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Title page

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Running title: Flight feather adaptations to migration

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ABSTRACT

Current avian migration patterns in temperate regions have been developed during the glacial retreat and subsequent colonization of the ice-free areas during the Holocene. This process resulted in a geographic gradient of greater seasonality as latitude increased that favoured migration-related morphological and physiological (co)adaptations. Most evidence of avian morphological adaptations to migration comes from the analysis of variation in the length and shape of the wings, but the existence of intra-feather structural adjustments has been greatly overlooked despite their potential to be under natural selection. To shed some light on this question, we used data from European robins *Erithacus rubecula* overwintering in Campo de Gibraltar (Southern Iberia), where sedentary robins coexist during winter with conspecifics showing a broad range of breeding origins and, hence, migration distances. We explicitly explored how wing length and shape, as well as several functional (bending stiffness), developmental (feather growth rate) and structural (size and complexity of feather components) characteristics of flight feathers varied in relation to migration distance, which was estimated from the hydrogen stable isotope ratios of the summer-produced tail feathers. Our results revealed that migration distance not only favoured longer and more concave wings, but also promoted primaries with a thicker dorsoventral rachis and shorter barb lengths, which in turn conferred more bending stiffness to these feathers. We suggest that these intra-feather structural adjustments could be an additional, largely unnoticed, adaptation within the avian migratory syndrome that might have the potential to evolve relatively quickly to facilitate the occupation of seasonal environments.

Keywords: feather mass, moult speed, moult-migration trade-offs, plumage quality.

1 | INTRODUCTION

Current avian migration patterns in temperate regions have been shaped over the last 10 000-14 000 years, coinciding with the start of the Holocene glacial retreat (Newton 2008). In the Western Palaearctic, glacier melting allowed the colonization of new lands by bird populations that had been confined within the Mediterranean refugia during millennia. As founder populations spread from low to high latitudes, the colonisation front gradually encountered more seasonal conditions. This shaped a latitudinal gradient of increased selection associated with longer migration distances towards the North, where individuals were able to take advantage of the summer surplus for breeding, but returned to southern latitudes annually to avoid the harsh winter conditions (Newton, 2008; Chapman, Brönmark, Nilsson, & Hansson, 2011). Subsequent changes in the environmental conditions at the Mediterranean Peninsulas could lead to the extinction of the ancestral sedentary populations that still remained in the refugia (Bell, 2000). However, there are still a few species in which the direct descendants of these ancestors persist and share their home ranges during winter with migratory conspecifics coming from different, more northern, breeding origins (Pérez-Tris & Tellería, 2002; Fandos & Tellería, 2019). These grounds of seasonal sympatry allow to simultaneously sample individuals with variable selection pressures associated with migration, whose analysis would contribute to strengthen our understanding of how avian life histories have evolved throughout this historical colonization process.

In order to effectively move between distant geographic locations, migratory birds have been selected for particular morphological, physiological and behavioural characteristics (Alerstam, Hedenström, & Åkesson, 2003; Dingle, 2014). The overall length of the wing and its outline has captured most of the research focus in the study of the external avian morphological adaptations facilitating an energy-efficient migratory flight (Lockwood, Swaddle, & Rayner, 1998; Milá, Wayne, & Smith, 2008). Thus, many inter and intraspecific studies support the idea that wings become longer and more pointed as the distance between breeding and wintering grounds (i.e. migration distance) increases (Fiedler, 2005; Forschler & Bairlein, 2011; Vágási et al., 2016). However, although some structural elements of the feathers (e.g. rachis width) can determine their mechanical behaviour (i.e. bending stiffness) and potentially be under natural selection (De la Hera, Hedenström, Pérez-Tris, &

Tellería, 2010a; Szép, Dobránszky, Møller, Dyke, & Lendvai , 2019), the existence of intra-feather structural adaptations to migration has been mostly overlooked, with only a few recent interspecific studies in the literature (Pap et al., 2015; 2019).

The complexity and size of feather structural components can be influenced by different, sometimes conflicting, factors. For example, migratory birds typically increase their wing span and obtain sharper wingtips by a differential elongation of the outer wing flight feathers (i.e. primaries; Lockwood, Swaddle, & Rayner, 1998). This feather lengthening is expected to be costly so that it might be associated with a simplification of feather structure (Aparicio, Bonal, & Cordero, 2003), which could have antagonistic effects on flight performance and other plumage functions. Feather elongation could be particularly detrimental for feather structure if birds undergo time or energy constraints during feather production (Pap, Vágási, Czirják, & Barta, 2008; De la Hera, Pérez-Tris, & Tellería, 2009). Indeed, migratory birds tend to grow their feathers faster than their sedentary counterparts as a consequence of the temporal constraints that the former experience between breeding an autumn migration for moulting (Kiat, Izhaki, & Sapir, 2019). In this respect, several aviary experiments have shown that an accelerated moult affects feather structure and quality (Dawson, Hinsley, Ferns, Bonser, & Eccleston, 2000; Griggio, Serra, Licheri, Campomori, & Pilastro, 2009; Vágási, Pap, & Barta, 2010; Vágási et al., 2012). This could explain why the only study comparing feather characteristics between migratory and sedentary conspecific natural populations (i.e. the blackcap *Sylvia atricapilla*) found that migrants had flight feathers with a thinner rachis than sedentary counterparts (De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a). Remarkably, however, the bending stiffness values were higher in the feathers of migratory blackcaps than in the sedentary fraction (De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a), which suggests the existence of feather structural adjustments that allow migrants to favour some feather properties (i.e. bending stiffness), maybe at the expense of other functions (e.g. resistance to wear and mechanical fatigue; Weber, Borgudd, Hedenström, Persson, & Sandberg, 2005; Weber, Kranenbarg, Hedenström, Waarsing, & Weinans, 2010). This also highlights that our understanding of the relationship among migration (distance), feather structural characteristics and mechanical properties is still very limited (Lees, Garner, Cooper, & Nudds, 2017).

In this study, we used data collected from European robins *Erithacus rubecula* seasonally sympatric during winter in *Campo de Gibraltar* (Southern Iberia), a region identified as a putative glacial refugia (Rodríguez-Sánchez, Pérez-Barrales, Ojeda, Vargas, & Arroyo, 2008; Médail & Diadema, 2009), to shed light into the morphological adaptations associated with migration that might have occurred in this species during the Holocene. Some mountains in this region sustain some relict submediterranean woodlands (De Dios, Benito-Garzón, & Sáinz-Ollero, 2009) that host sedentary robin populations that also receive during winter a huge number of migratory conspecifics with a broad range of breeding origins (Bueno, 1998; Tellería & Pérez-Tris, 2004). The breeding origin and, hence, the migration distance of each wintering robin can be estimated from the hydrogen stable isotope ratios of their feathers (δD_f; Catry et al., 2016; De la Hera et al., 2017), which are produced in the previous summer at the breeding grounds. We then explored how wing length and shape, as well as several functional (i.e. bending stiffness), developmental (i.e. feather growth rate) and structural (i.e. size and complexity of feather rachis and vane) characteristics of flight feathers varied in relation to δD_f. We predicted that migration distance will be strongly associated with longer and more pointed wings, as described in other broadly distributed Palaearctic avian species and partially tested in robins (Pérez-Tris, Carbonell, & Tellería, 2000; Catry et al., 2016). Likewise, we expect higher values of bending stiffness in the feathers of robins migrating longer distances, as previously outlined in blackcaps (De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a). We also tested whether ptilochronology-based measurements of tail feather growth rate, that are conservative proxies of moult speed (De la Hera et al., 2011), decrease with migration distance as expected from the existence of the abovementioned temporal constraints that might affect feather structure and quality. Finally, we explored the relationship between several feather structural characteristics and δD_f, predicting that those characteristics that might facilitate feather mechanical performance and, ultimately, long-sustained flight (e.g. longer feathers, wider rachis and more acute barb insertion angles) were favoured in birds migrating longer distances (Ennos, Hickson, & Roberts, 1995; Pap et al., 2019).

