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Variations in wing morphology among subspecies might reflect different migration distances in Bluethroat

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Long-distance migrants have a more pointed and concave wing than short-distance migrants. These pointed and concave wings are thought to minimize the energy-cost of flight. Detailed analyses of wing morphology among populations might therefore offer clues about the migratory behaviour of those populations whose wintering areas are not known. In this work we analysed variations of wing shape of three populations of Bluethroats (*Luscinia svecica*) from western Europe with different migration distances: *L. s. namnetum* (breeds mainly in W France, winters in W Portugal and Morocco, n = 31), *L. s. cyanecula* from central Europe (breeds in C Europe, winters in S Europe and N and C Africa, n = 182), *L. s. cyanecula* from Iberia (breeds in Iberia, but their wintering areas are still unknown, n = 39). To assess wing morphology we used C_2 and C_3 wingtip shape indices proposed by Lockwood *et al.* (1998), measuring wing pointedness and convexity, respectively. Males had more pointed and concave wings. As expected, *namnetum* was found to have a relatively more rounded wing than *cyanecula*, as well as a more convex wing, agreeing with the fact that *namnetum* moves shorter distances between its breeding and wintering areas. No significant differences were observed between *cyanecula* from C Europe and Iberia. Our results suggest that Bluethroats from Iberia are long-distance migrants.

1. Introduction

Wing morphology is well documented to be determined by selection pressures such as migration (Senar *et al.* 1994, Mönkkönen 1995, Calmaestra & Moreno 2001), predation (Alatalo *et al.* 1984) or foraging behaviour (Marchetti *et al.* 1995). In relation to migration, migrants tend to have a relatively more pointed wing than residents (Senar *et al.* 1994, Mönkkönen 1995), allowing them greater flight efficiency (e.g. Norberg 1989), a fact of particular importance when a bird must face a long-distance flight (Lockwood *et al.* 1998). By contrast, more rounded wings are known to improve take off ability and, hence, the capability to diminish the risk of being predated (Swaddle & Lockwood 1998, Hedenström & Rosen 2001), so this morphology is expected to be a selective advantage when distance of migration is short or even null (i.e. sedentary populations).

Migratory behaviour-dependent variations of wing morphology have been analysed either at inter-specific (Mönkkönen 1995, Calmaestra & Moreno 2001) or at intra-specific levels (Senar *et al.* 1994, Copete *et al.* 1999, Pérez-Tris & Tellería 2001). In this last case, most studies have considered bird populations with known migratory behaviour (such as resident opposite migrants, e.g. Senar *et al.* 1994, Copete *et al.* 1999). Alternatively, detailed analyses of wing morphology among populations might be of interest to offer clues about the possible migration distance (or at least to assess if its migratory distances are more or less pronounced) of a particular population whose wintering areas and, therefore, migratory behaviour, are still unknown

The Bluethroat (*Luscinia svecica*) is a polytypic Palearctic passerine (Cramp 1988), and migratory distances vary among subspecies. Thus, it is a good model to study the way in which wing shape varies among populations at the subspecific level. In W Europe, two subspecies are currently accepted to exist (Collar 2005). *L. s. namnetum* breeds in W France, establishes its wintering area in W Portugal and Morocco, and migrating on average 900 km (calculated from Cramp 1988). *L. s. cyanecula* breeds in C Europe to Belarus and Ukraine, as well as in C and NW Iberia, and establishes its wintering area mainly in S Europe and N and C Africa, displacing the population from C Europe an average of 3800 km (assuming, according to Cramp 1988, that most of the C European birds reach C Africa). In contrast to *namnetum* and the *cyanecula* from C Europe, it is still unknown where the birds which breed in Iberia overwinter (Hernández *et al.* 2003). Though Mayaud (1958) recommended that populations from Iberia should be considered as a separate subspecies (*L. s. azuricollis*), this is not actually accepted and, indeed, the validity of this subspecies remains unclear, as it is reported by Campos *et al.* (2005) in a recent work on biometrics of a breeding population from C Iberia. Thus, for practical reasons, we considered in this paper three populations of Bluethroats: *namnetum*, *cyanecula* from C Europe, *cyanecula* from Iberia.

