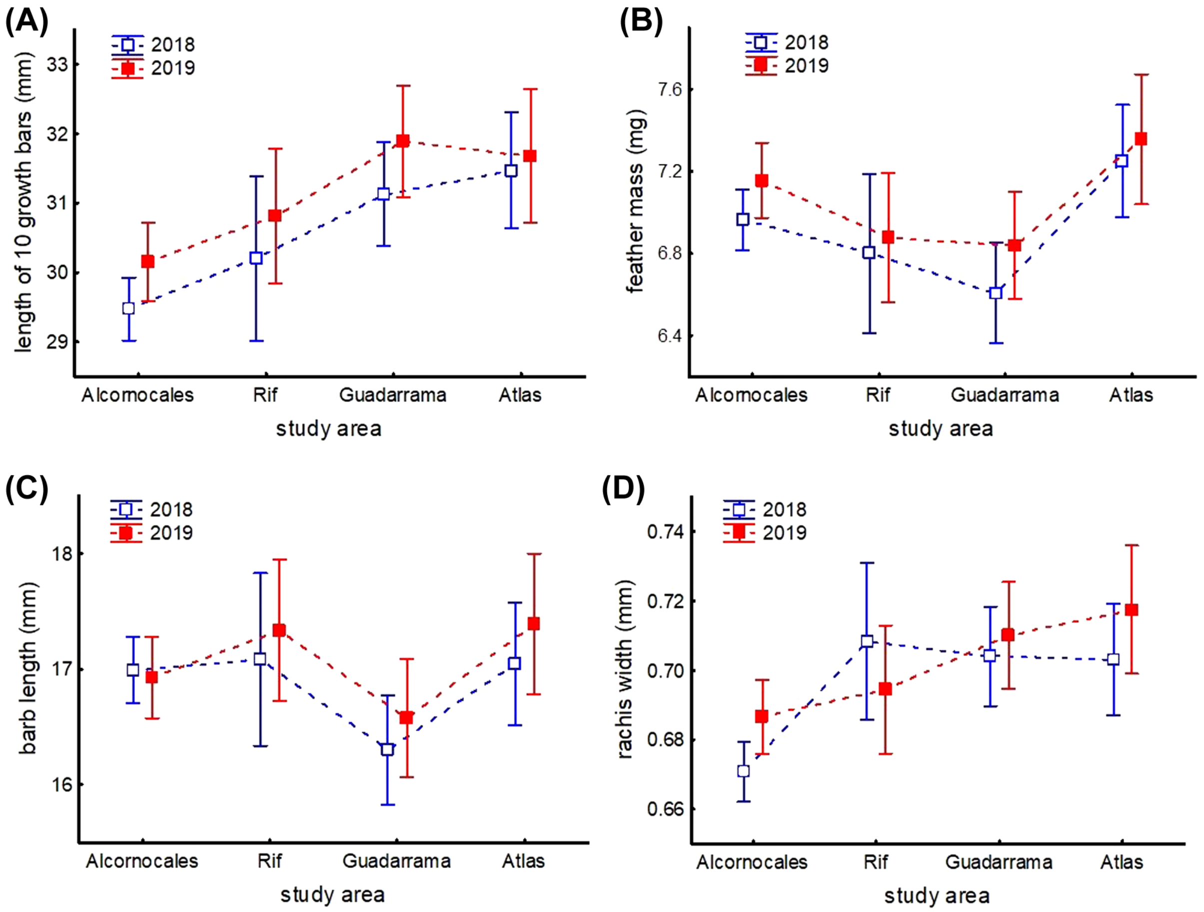

Figure 4. Variation between study areas in: (A) the length of ten growth bars, (B) feather mass, (C) barb length and (D) rachis width. In all cases, the results show mean and standard error for the absolute values of the study areas.

some differences in the way migration shapes wing morphological design in Iberian and African blackcaps inhabiting the highlands, perhaps because the distances that African populations have to travel are shorter as they are at the limit of their distribution area. Some preliminary analyses suggest that Atlas blackcaps disappear during winter from forests located over 1300 m a.s.l. (Supporting information), while the upper altitudinal limit of blackcap winter distribution in central Spain is located at around 600 m a.s.l. (Pérez-Tris 2012). Thus, the effect of latitude on winter severity could explain the differences in the extent of migratory movements and the concomitant changes in wing morphology. Despite these uncertainties, it can be concluded that changes in wing morphology support the

Table 2. Results of the linear models in which the differences between areas in growth bars, feather mass, rachis width and barb length have been analysed after controlling for the effect of year, age and sex.