2 | METHODS

2.1 | Study area and bird measurements

Birds were sampled using mist-nets and mesh-clap traps in four sites located in Campo de Gibraltar region, within the boundaries of *Los Alcornocales* and *Estrecho de Gibraltar* Natural Parks (Cádiz, Spain). There were less than 14 km in straight line between the farthest locations, so that these four sites could be effectively considered part of the same wintering region when inferring migration distances (see below). Two of these four localities represented woodlands, whereas the other two represented shrublands, the two main habitats that robins use for overwintering in this area (see De la Hera et al., 2018 for further details on the study sites). Given that the breeding origin of robins differs dramatically between woodlands and shrublands, obtaining samples from both habitats provided data from birds with a wide range of migration distances (De la Hera et al., 2018). Trapping sessions took place during two different winters (2006-07 and 2013-14) spanning the traditional winter season in this area (SEO/Birdlife, 2012). Thus, robins were sampled between mid-November and mid-February in winter 2006-07, and during January 2014 for winter 2013-14. Each captured Robin was aged as adult or juvenile using plumage features (Jenni & Winkler, 1994). We also measured tarsus length, maximum wing chord and wing shape considering the primary distances of the 9 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. In winter 2006-07, all morphological variables were obtained by two experienced ringers who have their measurements standardized; while the robins captured in winter 2013-14 were measured by only one of them. Additionally, we used a syringe to extract a sample of blood from the jugular vein which was used for molecular sexing (Griffiths, Double, Orr, & Dawson, 1998). We also collected two flight feathers. One innermost primary feather (primary 1) and one tail feather (the second outermost rectrix 5; Jenni & Winkler 1994) in order to obtain the feather traits and isotopic measurements detailed below. We could gather 146 individual robins with a complete set of data, plus one individual for which barb insertion angles could not be obtained for technical/logistical reasons. Maximum sample size was 147 (76 and 71 robins for winter 2006-07 and 2013-14, respectively).

2.2 | δD_f as estimator of migration distance

The isotopic particularities of each geographic location are transferred to the feathers through the diet during plumage production. In robins, feather production typically occurs during summer at their breeding grounds. Since avian feathers are inert once they are fully-grown, these isotopic signatures are maintained on feathers until the next moulting process (Catry et al., 2016). Hydrogen stable isotopes vary geographically across the Palaearctic, where the heavy isotope (i.e. Deuterium) becomes progressively less common in rainfall from south-western Europe, where Campo de Gibraltar is located, towards the northeast (Hobson, Bowen, Wassenaar, Ferrand, & Lormee, 2004). Conveniently, this hydrogen isotopic pattern overlaps with one of the main migratory routes of robins (Korner-Nievergelt, Liechti, & Thorup, 2014; Ambrosini et al., 2016), which probably follows the historical range expansion route of this species from the Iberian Peninsula during the Holocene (Newton, 2008). Consequently, it is reasonable to assume that the lower (the more negative) is the δD_f value of a robin wintering in Gibraltar, the more northern its breeding origin will be and, hence, a longer migration distance will have been travelled during autumn to arrive at Gibraltar (Hobson, Bowen, Wassenaar, Ferrand, & Lormee, 2004). Previous research strongly supports this assumption, although it also predicts the existence of some degree of variation in δD_f values between conspecifics growing their feathers in the same location (Catry et al., 2016; De la Hera et al., 2017; 2018). Although such circumstance might reduce the accuracy of the migration distance estimations made from δD_f values in our study, this would only lower the statistical power of our comparisons, making the study conservative.

In our study, migration distance was estimated from the δD_f values of the rectrix 5 feather, which were expressed in delta notation in units per mil (‰), and normalized according to the VSMOW-SLAP scale using the values obtained for three keratin standards (see De la Hera et al., 2018 for further details on the isotopic analyses). Isotopic analyses were performed in the Colorado Plateau Stable Isotope Laboratory (http://www.isotope.nau.edu/).

2.3 | Wing shape estimations

We used transformed values of the primary distances described above to estimate the variation in the wing shape of robins wintering in Campo de Gibraltar region. For this purpose, we opted for transforming primary distances into distances from the carpal joint (cP1-cP9) by subtracting, for each primary, its primary distance from the wing length. These transformed distances (cP1-cP9) were then standardized according to the method suggested by Senar and collaborators (1994), which provides more reliable measurements (cP1*-cP9*) that correct for the among-individual variation in wing size. These standardized values were included in a Principal Component Analysis (PCA) performed with the *prcomp* function in R, which gave rise to two principal components (wing concavity and wingtip pointedness) that reflected variation in wing shape among robins (see Results).

2.4 | Bending stiffness of Robin feathers

Bending stiffness is a major mechanical property of flight feathers that transmits the aerodynamic forces to the musculoskeletal system during flight (Videler, 2005). According to this, it is expected that the feathers of birds performing longer flights show more resistance to be bent (i.e. greater values of bending stiffness; De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a). Dorsoventral bending stiffness was estimated on the primary feather collected from each Robin using a two-point bending test. The system devised for this purpose consisted of a non-commercial feather testing equipment build specifically for this purpose mounted on an Instron 4411 Tensile Strength Tester (TST) machine that was connected to a high-resolution digital balance that measured the loads (Precisa XT220A; resolution of 0.1 mg). The feather testing equipment had two parts: (1) the clamping device, that was mounted in the mobile section of the TST machine and allowed clamping firmly the whole length of the calamus (inserted in the hole up to approximately the position of the superior umbilicus) using a small bolt; and (2) the loading platform, that was located on the digital balance and could be moved to the selected loading point of the feather. Each feather was tested during one minute, over which the TST machine was programmed to move the feather down at a speed of 4mm per minute, and the mass on the digital balance was automatically recorded every second. In all feathers the load was measured in the same position of the rachis (i.e. approximately 32mm from the superior umbilicus). This approach provided 60 (mass-time) points per feather. The slope of the relationship between mass (y) and time (x) for each feather was used to estimate bending stiffness (the steeper the slope, the higher the bending stiffness value). Bending stiffness was initially calculated in grams per second but it was transformed into miliNewton/mm using the appropriate conversion factors (original value in g/s * 60s/4mm * 1kg/1000g * 9.81 m/s2 * 1000mN/1N). Each feather was measured twice and the average values used in subsequent analyses. Repeatability of the bending stiffness of primary feathers was very high and significant (intraclass correlation coefficient $r_i = 0.86$, $F_{145,146} = 13.5$, $P < 0.001$), supporting the reliability of this measurement.