Concerning wing morphology, the following predictions should be expected to be found among the three groups mentioned above: (1) between *namnetum* and *cyanecula* from C Europe, the first is expected to show a relatively more rounded wing, since it moves shorter distances between its breeding and wintering areas, as we have said before; (2) *cyanecula* from Iberia is expected to show a more pointed wing than *namnetum*, if we assume that the population from Iberia is composed of long-distance migrants that overwinter in C Africa, as reported for the *cyanecula* subspecies (Cramp 1988, Collar 2005). By contrast, we should expect a more rounded wing (either similar to or shorter than *namnetum*) if the population from Iberia establishes its wintering area in W and S Iberia or N Africa.

2. Material and Methods

2.1. Sampling localities, ringing protocol

Bluethroats were captured at five localities in Iberia: (1) Central System in C Iberia (Piedrahita, 40º25'N 05º17'W; Béjar, 40º21'N 05º41'W; Candelario, 40º20'N 05º43'W); subspecies *cyanecula* (n = 39), caught with iron traps and vocal lures at breeding quarters, from May to July 2004–2005. (2) Ebro river basin in N Iberia (Villafranca, 42º16'N 01º42'W); individuals from *namnetum* (n = 11) and *cyanecula* (n = 173), caught with mist nets at a stopover site during the autumn migration period, from August to October 2004. (3) Txingudi marshlands in N Iberia (Fuenterrabía, 43º20'N 01º47'W); individuals from *namnetum* (n = 20) and *cyanecula* (n = 9), mist netted at a stopover site during the autumn migration period, from August to October 2005. It is unlikely that *cyanecula* individuals from Iberia were caught at Villafranca and Fuenterrabía, since these birds breed in NW Iberia, as these sampling sites are in NE Iberia and migration movements are expected to be performed along a latitudinal axis, rather than a longitudinal axis.

Once captured, the age and sex of each bird was determined according to Svensson (1998). We considered two age categories: adults (EURING 4 or 6) and juveniles (EURING 3 or 5). Thereafter, we recorded wing length (method III following Svensson 1998) with a metal ruler to 0.5 mm accuracy, and the primary feather lengths (P1 to P8, numbered from outermost to innermost, just like Lockwood *et al.* 1998; most-distal [vestigial] primary was ignored), measured from the tip to the point where it enters skin, to 0.5 mm accuracy. In contrast to distances of primaries (recorded for each primary feather, from its tip to the tip of the longest primary, in a folded wing), also commonly used in studies on wing morphology (e.g. Senar *et al.* 1994, Pérez-Tris & Tellería 2001), primary feather lengths provide more statistical consistency, since they allow a lower measurement error (the distances are much shorter than primary lengths) as well as higher repeatability (Swaddle & Witter 1994, Lockwood *et al.* 1998).

At Villafranca and Fuenterrabía, we used wing length to separate *namnetum* from *cyanecula* from C Europe (for further details see Eybert *et al.* 1999): adult males < 72 mm, adult females < 68 mm, juvenile males < 71 mm, and juvenile females < 67 mm. Nominate *L. s. svecica* is absent from all the sampling localities (pers. obs.). Individuals with some missing data and unknown age were removed from this work.

