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Are Iberian Chiffchaffs *Phylloscopus (collybita) brehmii* long-distance migrants? An analysis of flight-related morphology

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Capsule Iberian Chiffchaffs *Phylloscopus* (*collybita*) *brehmii* are genetically, morphologically and bioacoustically different from European Chiffchaffs (*P. [c.] collybita*).

Aim To examine the difference in migratory pattern between *brehmii* and *collybita*.

Methods We inferred variation in distance of migration between *brehmii* and *collybita* by analysing differences in flight-related morphology (wing-length, wing shape and tail-length) between individuals breeding or wintering in the Iberian Peninsula.

Results Controlling for body size and allometry of feather dimensions, birds captured in spring had more pointed wings (more concave wing shapes and pointed wing tips) and a shorter tail than birds caught in winter, although no spring-to-winter difference was found for wing-length.

Conclusion Iberian breeders appear better suited to long-distance migration (their traits are likely to give a higher speed and a lower energy consumption during long non-stop flights) than wintering individuals, which strongly supports the hypothesis that *brehmii* move south of the Sahara in autumn and are substituted by central European *collybita* populations in winter. This different migration pattern of *brehmii* and *collybita* has important implications for the maintenance of differentiation in their contact zone, because selection against hybrids with maladaptive, intermediate migratory behaviours might contribute to reproductive isolation.

The study of differentiation between two closely related species or subspecies meeting at hybrid zones may shed light on the processes contributing to reproductive isolation and speciation (Barton & Hewitt 1989, Harrison 1993). During the last decade, Old World leaf warblers (birds of the genus *Phylloscopus*) have become a model in this kind of studies. Leaf warblers include many closely related forms, some of which are considered to be species and others to be subspecies, whose ranges usually overlap in confined areas (Helbig *et al.* 1996, Bensch *et al.* 1999, Irwin *et al.* 2001).

Among these, the contact zone between European Chiffchaffs (*P. [collybita] collybita* Vieillot, 1817) and Iberian Chiffchaffs (*P. [c.] brehmii* Homeyer, 1871) has been extensively studied in recent times. The form *brehmii* is endemic to the Iberian Peninsula and southwestern France, and contacts with *collybita* in a narrow belt located at the southwestern edge of the Pyrenees (Salomon *et al.* 1997, Balmori *et al.* 2002). These two forms differ at the molecular level (4.6% divergence in the cytochrome b gene), and also have a different song (Helbig *et al.* 1996). Remarkably, these differences have persisted over time despite noticeable gene flow, as shown by microsatellite analyses and direct identification of hybrids (Helbig *et al.* 2001, Bensch *et al.* 2002).

Because the molecular and bioacoustic differences existing between *brehmii* and *collybita* were unknown until very recently, possible variation between these forms in other basic biological aspects has never been investigated in detail. In particular, the migratory behaviour of *brehmii* is still a major uncertainty. The majority of Chiffchaffs are short-distance migrants, which breed all across Europe and have their main wintering grounds in the Mediterranean area, including the Iberian Peninsula where they could mix with *brehmii* populations. However, it has been suggested that *brehmii* populations could be long-distance migrants, which spend the winter south of the Sahara in Africa (Salomon *et al.* 1997, Balmori *et al.* 2002 and

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*Author for correspondence. Present address: Department of Animal Ecology, Lund University, Ecology Building SE-223 62 Lund, Sweden. Email: javier.perez-tris@zooekol.lu.se references therein). Such a difference in migratory behaviour would have important implications for the maintenance of differentiation between *brehmii* and *collybita* at either side of their contact zone. Because hybrids between birds with different migratory behaviours show an intermediate migratory pattern (and hence are likely to face a much higher mortality than either parental phenotype; Berthold 1996), migratory divergence might be an important reproductive isolating mechanism.