2.5 | Feather structural and developmental traits

Primary feathers were weighed in a high-resolution digital balance (Mettler Toledo AG-245; resolution 0.01 mg) and their full length measured (from inferior umbilicus to the distal tip) using a digital caliper (resolution 0.01 mm). For primary feathers, we also took a set of structural measurements that could show variation in relation to migration distance. Thus, we used a digital caliper to measure the dorsoventral and lateral width of the rachis at its base (at the position of superior umbilicus). We also used a binocular magnifier (x10) to count the number of barbs in the central centimetre of the feather, and 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). We also estimated the insertion angle of the central barb into the rachis by means of a Powerfix Prof angle conveyor (resolution of 0.1°). This was done on pictures taken using a LEICA DFC295 camera adapted to a LEICA DM2500 microscope. The density, length and angle of the barbs were measured in both the inner and the outer vane of each feather. Outer barbs insertion angles were measured in relation to the distal part of the rachis, considering a straight line from the insertion point of the barb to its position at 0.5 and 1.5 mm of rachis length towards its tip. We selected two different positions for estimating outer barb angles to explore the consistency of the measurement. Outer barb angles did not differ when they were measured at 0.5 or 1.5mm (paired $t_{145} = 0.11$, $P = 0.911$) and were also significantly correlated with each other ($r = 0.60$, $P < 0.001$). For simplifying subsequent analyses, we opted for using a combination of both measurements that was obtained from a PCA (eigenvalue = 1.60; explained variance = 0.80; factor loadings = 0.71). Only the 0.5 mm measurement could be obtained from the pictures for the inner barb insertion angle, given its larger angle compared to the outer barbs. Since outer insertion barb angles did not correlate with inner ones (*r* = 0.06, *P* = 0.508), inner and outer angles were analysed independently. We followed a similar variable simplification procedure for outer and inner barb lengths (PCA: eigenvalue = 1.29; explained variance = 0.65; factor loadings = 0.71) and outer and inner barb densities (eigenvalue = 1.56; explained variance = 0.78; factor loadings = 0.71), which additionally provided a much better fit to a normal error distribution of these two variables (i.e. barb length and barb density) in the subsequent statistical analyses.

For tail feathers, we also measured their length and mass, following the same procedure described above, and obtained the width of 10 growth bars according to Grubb (2006). Juvenile birds (n = 72) were ruled out from this part of the study because growth bars are hardly visible in juvenile feathers and they might not follow a daily cycle (Elderbrock, Kern, & Lynn, 2012). Unlike juvenile feathers, growth bars are much more conspicuous in adult feathers (i.e. those feathers produced during a complete postbreeding moult; n = 75) and it has been shown that their (length-corrected) growth rate estimates are correlated with overall moult speed both within and between bird species (De la Hera et al., 2011).

2.6 | Statistical analyses

We used linear models to test whether migration distance (δD_f) correlated with observed variation in wing length and shape (wing concavity and wingtip pointedness), primary feather characteristics (feather length, feather mass, dorsoventral and lateral rachis width independently, combined barb density, combined barb length, combined outer barb insertion angle, and inner barb insertion angle) and tail feather growth rate during the complete moult. All models included age (adult, juvenile), winter (2006-07, 2003-14), sex (male, female) and age-sex interaction as fixed effects factors. Winter-age and winter-sex interactions were excluded to avoid over-parameterization, but their inclusion in the models did not affect the results qualitatively. Tarsus length was included as a covariate representing bird body size in the wing length and primary feather length statistical models (see Table 1). Similarly, feather length was used as covariate in the remaining feather trait analyses (see Table 2). The only exception to this model structure was the analysis of tail feather growth rate, where only adults were considered, so that the age and the age-sex interaction terms were not computed. We finally explored the quantity of variance in bending stiffness that could be explained by length-corrected (where appropriate, see Results) feather structural characteristics (as size-independent measures of these traits) after accounting for feather length, age, winter, sex, age-sex interaction effects, and including or not migration distance (δD_f) in the model. The purpose of these last analyses was to explore whether observed variation in bending stiffness was better predicted by among-individual differences in these feather structural traits, by migration distance (δD_f) alone, or by a combination of both. The latter two options would suggest the existence of non-measured variation associated with δD_f in feather structure/configuration contributing to bending stiffness (De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a). We did this by comparing the coefficients of determination (R^2) of each of the three models (see Results). All analyses were performed in R version 3.4.3 (R Core Team 2017) using the default *stats* package and considering a threshold for statistical significance of $\alpha = 0.05$.

3 | RESULTS

The PCA on the standardized primary distances provided two principal components (PC). PC1 was interpreted as an index of wing concavity (eigenvalue = 4.09; explained variance = 0.45; factor loadings: cP9* = 0.17, cP8* = 0.19, cP7* = 0.17, cP6* = -0.12 , cP5* = -0.37, cP4* = -0.44, cP3* = -0.45, cP2* = -0.44, cP1* = -0.40,), where individuals with higher PC1 scores showed proportionally shorter inner primaries, i.e. more concave wings. On the other hand, PC2 reflected variation in wingtip pointedness (eigenvalue = 1.95; explained variance = 0.22; factor loadings: cP9* = 0.52, cP8* = 0.57, cP7* = 0.49, cP6* = -0.17, cP5* = 0.03, cP4* = 0.12, cP3* = 0.16, cP2* = 0.21, cP1* = 0.21), whereby higher PC2 scores were associated with longer outer primaries for a given degree of wing concavity, or more pointed wingtips. Wing length was not correlated with wing concavity (PC1; wing effect: estimate ± se = -0.04 ±

0.08, t_{145} = -0.53, P = 0.595) or wingtip pointedness (PC2 wing effect: estimate ± se = 0.05 ± 0.05, t_{145} = 0.83, P = 0.407) supporting the success of the standardization procedure.

After controlling for other confounding factors, robins with lower δD_f values exhibited longer (Fig. 1A) and more concave wings (PC1, Fig. 1B), but no significant association between δD_f and wingtip shape (PC2) was detected (Table 1). In parallel to the pattern observed for wing length, the innermost primary feathers also became longer with migration distance (Table 1, Fig. 1C).

Rachis dorsoventral width and bending stiffness increased significantly with migration distance (Fig. 1D and 1F), whereas the combined measure of outer and inner barb lengths decreased (Fig. 1E) after accounting for feather length and other factors affecting each trait variation (Table 2). No significant effects of δD_f were detected for primary feather mass, rachis lateral width or (inner or outer combined) barb insertion angles (Table 2). Neither was feather growth rate of adult feathers significantly correlated with migration distance (δD_f effect: estimate ± se = -0.01 ± 0.01, t_{70} = -1.39, P = 0.169) after accounting for other fixed effects (feather length effect: estimate ± se = 0.38 ± 0.07, t_{70} = 5.34, $P < 0.001$; sex effects: estimate ± se =-0.80±0.32, t_{70} = -2.47, P = 0.016; winter effect: estimate ± se = 0.27± 0.28, t_{70} = 0.99, P = 0.325).