	Growth bars (estimate ± SE)	Feather mass (estimate ± SE)	Barb length (estimate ± SE)	Rachis width (estimate ± SE)
Intercept[1]	15.085 ± 3.603***	2.750 ± 0.908**	8.135 ± 2.154***	0.562 ± 0.074***
Year (2018)	−0.372 ± 0.129**	−0.004 ± 0.003	0.079 ± 0.077	−0.004 ± 0.003
Age (5)	0.369 ± 0.141**	−0.000 ± 0.005	−0.260 ± 0.04**	−0.001 ± 0.003
Sex (male)	−0.249 ± 0.124*	−0.000 ± 0.003	0.173 ± 0.074*	0.004 ± 0.003
Alcornocales	−0.981 ± 0.181***	0.010 ± 0.005*	0.022 ± 0.108	−0.020 ± 0.004***
Rif	−0.252 ± 0.285	−0.016 ± 0.007*	0.183 ± 0.170	0.001 ± 0.006
Guadarrama	0.953 ± 0.237***	0.006 ± 0.006	−0.324 ± 0.142*	0.012 ± 0.005*
Feather length	0.271 ± 0.062***	0.0168 ± 0.016***	0.152 ± 0.037***	0.002 ± 0.001
R^2 × 100	39.17	58.24	31.90	27.68
$F_{7,124}$	11.4	24.70	8.30	6.78
p	<0.001	<0.001	<0.001	<0.001

[1] Averaged intercept value according to sum to zero contrasts for study areas, sex categories, age classes and years. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

existence of different migratory strategies in the Eurasian blackcap populations of the southwestern Palaearctic.

Results in this paper show a concordance between feather traits (measured in tail feathers) and some constraints usually related to continental migration in birds. For instance, time constraints to moult after breeding and before the onset of migratory movements have been usually linked to faster moult and the production of lighter feathers in populations involved in latitudinal movements (de la Hera et al. 2010, Terrill 2018, Kiat et al. 2019). In our case, blackcap populations involved in altitudinal movements reported wider growth bars, which could suggest faster feather production in a context of time constraints. However, feather mass did not show the expected pattern as the two highland populations (Atlas and Guadarrama) had the heaviest and lightest feathers, respectively (Fig. 4B). Feather mass showed an atypical pattern in the Atlas populations, with feathers that are both fast growing and heavier than the rest (Fig. 4B). This suggests that light feathers are not the by-product of faster moults (Dawson et al. 2000, Serra et al. 2007, 2010, Vagasi et al. 2012, Moller and Nielsen 2018) but the putative result of other physiological and evolutionary processes (de la Hera et al. 2013, Jenni et al. 2020). Likewise, a recent study detected wider rachises and shorter barbs in migratory populations of the European robin (de la Hera et al. 2020), which is consistent with our results, although their functional role remains poorly understood. Tail evolution in birds is a balance between manoeuvrability and drag reduction, so that narrow tail feathers could be useful to reduce drag in migratory birds (e.g. Guadarrama, Fig. 4C). In any case, this trait seems linked to the effects of sex and age (Table 2; Tobalske 2007) so that it remains unclear whether it is actually associated with flight efficiency in migratory birds. Finally, an increased diameter of the rachis would be a straightforward solution to improve bending stiffness in flight feathers (Tubaro 2003, Weber et al. 2005), which would improve the transmission of the aerodynamic forces to the musculoskeletal system during flight (Videler 2005). Consequently, rachis width is expected to increase in birds performing longer migratory journeys to obtain better mechanical properties (de la Hera et al. 2010). Our results support this view as rachis width, a trait unrelated to age or sex (Table 2), increased from lowland to highland populations (Fig. 4D). However, it is important to note that, while rachis width and bending stiffness are positively associated with migration distance in robins (de la Hera et al. 2020), the opposite pattern was detected in blackcaps, where migrants showed, on average, narrower rachis than the sedentary counterparts with which they wintered in sympatry in southern Spain (de la Hera et al. 2010). This contrasting patterns of rachis width variation between migratory and sedentary blackcaps could be influenced by the more northern origin of the migrant populations in the older study, where the allegedly central European migrants could use other mechanisms, apart from enhancing rachis diameter, to increase bending stiffness (de la Hera et al. 2010). Still this raises a doubt on the actual role of rachis width in the flight mechanics of birds and if it can always be considered an adaptive trait related to migration in birds (Lees et al. 2017, Jenni et al. 2020). In view of the above, our results show that certain feather traits (such as accelerated growth rate or wide rachis) are maintained in both latitudinal and altitudinal migrants, but other traits (such as feather mass or barbs length) do not fit this scheme. It would be interesting to check whether the results obtained are really a pattern of the populations in this context or a specific condition of this species.

Concluding remarks

Moulting is an important landmark in bird life cycle that interacts with other processes (reproduction, migration) and provides feathers that can be useful for monitoring several aspects of bird biology. Unfortunately, the processes that modulate feather structure and production are far from being understood, probably because they result from some idiosyncratic traits of species (e.g. size, physiology, diet), individuals (e.g. sex, age), scales of approach (within versus between population), particular adaptations (e.g. migration) or environmental settings (e.g. food availability, time constraints, competence, predation; see chapter 3.2.7 Jenni and Winkler 2020). This makes difficult to get plain links between different environmental or evolutionary settings and feather traits. Regardless, the results of this work demonstrate that there is variability in these traits among southwestern Palearctic populations of the Eurasian blackcap and suggest the inspiring idea that several of the study traits are better interpreted as adaptations to altitudinal movements of Eurasian blackcap populations.

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Author contributions

Irene Hernández-Téllez: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (lead); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **José I. Aguirre**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Iván De la Hera**: Conceptualization (equal); Methodology (supporting); Supervision (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Alejandro Onrubia**: Conceptualization (equal); Data curation (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal). **José Luis Tellería**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.z8w9ghxd3> (Hernández-Tellez et al. 2021).

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