Unfortunately, it is difficult to unravel the migratory patterns of small bird populations (like those living in Iberian forests), as they usually produce very few ringing recoveries (Tellería *et al.* 2001). This problem is further accentuated when birds migrate to Africa, where ring reporting rates are low, as shown by Willow Warblers *Phylloscopus trochilus* – one of the most extensively ringed species within the genus – for which other methods have been necessary to ascertain the migratory patterns of different populations (Chamberlain *et al.* 2000). As for many other species, ringing data for the small and sparse breeding populations of Iberian Chiffchaffs are few, leading to few recoveries. Among the 1188 recovery cards available at the Spanish Ringing Scheme up to 1998, corresponding to Chiffchaffs ringed or recovered in Spain since 1940 (excluding the Canary Islands), less than 1% (seven birds) may be assigned to the Iberian breeding population (as they have been captured in Spain at least once during the breeding season, from May to July according to the phenology of the species; Cantos 1992). All these birds were always recaptured in spring and at the site of ringing, giving no information about flight ranges or the orientation of migrants.

One alternative to the use of ringing recoveries when studying variation in migratory behaviour is the analysis of flight-related morphology. The shape of the wings and tails vary between species and populations in relation to their migratory behaviour, even though these behavioural differences may be small (Marchetti *et al.* 1995, Tellería *et al.* 2001). Migratory birds benefit from having longer and more pointed wings and shorter tails, as this increases speed and reduces energy consumption during long-distance flights (Winkler & Leisler 1992, Mönkkönen 1995, Norberg 1995). In the absence of costs of migration, shorter and rounded wings and longer tails are favoured because they improve manoeuvrability and hence predator avoidance and foraging efficiency (Marchetti *et al.* 1995, Swaddle & Lockwood 1998, Pérez-Tris & Tellería 2001). Consistent with these relationships, short-distance migrants have shorter and more rounded wings than long-distance migrants (Winkler & Leisler 1992, Mönkkönen 1995; for an example with *Phylloscopus* warblers, see Marchetti *et al.* 1995).

Previous studies on the morphological variation between *brehmii* and *collybita* Chiffchaffs have compared males of both forms, showing that Iberian Chiffchaffs have longer and more pointed wings than southern French Common Chiffchaffs (Salomon *et al.* 1997). However, these differences in wing dimensions just could be indicating variation in body size between both forms (as discussed by Salomon *et al.* 1997). Large birds are likely to have longer wings or tails, and the tips of their primaries are likely to be more separated from the wing tip (giving apparently more pointed wings) due to allometric growth of each primary at different wing sizes (Senar *et al.* 1994). If overall variation in body size accounts for differences in body dimensions, the wing-shape variation observed in male Chiffchaffs by Salomon *et al.* (1997) would not be interpretable in relation to variation in migratory behaviour (Senar *et al.* 1994, Norberg 1995).

We analysed variation in flight-related morphology of birds breeding or wintering in different Iberian areas. If *brehmii* Chiffchaffs are trans-Saharan migrants, variation in wing and tail morphology should be consistent with this behaviour. Thus, individuals breeding in the Iberian Peninsula should have longer and more pointed wings and a shorter tail than birds wintering in the same area, which arrive there from central and northern Europe (moving an average distance of 1533 km, se = ± 45 km, as estimated from ringing recovery data for birds of known breeding-site origin wintering in Spain, see also Cantos 1992).

METHODS

Capture and measurement of birds

During 1997 to 2002, we mist-netted Chiffchaffs at different localities in the Iberian Peninsula (Fig. 1). Mist-nets were worked without any luring mechanism (such as song playbacks) that could have biased our sampling. During the breeding season (in July), we captured birds in the northern half of Iberia (in Álava, 42°55′N 2°29′W) and in the southern half of Iberia (in Tarifa, 36°01′N 5°36′W). Wintering birds were captured from December to January also in the north (in Las Minas, 40°18′N 3°35′W) and in the south (in Tarifa).

In total, we captured, ringed and measured 77 birds.