The model that included length-corrected feather structural characteristics explained 13% more variance in bending stiffness (Table 3; R^2 = 0.75) than the previous model that considered δD_f instead (Table 2; R^2 = 0.62). However, the residuals derived from the model shown in Table 3 were still significantly correlated with δD_f (r = -0.20, P = 0.016), although the addition of this term to the data structure shown in Table 3 only increased the coefficient of determination by 2% (R^2 = 0.77; see Table S1).

4 | DISCUSSION

Our results revealed that migration distance not only favours a specific configuration of wing size and shape, but also predicts the variation of some intra-feather structural characteristics that could benefit long-sustained migratory flights.

By accounting in our statistical tests for the large variation between age and sex in wing size using molecular methods to discriminate between male and female robins

(Griffiths et al., 1998) and standardization procedures (Senar, Lleonart, & Metcalfe, 1994), we could uncover the existence of longer and more concave wings, but not sharper wingtips, as migration distance increased in this passerine species. This widely acknowledged pattern across avian taxa had not been appropriately addressed in robins so far (Pérez-Tris et al., 2000; Catry et al., 2016), probably because of the difficulty of estimating the migration distance of specific robin individuals and populations (Korner-Nievergelt, Liechti, & Thorup, 2014; Ambrosini et al., 2016), and because this pattern can be easily blurred by the large variation between sex and age in wing length (Ellrich, Salewski, & Fiedler, 2010; De la Hera et al., 2017). The use of δD_f values as indirect surrogates of breeding origin in Campo de Gibraltar, where robins with a wide range of geographic origins concur in sympatry during winter, has significantly facilitated this purpose.

Apart from these differences in the size and shape of the wings, the comparison of feather structural characteristics between conspecific individuals sharing the same wintering grounds but differing in migration distance allowed us to identify candidate feather traits that could have been favoured by the selective pressures of migration. Thus, we found that migration could have promoted a thicker dorsoventral rachis, shorter barb lengths and also longer inner primaries (P1). It could be argued that observed variation in these traits was not mediated by selection, but by geographic differences in food availability that might affect feather characteristics. However, we think this possibility is unlikely, since feather mass and feather growth rate (two potential body condition indexes; Grubb, 2006; De la Hera, Pérez-Tris, & Tellería, 2009) did not vary significantly in relation to migration distance (see below).

An increased diameter of the rachis would be a straightforward adaptive solution to improve the bending stiffness of flight feathers (Tubaro, 2003; Weber et al., 2005). This possibility does not seem to be hampered in robins by the temporal and energetic constraints that migration could exert during moulting and the fledging period (De la Hera, Pérez-Tris, & Tellería, 2010b). This is additionally supported by the fact that length-corrected feather growth rate, a surrogate of moult speed (De la Hera et al., 2011), and migration distance were not correlated in adult robins. Migration-constraints have been suggested to potentially limit the quantity of material available for feather production (Serra, 2001; Hall & Fransson, 2000), which would explain the narrower (dorsoventral) rachis in migratory blackcaps and the lighter mass of some of their feather tracts (i.e. tail feathers) in relation to sedentary conspecifics (De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a; De la Hera, Pérez-Tris, & Tellería, 2010b). Contrary to what was observed in blackcaps, migration was positively correlated with the dorsoventral width of the rachis in robins and, although non-significant, there was also a tendency in more migratory birds to show heavier primary (Table 2) and tail flight feathers (see Table S2). These contrasting patterns between these two species may represent different ways in which (sedentary) populations of European passerines are adapted to living at the edge of their breeding range. Thus, body condition deteriorates in Campo de Gibraltar for robins (Pérez-Tris et al., 2000) but not for blackcaps (Carbonell, Pérez-Tris, & Tellería, 2003), which not only could set limitations on feather production counterbalancing the benefits of a non-temporally constrained moult, but might also explain the recent population decline observed in local sedentary robins at this peripheral area (Tellería, 2015). However, in spite of these differences between robins and blackcaps in the relationship of migration with rachis width and feather mass, bending stiffness values were higher in the feathers of the migrants for both species. This suggests that the way whereby migration determines the configuration and distribution of feather structural resources to obtain feathers with better mechanical behaviour (i.e. increased bending stiffness) would vary among species (Lees, Garner, Cooper, & Nudds, 2017).

We did not predict the existence of a significant association between barb length and migration distance. The few studies that compared feather structural characteristics across multiple avian taxa with variable flight types and life histories did not consider this trait (Pap et al., 2015; 2019), so it is difficult to elucidate at this point how shorter barbs could contribute to a more efficient migratory flight. Tentatively, barb length reduction might be explained as a counterbalance for obtaining thicker rachises and longer feathers that would impact on other feather functions not relevant for migration (Weber et al., 2005). Our results did not find evidence supporting that migration favoured the lateral width of the rachis, barb density or barb insertion angles, which suggests that the configuration of these traits could be more influenced by some life-history characteristics that would be more homogenous between robins differing in migration distance.

Our results additionally showed that observed variation in bending stiffness between robins was mostly explained by differences in the feather traits analyses (see Table 3 and Table S1), although there is still some room for additional, less perceptible (De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a; Lees, Garner, Cooper, & Nudds, 2017), structural adjustments at microscopic level that would require additional research with the appropriate technology (e.g. tomography of the feather shaft; Weber et al., 2010). Together with previous evidence in blackcaps (De la Hera, Hedenström, Pérez-Tris, & Tellería, 2010a), this study provides additional support to the idea that the acquisition of flight feathers with better bending stiffness in migratory birds could have been a general pattern in birds during the Holocene to facilitate their migratory flights and the subsequent colonization of geographic grounds recently freed from ice. Thus, the adoption of migration in avian life histories not only has pervasive consequences on the physiology, behaviour and general morphology of birds, but its selective pressures would also have repercussions in the configuration of flight feather structure, a pattern that had been largely ignored so far. In a similar way to what has been reported for the size and shape of the flight apparatus, the structure and mechanical properties of flight feathers might also be affected in migratory birds by ongoing anthropogenic alterations, such as the widespread landscape changes (Desrochers, 2010) or global warming (Møller, Fiedler, & Berthold, 2010; Remacha, Rodríguez, de la Puente, & Pérez-Tris, 2020), which would deserve further investigation. These intra-feather adjustments could have an adaptive nature and be part of the group of integrated adaptations that constitute the migratory syndrome in birds (Piersma, Pérez-Tris, Mouritsen, Bauchinger, & Bairlein, 2005). A coordinated evolution of all these traits might have occurred relatively quickly reducing the energetic costs of long-sustained flights, increasing fitness and, hence, allowing the colonization of seasonal environments.

REFERENCES

Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: evolution and determinants. Oikos, 103, 247-260. https://doi.org/10.1034/j.1600-0706.2003.12559.x

Ambrosini, R., Cuervo, J. J., du Feu, C., Fiedler, W., Musitelli, F., Rubolini, D., Sicurella, B., Spina, F., Saino, N., & Møller, A. P. (2016). Migratory connectivity and effects of winter temperatures on migratory behaviour of the European Robin *Erithacus rubecula*: a continent-wide analysis. Journal of Animal Ecology, 85, 749–60. https://doi.org/10.1111/1365-2656.12497

Aparicio, J. M., Bonal, R., & Cordero, P. J. (2003). Evolution of the structure of tail feathers: implications for the theory of sexual selection. Evolution, 57, 397-405. https://doi.org/10.1554/0014-3820(2003)057[0397:EOTSOT]2.0.CO;2

Bell, C. P. (2000). Process in the evolution of bird migration and pattern in avian ecogeography. Journal of Avian Biology, 31, 258-265. https://doi.org/10.1034/j.1600-048X.2000.310218.x

Bueno, J. M. (1998). Migración e invernada de pequeños turdinos en la Península Ibérica. V. Petirrojo (*Erithacus rubecula*). Ardeola, 45, 193–200.

Carbonell, R., Pérez-Tris, J., & Tellería, J. L. (2003). Effects of habitat heterogeneity and local adaptation on the body condition of a forest passerine at the edge of the range. Biological Journal of the Linnean Society, 79, 479–488. https://doi.org/10.1046/j.0024-4066.2002.00156.x

Catry, P., Campos, A. R., Granadeiro, J. P., Neto, J. M., Ramos, J., Newton, J., & Bearhop, S. (2016). Provenance does matter: links between winter trophic segregation and the migratory origins of European robins. Oecologia, 182, 985–994. https://doi.org/10.1007/s00442-016-3725-z

Chapman, B. B., Brönmark, C., Nilsson, J-Å., & Hansson, L-A. (2011). The ecology and evolution of partial migration. Oikos, 120, 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Dawson, A., Hinsley, S. A., Ferns, P. N., Bonser, R. H. C., & Eccleston, L. (2000). Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society of London B, 267, 2093-2098. https://doi.org/10.1098/rspb.2000.1254

De Dios, R. S., Benito-Garzón, M., & Sáinz-Ollero, H. (2009). Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. Plant Ecology, 204, 189–205. https://doi.org/10.1007/s11258-009-9584-5

De la Hera, I., Fandos, G., Fernández-López, J., Onrubia, A., Pérez-Rodríguez, A., Pérez-Tris, J., & Tellería, J. L. (2017). Stable isotope analysis reveals biases in the performance of a morphological method to distinguish the migratory behaviour of European robins *Erithacus rubecula*. Ardeola, 64, 67-76. https://doi.org/10.13157/arla.64.2.2017.sc1

De la Hera, I., Fandos, G., Fernández-López, J., Onrubia, A., Pérez-Rodríguez, A., Pérez-Tris, J., & Tellería, J. L. (2018). Habitat segregation by breeding origin in the declining populations of European robins wintering in southern Iberia. Ibis, 160, 355-364. https://doi.org/10.1111/ibi.12549

De la Hera, I., Hedenström, A., Pérez-Tris, J., & Tellería, J. L. (2010a). Variation in the mechanical properties of flight feathers of the Blackcaps *Sylvia atricapilla* in relation to migration. Journal of Avian Biology, 41,342-347. https://doi.org/10.1111/j.1600-048X.2009.04835.x

De la Hera, I., Pérez-Tris, J., & Tellería, J. L. (2010b). Migratory behavior and differential resource allocation between wing and tail feathers in a passerine bird. The Auk, 127, 647-652. https://doi.org/10.1525/auk.2010.09120

De la Hera, I., Pérez-Tris, J., & Tellería, J. L. (2009). Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. Biological Journal of the Linnean Society, 97, 98-105. https://doi.org/10.1111/j.1095-8312.2008.01189.x

De la Hera, I., Schaper, S. V., Díaz, J. A., Pérez-Tris, J., Bensch, S., & Tellería, J. L. (2011). How much variation in the molt duration of passerines can be explained by the growth rate of tail feathers? The Auk, 128, 321-329. https://doi.org/10.1525/auk.2011.10181

Desrochers, A. (2010). Morphological response of songbirds to 100 years of landscape change in North America. Ecology, 91, 1577-1582. https://doi.org/10.1890/09-2202.1

Dingle, H. (2014). Migration: the biology of life on the move (2nd ed.). Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199640386.001.0001

Elderbrock, E. K., Kern, M. D., & Lynn, S. E. (2012). Problems with using ptilochronology to measure the growth and nutritional status of nestling bluebirds. The Condor, 114, 823–830. https://doi.org/10.1525/cond.2012.110191

Ellrich, H., Salewski, V., & Fiedler, W. (2010). Morphological sexing of passerines: not valid over larger geographical scales. Journal of Ornithology, 151, 449–458. https://doi.org/10.1007/s10336-009-0478-z

Ennos, R. A., Hickson, J. R. E., & Roberts, A. (1995). Functional morphology of the vanes of the flight feathers of the pigeon *Columba livia*. Journal of Experimental Biology, 198, 1219–1228.

Fandos, G., & Tellería, J. L. (2019). Seasonal niche-tracking behaviour of two partially migratory passerines. Ibis, in press. https://doi.org/10.1111/ibi.12721

Fiedler, W. (2005). Ecomorphology of the external flight apparatus of Blackcap (*Sylvia atricapilla*) with different migratory behavior. Annals of the New York Academy of Sciences, 1046, 253-263. https://doi.org/10.1196/annals.1343.022

Forschler, M. I., & Bairlein, F. (2011). Morphological shifts of the external flight apparatus across the range of a passerine (Northern Wheatear) with diverging migratory behaviour. PLoS One, 6, e18732. https://doi.org/10.1371/journal.pone.0018732

Griffiths, R., Double, M. C., Orr, K., & Dawson, R. J. G. (1998). A DNA test to sex most birds. Molecular Ecology, 7, 1071–1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Griggio, M., Serra, L., Licheri, D., Campomori, C., & Pilastro, A. (2009). Moult speed affects structural feather ornaments in the blue tit. Journal of Evolutionary Biology, 22, 782-792. https://doi.org/10.1111/j.1420-9101.2009.01700.x

Grubb, T. C. Jr. (2006). Ptilochronology. Feather time and the biology of birds. New York, NY: Oxford University Press.

Hall, K. S. S., & Fransson, T. (2000). Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. Journal of Avian Biology, 31, 583-587. https://doi.org/10.1034/j.1600-048X.2000.310419.x

Hobson, K. A., Bowen, G. J., Wassenaar, L. I., Ferrand, Y., & Lormee, H. (2004). Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. Oecologia, 141, 477–488. https://doi.org/10.1007/s00442-004-1671-7

Jenni, L., & Winkler, R. (1994). Moult and Ageing of European Passerines. London, UK: Academic Press.