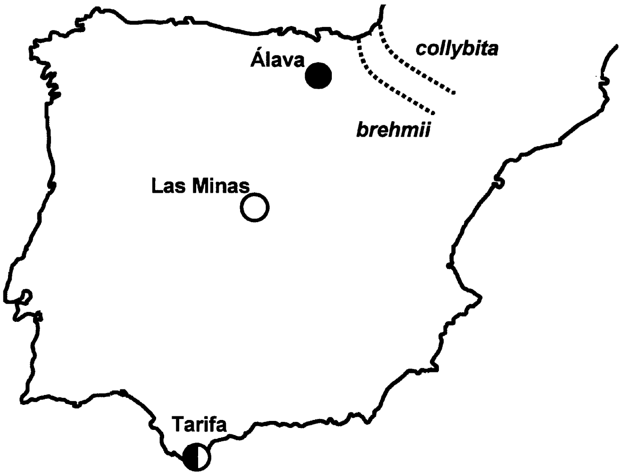

Figure 1. Location of the sites where Chiffchaffs were captured in spring (●), in winter (○) and in both seasons (split circle). The approximate location of the contact zone between *collybita* and *brehmii* at the Pyrenees is also shown (- - - , for further details see Salomon *et al.* 1997, Balmori *et al.* 2002).

We measured tarsus-length (to the last scale), using a digital calliper with 0.01 mm precision. We also measured tail-length, wing maximum chord and the distances between the wing tip and the tip of each primary feather from the first to the ninth (primary distances 1 to 9, numbered from the body), with the appropriate rulers and to the nearest 0.5 mm (see Svensson 1992 for details).

Analysis of morphology

Variation in body size has to be taken into account when studying differences in flight-related morphology between populations of different breeding-site origin. We obtained an index of structural body size of Chiffchaffs using principal components analysis (PCA) with body dimensions (wing-length, tail-length and tarsus-length). This analysis extracted a single component with eigenvalue above 1 (eigenvalue = 2.36, variance explained 78.5%, n = 77), on which all body dimensions were weighed with a large and positive loading (tarsus = 0.90, wing = 0.90, tail = 0.87). Therefore, this component could be interpreted as a measure of body size (for further details see Rising & Sommers 1989).

We used primary distances to derive indices of wing-pointedness by means of PCA (Senar *et al.* 1994). In this analysis, we took into account the possibility that birds with wings of different sizes have differing potential to manifest variation in wing-pointedness due to allometric growth of each primary.[a]

Chiffchaffs cannot be sexed in the hand outside the breeding season, so we did not take into account possible sexual differences. We did not consider age-related variation because ageing was difficult in many instances (particularly in July when trying to identify post-juvenile and adult plumages, see Svensson 1992), and hence our sample size decreased dramatically if we considered only birds of known age. Nevertheless, omitting age from the analyses should not have substantially affected our results, as its effect on morphology is much smaller than the effect of migratory behaviour in passerines (Pérez-Tris & Tellería 2001).

In our study, flight-related morphology was defined by the covariation of tail-length, wing-length and wing-pointedness. Because of this, we first tested whether Chiffchaffs vary in flight-related morphology from spring to winter, using general linear models (GLMs)[b] with tail-length, wing-length and wing-pointedness as dependent variables, season and locality as factors, and structural body size (PC scores extracted from body dimensions) as a covariate. Locality was included in the design in order to use the correct error term when testing for seasonal variation in morphology. Because of the existence of missing cells, we tested for seasonal variation in flight-related morphology using a type-IV sum of squares. After this, we conducted univariate protected GLMs to check which particular components of flight-related morphology contribute to the observed variation.[b]

RESULTS

The PCA with primary distances corrected for allometry identified two components (Table 1). PC1 was inter-

Table 1. Results of PCA with primary distances corrected for allometry (feathers numbered from the body to the wing tip). The correlation between each variable and each component is shown (significant correlations have been labelled with asterisks, all with $P < 0.0001$).

	PC1	PC2
Primary 9	–0.176	–0.882*
Primary 8	–0.226	–0.863*
Primary 7	0.202	–0.097
Primary 6	0.721*	0.036
Primary 5	0.827*	0.016
Primary 4	0.914*	–0.075
Primary 3	0.934*	–0.130
Primary 2	0.886*	–0.122
Primary 1	0.833*	–0.086
Eigenvalue	4.514	1.579
Variance explained (%)	50.16	17.54

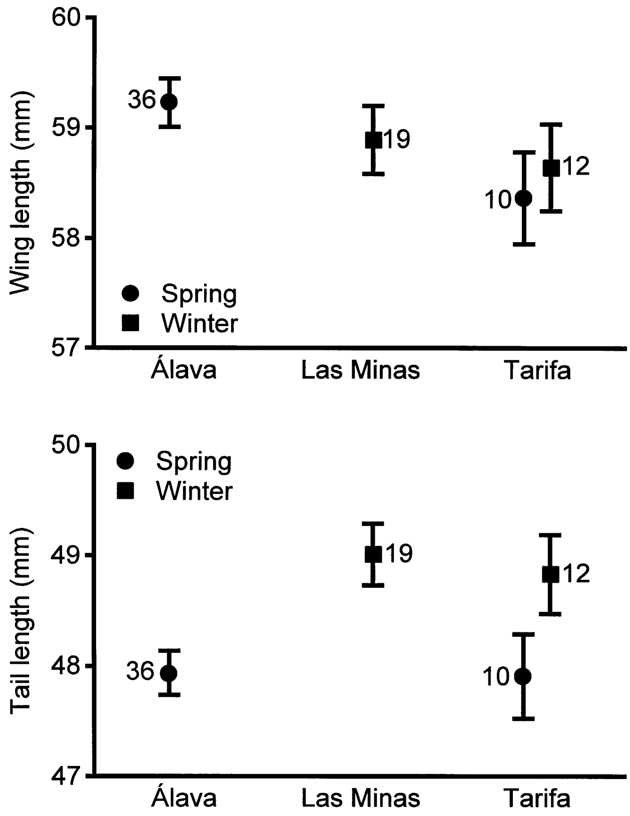

Figure 2. Variation in wing-length and tail-length between Chiffchaffs captured in spring and in winter. Means adjusted for by body size, standard errors and sample sizes are shown.

preted as an index of wing concavity, as inner primary distances had high positive loadings. PC2 was an index of wing-tip pointedness; the higher this score, the closer were the tips of the outer primaries to the wing tip (Table 1). Thus, the two principal components extracted were complementary measures of wing shape.

Covariation among tail-length, wing-length, wing concavity and wing-tip pointedness was higher than expected through random effects (Mauchley sphericity test[b]: $\chi^2 = 63.64$, df = 5, $P < 0.0001$). The multivariate GLM with all four traits together showed that, controlling for body size (Wilks' lambda = 0.05, Rao's approximated $F_{4,69} = 309.36$, $P < 0.0001$) Chiffchaffs captured in spring had a different morphology to those captured in winter (Wilks' lambda = 0.72, $F_{4,69} = 6.61$, $P < 0.001$). Although individual variation in flight-related morphology was dependent on body size, Chiffchaffs breeding in the Iberian Peninsula had a similar body size to those arriving from Europe to spend the winter ($F_{1,76} = 0.01$, $P = 0.96$).

Table 2. Results of protected GLM testing for seasonal variation in the four components of flight-related morphology studied.

	Season		Body size	
	$F_{1,72}$	P	$F_{1,72}$	P
Wing-length	0.01	0.929	264.02	< 0.0001
Tail-length	10.48	0.002	221.19	< 0.0001
Wing concavity	8.13	0.006	0.66	0.420
Wing-tip pointedness	8.78	0.004	1.55	0.217

Univariate protected analyses[b] showed that wing-length did not contribute to spring-to-winter differences in flight-related morphology of Chiffchaffs (Fig. 2), which were due to variation in the other three traits (Table 2). Birds captured in spring had a shorter tail than birds captured in winter (Fig. 2), and they also showed more pointed wings (as shown by both wing concavity and wing-tip pointedness; Fig. 3). Large birds had longer wings and tails but body size did not influence variation in wing concavity or wing-tip