Kiat, Y., Izhaki, I., & Sapir, N. (2019). The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. Biological Reviews, 94, 700-720. https://doi.org/10.1111/brv.12474

Korner-Nievergelt, F., Liechti, F., & Thorup. K. (2014). A bird distribution model for ring recovery data: where do the European robins go? Ecology and Evolution, 4, 720–73. https://doi.org/10.1002/ece3.977

Lees, J., Garner, T., Cooper, G., & Nudds, R. (2017). Rachis morphology cannot accurately predict the mechanical performance of primary feathers in extant (and therefore fossil) feathered flyers. Royal Society Open Science, 4, 160927. https://doi.org/10.1098/rsos.160927

Lockwood, R., Swaddle, J. P., & Rayner, J. M. V. (1998). Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. Journal of Avian Biology, 29, 273-292. https://doi.org/10.2307/3677110

Médail, F., & Diadema, K. (2009). Glacial Refugia Influence Plant Diversity Patterns in the Mediterranean Basin. Journal of Biogeography, 36, 1333-1345. https://doi.org/10.1111/j.1365-2699.2008.02051.x

Milá, B., Wayne, R. K., & Smith, T. B. (2008). Ecomorphology of Migratory and Sedentary Populations of the Yellow-Rumped Warbler (*Dendroica Coronata*). The Condor, 110, 335–344. https://doi.org/10.1525/cond.2008.8396

Møller, A.P., Fiedler, W., & Berthold, P. (2010). Effects of climate change on birds. Oxford, UK: Oxford Univ. Press. https://doi.org/10.1093/oso/9780198824268.001.0001

Newton, I. (2008). The migration ecology of birds. London, UK: Academic Press. https://10.1016/B978-0-12-517367-4.X5000-1

Pap, P. L., Vágási, C. I., Czirják, G. A., & Barta, Z. (2008). Diet quality affects postnuptial molting and feather quality of the house sparrow (*Passer domesticus*): interaction with humoral immune function? Canadian Journal of Zoology, 86, 834-842. https://doi.org/10.1139/Z08-060

Pap, P. L., Osváth, G., Sándor, K., Vincze, O., Bărbos, L., Marton, A., Nudds, R. L., & Vágási, C. I. (2015). Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. Functional Ecology, 29, 746–757. https://doi.org/10.1111/1365-2435.12419

Pap, P. L., Vincze, O., & Vágási, C. I., Salamon, Z., Pándi, A., Bálint, B., Nord, A., Nudds, R. L., & Osváth, G. (2019). Vane macrostructure of primary feathers and its adaptations to flight in birds. Biological Journal of the Linnean Society, 126, 256-267. https://doi.org/10.1093/biolinnean/bly189

Pérez-Tris, J., Carbonell, R., & Tellería, J. L. (2000). Abundance distribution, morphological variation, and juvenile condition of robins *Erithacus rubecula* (L.) in their Mediterranean range boundary. Journal of Biogeography, 27, 879–888. https://doi.org/10.1046/j.1365-2699.2000.00457.x

Pérez Tris, J., & Tellería, J. L. (2002). Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. Journal of Animal Ecology, 71, 211-224. https://doi.org/10.1046/j.1365-2656.2002.00590.x

Piersma, T., Pérez-Tris, J., Mouritsen, H., Bauchinger, U., & Bairlein, F. (2005). Is there a "migratory syndrome" common to all migrant birds? Annals of the New York Academy of Sciences, 1046, 282–293. https://doi.org/10.1196/annals.1343.026

R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Remacha, C., Rodríguez, C., de la Puente, J., & Pérez-Tris, J. 2020. Climate change and maladaptive wing shortening in a long-distance migratory bird. Auk, in press. https://doi.org/10.1093/auk/ukaa012

Rodríguez-Sánchez, F., Pérez-Barrales, R., Ojeda, F., Vargas, P., & Arroyo, J. (2008). The Strait of Gibraltar as a melting pot for plant biodiversity. Quaternary Science Reviews, 27, 2100–2117. https://doi.org/10.1016/j.quascirev.2008.08.006

SEO/BIRDLIFE. (2012). Atlas de las aves en invierno en España 2007-2010. Madrid, Spain: Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/Birdlife.

Senar, J. C., Lleonart, J., & Metcalfe, N. B. (1994). Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. Journal of Avian Biology, 25, 50-54. https://doi.org/10.2307/3677293.

Serra, L. (2001). Duration of primary moult affects primary quality in grey plovers *Pluvialis squatarola*. Journal of Avian Biology, 32, 377-380. https://doi.org/10.1111/j.0908-8857.2001.320415.x

Szép, T., Dobránszky, J., Møller, A. P., Dyke, G., & Lendvai, Á. Z. (2019). Older birds have better feathers: A longitudinal study on the long-distance migratory Sand Martin, *Riparia riparia*. PLoS ONE 14(1), e0209737. https://doi.org/10.1371/journal.pone.0209737

Tellería, J. L. (2015). The decline of a peripheral population of the European Robin *Erithacus rubecula*. Journal of Avian Biology, 45, 159–166. https://doi.org/10.1111/jav.00451

Tellería, J. L., & Pérez-Tris, J. (2004). Consequences of the settlement of migrant European robins *Erithacus rubecula* in wintering habitats occupied by conspecific residents. Ibis 146, 258–268. https://doi.org/10.1111/j.1474-919x.2003.00249.x

Tubaro, P. L. (2003). A comparative study of aerodynamic function and flexural stiffness of outer tail feathers in birds. Journal of Avian Biology, 34, 243–250. https://doi.org/10.1034/j.1600-048X.2003.03084.x

Vágási, C. I., Pap, P. L., & Barta, Z. (2010) Haste Makes Waste: Accelerated Molt Adversely Affects the Expression of Melanin-Based and Depigmented Plumage Ornaments in House Sparrows. PLoS ONE 5(12), e14215. https://doi.org/10.1371/journal.pone.0014215

Vágási, C. I., Pap, P. L., Vincze, O., Benkő, Z., Marton, A., & Barta, Z. (2012). Haste Makes Waste but Condition Matters: Molt Rate–Feather Quality Trade-Off in a Sedentary Songbird. PLoS ONE, 7, e40651. https://doi.org/10.1371/journal.pone.0040651

Vágási, C. I., Pap, P. L., Vincze, O., Osvath, G., Erritzoe, J., & Moller, A. P. (2016). Morphological Adaptations to Migration in Birds. Evolutionary Biology, 43, 48-59. https://doi.org/10.1007/s11692-015-9349-0

Videler, J. J. (2005). Avian flight. Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199299928.001.0001

Weber, T. P., Borgudd, J., Hedenström, A., Persson, K., & Sandberg, G. (2005). Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. Biology Letters, 1, 27-30. https://doi.org/10.1098/rsbl.2004.0244

Weber, T. P., Kranenbarg, S., Hedenström, A., Waarsing, J. H., & Weinans, H. (2010). Flight feather shaft structure of two warbler species with different moult schedules: a study using high-resolution X-ray imaging. Journal of Zoology, 280, 163-170. https://doi.org/10.1111/j.1469-7998.2009.00644.x

Table 1. Results of the Linear Models that analysed the relationship between an isotopic proxy of migration distance (δD_f) and wing length, wing concavity (PC1), wintip pointedness (PC2) and primary feather length, after accounting for other potential confounding effects. Significant effects were additionally highlighted in bold letter. Sample size was 147 for all the analyses. N.A. (not applicable) indicates effects that were not tested for some response variables according to the rationale raised in the Methods section.

Fixed effects		Wing length	Wing concavity (PC1)	Wingtip pointedness (PC2)	Primary length (P1)
Intercept (adult, female, 2006-07)	Estimate ± se	56.08 ± 4.90	-2.39 ± 0.55	-0.84 ± 0.37	48.79 ± 3.95
δD_f	Estimate ± se	**-0.04 ± 0.01**	**-0.04 ± 0.01**	-0.01 ± 0.00	**-0.01 ± 0.00**
	t	**-6.67**	**-5.18**	-1.39	**-2.99**
	P	**<0.001**	**<0.001**	0.167	**0.003**
Tarsus length	Estimate ± se	**0.51 ± 0.20**	*N.A.*	*N.A.*	0.23 ± 0.16
	t	**2.62**			1.44
	P	**0.010**			0.153
Age (juv)	Estimate ± se	**-0.79 ± 0.34**	0.61 ± 0.39	**1.24 ± 0.26**	-0.33 ± 0.27
	t	**-2.34**	1.55	**4.74**	-1.20
	P	**0.021**	0.123	**<0.001**	0.231
Sex (male)	Estimate ± se	**2.24 ± 0.38**	0.32 ± 0.44	-0.17 ± 0.30	**1.33 ± 0.31**
	t	**5.85**	0.73	-0.83	**4.31**
	P	**<0.001**	0.467	0.559	**<0.001**
Winter (2013-14)	Estimate ± se	-0.15 ± 0.27	-0.10 ± 0.31	-0.17 ± 0.21	-0.36 ± 0.22
	t	-0.56	-0.33	-0.83	-1.65
	P	0.574	0.740	0.410	0.102
Age × sex	Estimate ± se	0.40 ± 0.54	-0.88 ± 0.63	-0.04 ± 0.42	0.47 ± 0.44
	t	0.74	-1.40	-0.10	1.07
	P	0.463	0.165	0.920	0.288
Model R-squared (R^2)		0.47	0.19	0.25	0.30

Table 2. Results of the Linear Models that analysed the relationship between an isotopic proxy of migration distance (δD_f) and some structural and functional feather characteristics (primary mass, dorsoventral (dv) and lateral (lat) rachis width, barb length, barb density, outer and inner barb insertion angles, and bending stiffness), after accounting for feather length and other effects. Sample size was 147 for all the analyses, except for the outer and inner barb angle analyses, whose samples sizes were 146.

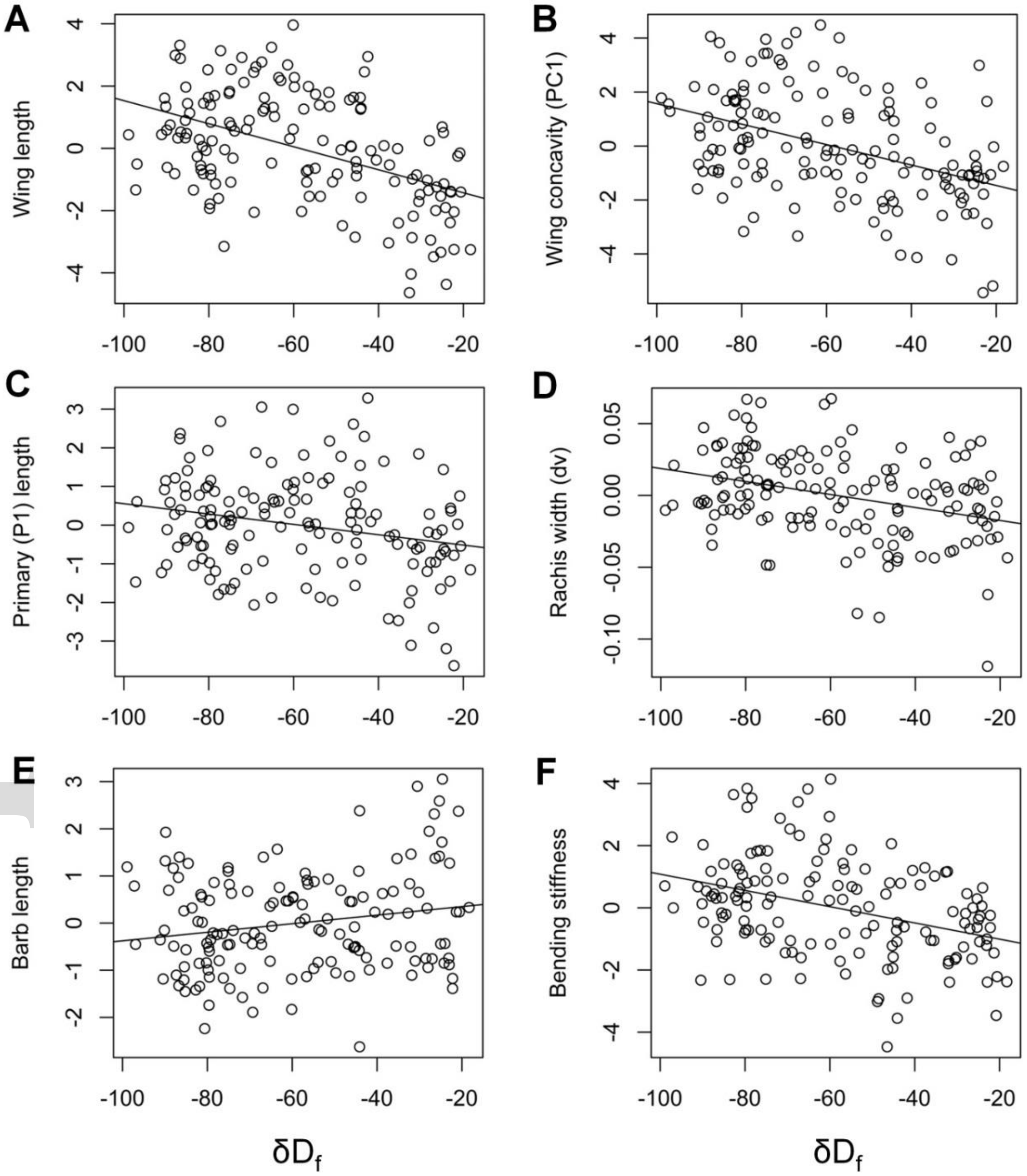
Fixed effects		Primary mass	Rachis width (dv)	Rachis width (lat)	Barb length (combined)	Barb density (combined)	Outer barb angle (combined)	Inner barb angle	Bending stiffness
Intercept (adult, female, 2006-07)	Estimate±se	-2.55 ± 0.79	0.57 ± 0.10	0.37 ± 0.15	-7.39 ± 3.80	10.72 ± 4.21	-0.91 ± 4.55	29.3 ± 8.71	-33.1 ± 5.41
δD_f	Estimate ± se	-0.00 ± 0.00	**-0.00 ± 0.00**	-0.00 ± 0.00	**0.01 ± 0.00**	-0.00 ± 0.00	-0.00 ± 0.01	0.00 ± 0.01	**-0.03 ± 0.01**
	t	-1.73	**-4.56**	-0.04	**2.52**	-1.03	-0.14	0.14	**-5.09**
	P	0.086	**<0.001**	0.973	**0.013**	0.305	0.885	0.889	**<0.001**
Feather length	Estimate ± se	**0.14 ± 0.01**	**0.00 ± 0.00**	**0.01 ± 0.00**	**0.15 ± 0.07**	**-0.19 ± 0.08**	0.02 ± 0.08	-0.12 ± 0.16	**0.81 ± 0.10**
	t	**9.57**	**2.12**	**2.19**	**2.10**	**-2.49**	0.28	-0.77	**8.16**
	P	**<0.001**	**0.036**	**0.030**	**0.037**	**0.014**	0.783	0.444	**<0.001**
Age (juv)	Estimate ± se	**-0.18 ± 0.05**	-0.01 ± 0.01	**0.02 ± 0.01**	-0.29 ± 0.23	**-0.66 ± 0.25**	-0.30 ± 0.27	0.38 ± 0.52	-0.24 ± 0.32
	t	**-3.83**	-0.86	**2.23**	-1.29	**-2.63**	-1.12	0.72	-0.74
	P	**<0.001**	0.393	**0.027**	0.199	**0.009**	0.266	0.470	0.458
Sex (male)	Estimate ± se	**0.14 ± 0.06**	**0.03 ± 0.01**	**0.03 ± 0.01**	0.27 ± 0.27	-0.16 ± 0.30	-0.52 ± 0.32	-0.01 ± 0.62	**1.96 ± 0.39**
	t	**2.53**	**4.16**	**2.60**	0.99	-0.54	-1.59	-0.02	**5.06**
	P	**0.012**	**<0.001**	**0.011**	0.326	0.588	0.115	0.986	**<0.001**