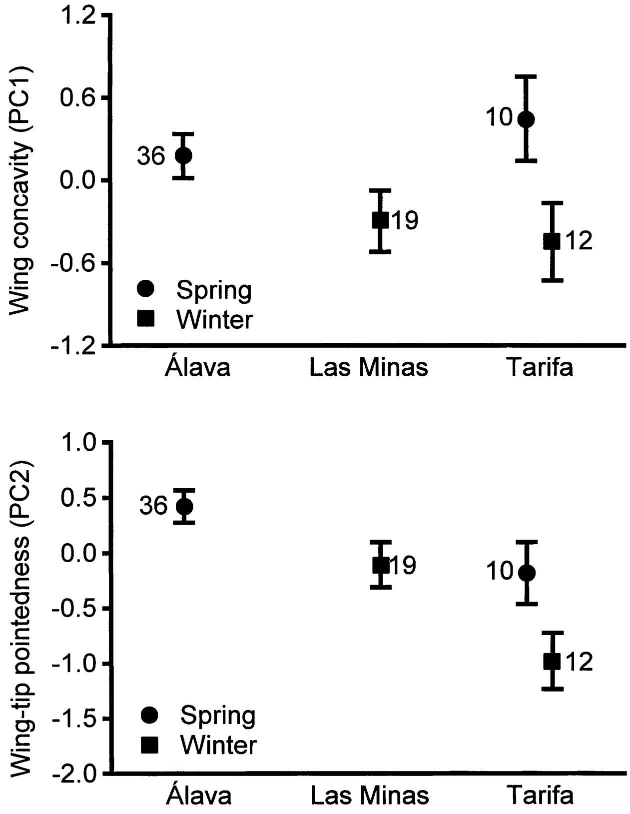

Figure 3. Variation in the two components of wing-pointedness between Chiffchaffs captured in spring and in winter. Wing concavity increases with distance from the tip of the inner primaries (1 to 6 numbered from the body) to the wing tip, and wing-tip pointedness increases with decreasing distance from the outer primaries (8 and 9) to the wing tip. Means, standard errors and sample sizes are shown.

pointedness (Table 2), as these two measures were derived taking into account allometric effects on primary distances.

DISCUSSION

At present, the migratory pattern of Iberian Chiffchaffs cannot be resolved based on ringing recoveries alone. Only seven out of more than 1000 ringing recoveries could be assigned to local individuals, which were always recovered at the same site and hence gave no information on movements (see Introduction).

Based on the established evidence for a correlation between flight-related morphology and migratory behaviour (Winkler & Leisler 1992, Marchetti *et al.* 1995, Mönkkönen 1995, Tellería *et al.* 2001), our results support the idea that Chiffchaffs breeding in the Iberian Peninsula (*brehmii*) migrate longer distances than individuals wintering in this area (*collybita*). After controlling for body size and allometry of feather dimensions, breeding Iberian Chiffchaffs had a shorter tail and more pointed wings than birds wintering in the same areas. These results conflict with the idea that *brehmii* are sedentary and mix with European migrants in winter, as this would not explain why Iberian Chiffchaffs are better suited for long-distance travelling (Swaddle & Lockwood 1998, Pérez-Tris & Tellería 2001). The most plausible explanation for our results is that *brehmii* Chiffchaffs winter in Africa south of the Sahara, and hence move longer distances than European *collybita* wintering in the Iberian Peninsula.

We observed more variation in wing-pointedness and tail-length than in wing-length. This is consistent with comparative studies, which have shown that wing-pointedness is more sensitive than wing-length to variation in distance of migration (Mönkkönen 1995). Besides, all Chiffchaffs wintering in the Iberian Peninsula are migrants, which sometimes may travel thousands of kilometres in their journeys as shown by ringing recoveries (see Introduction). Hence, it is not surprising that they have wings as large as other migrant relatives. However, if *brehmii* Chiffchaffs move to sub-Saharan Africa while *collybita* move to the Mediterranean area, their migratory strategies are likely to differ strongly. European passerines wintering in the Mediterranean are usually slower in their migrations than trans-Saharan migrants (Ellegren 1993). Moreover, the latter are obliged to make longer journeys, at least when faced with the crossing of the Sahara desert. These differences might explain why Iberian Chiffchaffs have shorter tails and more pointed wings than wintering Chiffchaffs, as these traits decrease energy expenditure and increase speed during long non-stop flights (Norberg 1995).