Winter (2013-14)	Estimate ± se	0.02 ± 0.04	**0.01 ± 0.01**	0.01 ± 0.01	0.07 ± 0.18	0.13 ± 0.20	-0.25 ± 0.22	**1.61 ± 0.42**	-0.41 ± 0.26
	t	0.57	**2.27**	0.78	0.40	0.66	-1.14	**3.86**	-1.58
	P	0.572	**0.025**	0.438	0.690	0.510	0.255	**<0.001**	0.117
Age × sex	Estimate ± se	0.00 ± 0.08	-0.00 ± 0.01	**-0.03 ± 0.01**	-0.60 ± 0.36	-0.07 ± 0.40	0.36 ± 0.44	0.42 ± 0.0.83	-0.90 ± 0.52
	t	0.05	-0.33	**-2.39**	-1.65	-0.17	0.84	0.50	-1.74
	P	0.958	0.744	**0.018**	0.102	0.868	0.403	0.618	0.084
Model R-squared (R^2)		0.61	0.36	0.12	0.16	0.15	0.04	0.12	0.62

Table 3. Relationship between feather structural characteristics and bending stiffness of primary feathers after accounting for age, sex, winter and age-sex interaction effects. The length-corrected residuals of feather mass, rachis width (dv and lat), barb length and barb density were included in the models to obtain size-independent measures of these traits as shown in Table 2. Sample size was 146 for this analysis.

	Bending stiffness (Model R^2= 0.75)		
Fixed effects	Estimate ± se	*t*	*P*
Intercept (adult, female, 2006-07)	-44.92 ± 4.72		
Feather length	**1.07 ± 0.08**	**13.22**	**<0.001**
Age (juv)	0.38 ± 0.30	1.28	0.204
Sex (male)	**0.84 ± 0.33**	**2.52**	**0.013**
Winter (2013-14)	**-0.68 ± 0.23**	**-2.97**	**0.004**
Residuals feather mass	**3.38 ± 0.54**	**6.32**	**<0.001**
Residuals rachis width (dv)	**16.77 ± 3.67**	**4.57**	**<0.001**
Residuals rachis width (lat)	1.46 ± 2.68	0.55	0.586
Residuals barb length	**-0.36 ± 0.11**	**-3.21**	**0.002**
Residuals barb density	-0.11 ± 0.11	-1.07	0.285
Outer barb insertion angle	0.03 ± 0.09	0.33	0.741
Inner barb insertion angle	-0.03 ± 0.05	-0.61	0.543
Age × sex	**-0.99 ± 0.44**	**-2.24**	**0.027**

Figure 1. Relationship between an isotopic proxy of migration distance (δD_f) and a set of migration-related morphological and functional traits: (A) wing length, (B) wing concavity, (C) primary feather length, (D) dorsoventral rachis width, (E) barb length, and (F) bending stiffness. These traits were represented in the graphs as the residuals derived from the corresponding models shown in Table 1 and 2, but excluding δD_f effects, whose variation is represented in the Y axis.



Supplementary materials. “Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine”

Table S1. Relationship between feather structure and migration distance with bending stiffness. Results of the analysis of bending stiffness of primary feathers in relation to feather structural characteristics and an isotopic proxy of migration distance (δD_f) after accounting for age, sex, winter and age-sex interaction effects. The length-corrected residuals of feather mass, rachis width (dv and lat), barb length and barb density were included in the models to obtain size-independent measures of these traits as shown in Table 2 and 3. The overall sample size was 146.

	Bending stiffness (Model R^2= 0.77)		
Fixed effects	Estimate ± se	t	P
Intercept (adult, female, 2006-07)	-41.76 ± 4.73		
δD_f	**-0.02 ± 0.01**	**-2.85**	**0.005**
Feather length	**0.99 ± 0.08**	**11.94**	**<0.001**
Age (juv)	0.30 ± 0.29	1.02	0.309
Sex (male)	**1.13 ± 0.34**	**3.33**	**0.001**
Winter (2013-14)	**-0.58 ± 0.23**	**-2.56**	**0.012**
Residuals feather mass	**3.25 ± 0.52**	**6.20**	**<0.001**
Residuals rachis width (dv)	**13.32 ± 3.78**	**3.53**	**<0.001**
Residuals rachis width (lat)	1.98 ± 2.62	0.76	0.450
Residuals barb length	**-0.28 ± 0.11**	**-2.50**	**0.014**
Residuals barb density	-0.10 ± 0.10	-0.97	0.335
Outer barb insertion angle	0.04 ± 0.08	0.50	0.620
Inner barb insertion angle	-0.03 ± 0.05	-0.58	0.564
Age:sex	**-1.03 ± 0.43**	**-2.37**	**0.019**

Table S2. **Relationship between tail feather mass and migration distance in robins.** Results of the analysis of tail (rectrix) feather mass in relation to an isotopic proxy of migration distance (δD_f) for all robins (n=147) and restricted to adults (n=75), after accounting for other appropriate fixed effects. N.A. (not applicable) indicates effects that were not tested for some response variables according to the rationale raised in the Methods section.

Fixed effects		Feather mass (All robins)	Feather mass (only adults)
Intercept (adult, female, 2006-07)	Estimate ± se	-1.97 ± 0.66	-3.30 ± 0.92
δD_f	Estimate ± se	-0.00 ± 0.00	-0.00 ± 0.00
	t	-1.18	-1.87
	P	0.242	0.065
Feather length	Estimate ± se	**0.12 ± 0.01**	**0.13 ± 0.02**
	t	**10.55**	**8.93**
	P	**<0.001**	**<0.001**
Age (juv)	Estimate ± se	-0.07 ± 0.05	*N.A.*
	t	-1.30	
	P	0.198	
Sex (male)	Estimate ± se	**0.23 ± 0.07**	**0.20 ± 0.07**
	t	**3.50**	**2.84**
	P	**<0.001**	**0.006**
Winter (2013-14)	Estimate ± se	0.01 ± 0.04	0.05 ± 0.06
	t	0.27	0.77
	P	0.787	0.444
Age:sex	Estimate ± se	0.07 ± 0.09	*NA*
	t	0.86	*NA*
	P	0.392	*NA*
Model R-squared (R^2)		0.67	0.71