Our results support the idea that *brehmii* and *collybita* Chiffchaffs have a similar body size, at least when *collybita* from the central and northern range are studied. Differences in single body dimensions have been used to conclude that Iberian Chiffchaffs have a larger body size than northern populations (Salomon *et al.* 1997). However, these differences are more probably due to varying body proportions than to varying body size. Salomon *et al.* (1997) compared *brehmii* individuals with southern French *collybita* Chiffchaffs. But given that these latter birds are the least migratory of all *collybita* (they are principally residents, Cramp 1992) and hence are likely to have comparatively short wings, wing-length alone was inappropriate to assess differences in body size. The results would probably have been rather different if birds breeding in northern Europe had been compared to *brehmii* Chiffchaffs (Erard & Salomon 1989). For example, birds wintering in Spain (used in this study) come from central and northern Europe (Cantos 1992, this study), and thus they have longer wings for their body size, and also in absolute terms, than those breeding in southern France (cf. Salomon *et al.* 1997). This is relevant to methods proposed to recognize both species based on morphometrics. Salomon *et al.* (1997) reported that male *brehmii* and *collybita* may be separated with a suite of morphological characters, but our results suggest that such a method might be applicable only to *collybita* from the southern range.

The different migratory behaviour of *brehmii* and *collybita* Chiffchaffs suggested in this study has important implications in the maintenance of differences at either side of their contact zone. Migratory behaviour is a highly heritable trait in birds, to the point that both the direction and distance of the migration of hybrids is intermediate between those of their parents (Berthold 1996). Consequently, hybrids between trans-Saharan migrant *brehmii* and pre-Saharan migrant *collybita* are likely to have an inappropriate migratory behaviour, and hence a very low survival. This type of selection against hybrids has been suggested to be involved in the maintenance of morphological differences at either side of a migratory divide in Willow Warblers despite existing gene flow (Bensch *et al.* 1999). Among leaf warblers, song divergence seems to be the major pre-reproductive isolating mechanism (Helbig *et al.* 2001, Irwin *et al.* 2001). However, song differences are not sufficient for *brehmii* and *collybita* to remain isolated, as they are unable to completely discriminate each other by song alone (Helbig *et al.* 2001, Bensch *et al.* 2002). The high frequency of hybrids between *brehmii* and *collybita* in the contact zone suggests that post-reproductive isolating mechanisms are important, and our results support the idea that migratory divergence might contribute to the maintenance of the divide at the Pyrenees, despite considerable genetic interchange.

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ENDNOTES

a. In order to take into account allometric growth of primary feathers, we standardized primary distances before analysing wing shape, using the expression:

$$P^*_{ji} = P_{ji}\left(\frac{l_0}{l_i}\right)^{b_j}$$

where P_{ji} is the original primary distance j in the individual i, P^*_{ji} is the standardized value, l_i is the wing-length of the individual i, l_0 is a standard wing-length to which all individuals are reduced or increased (which we conventionally set at 58.5 mm, the average wing-length of Chiffchaffs in our sample) and b_j is the allometry coefficient of the primary j according to the growth model $P_{ji} = a_j l_i^{b_j}$, where a_j is a parameter (for further details see Senar *et al.* 1994).

b. Multivariate GLMs test for the effect of a set of independent variables on a non-measurable variable defined by the covariation between several dependent variables (e.g. the covariation among wing-length, tail-length and two components of wing shape define flight-related morphology in our study). The multivariate GLM only makes sense if dependent variables are not independent (orthogonal) components or, in other words, if their correlation matrix deviates from sphericity. This assumption may be evaluated using the Mauchley test; if the test is significant, our dependent variables can be regarded as more correlated to one another than expected through random effects. Once a multivariate effect has been examined using GLM (e.g. variation in flight-related morphology in our study), we can be interested in knowing which particular independent variables contribute best to such an effect. This may be done *a posteriori* using the so-called protected analyses, which test for univariate effects protecting us from potential misleading conclusions attained by multiple estimation of probability, as long as the overall, multivariate effect investigated was proved to be significant *a priori* (for further details, see Finn 1974, Statsoft 1999).

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