2.2. Statistics

Though Principal Component Analyses (PCA) have been commonly used to assess wing morphology (Chandler & Mulvihill 1988, Senar *et al.* 1994, Marchetti *et al.* 1995), it is well reported that PCA, even if primary lengths (or distances) are corrected for size allometric effect (Senar *et al.* 1994, Mönkkönen 1995), is susceptible to show some statistical-associated errors (see for a review Lockwood *et al.* 1998). This is mainly due to the fact that size-effect is usually assumed to be included at all in wing length, though this is unlikely to be true (Lockwood *et al.* 1998), at least in general. Thus, we used data on the length of primaries one to eight (hereafter abbreviated as P1 to P8) to estimate C_2 and C_3 size-independent indices of wingtip morphology (Lockwood *et al.* 1998) used to assess, respectively, wing pointedness and convexity (see also for similar studies Copete *et al.* 1999). Both indices are derived from a modified PCA, the size-constrained component analysis (SCCA, for further details see Lockwood *et al.* 1998). Higher values of C_2 relate to a relatively more rounded wing, whilst higher values of C_3 correspond to a more convex wing.

Wing morphology is likely to be affected by either sex or age or both (e.g. Pérez-Tris & Tellería 2001) so, in addition to subspecies, data analyses should also include these factors. To maintain a sufficient sample size for each subspecies, we performed an ANOVA on C_2 and C_3 scores (calculated in each individual) with sex and age as selection variables, and used the residuals (i.e. C_2 and C_3 values once corrected for sex and age effect; for similar methods see Marquiss & Rae 2002, Alonso *et al.* 2006) to analyse wing morphology among subspecies. In all cases the ANOVA fitted well statistical assumptions (Levene's test: all $P > 0.05$).

Additionally, wing length-associated variations in relation to subspecies were also analysed. As argued before for the case of primary lengths, we performed an ANOVA on residual wing length once sex and age effects were removed (Levene's test. all $P > 0.05$).

Bird plumage is exposed to wear, so lengths of feathers (and therefore the associated measurements, such as wing length) are expected to change over time (Martin 1996), a fact that should be considered here since the birds at Fuenterrabía and Villafranca were captured in autumn (following either post-breeding moult by adult birds or recent feather growth in nest by juveniles), while the birds at C Iberia were caught in spring, a date when feathers show a higher degree of abrasion (Jenni & Winkler 1994).

Abrasion, however, is expected to affect wing morphology to a lesser extent (wingtip shape indices are independent of size), unless it would be higher in outermost primaries than in innermost primaries. Unfortunately, information on this is fairly scarce (Martin 1996), and, in addition, is subjected to variation between species (e.g. due to the specific flight performance). Thus, we considered here that whilst having a possible impact on wing length (for further details see Discussion), wingtip morphology indices were independent of capture date.

Statistical analyses were conducted with software SPSS v.13.0 for Windows and means are shown ± SE.

Table 1. Sample size (n), and mean ± SE (mm) of C_2 (wing pointedness) and C_3 (wing convexity) indices (Lockwood *et al.* 1998), in three populations of Bluethroats from W Europe, after correcting for age and sex differences. Results from Tukey-B tests are shown (groups between which no significant differences were found are shown with the same superscripts).

Index	*L. s. namnetum* (W France)	*L. s. cyanecula* (C Europe)	*L. s. cyanecula* (Iberia)
n	31	182	39
C_2	$0.098^{a} \pm 0.030$	$-0.006^{b} \pm 0.009$	$-0.050^{b} \pm 0.015$
C_3	$0.076^{a} \pm 0.021$	$-0.004^{b} \pm 0.007$	$-0.041^{b} \pm 0.013$

3. Results

ANOVA on the C_2 scores showed that, overall, wing pointedness only varied in relation to sex (sex: $F_{1,248} = 13.8$, $P < 0.001$; age: $F_{1,248} = 0.022$, $P = 0.88$; interaction: $F_{1,248} = 3.8$, $P = 0.051$), with males showing more pointed wings than females (1.20 ± 0.010, n = 167; 1.26 ± 0.012, n = 85, respectively). Similarly, wing convexity (C_3) also varied only between sex classes (sex: $F_{1,248} = 14.3$, $P < 0.001$; age: $F_{1,248} = 0.006$, $P = 0.94$; interaction: $F_{1,248} = 3.5$, $P = 0.06$), with males showing more concave wings than females (0.18 ± 0.008, n = 167; 0.23 ± 0.010, n = 85, respectively).

Once the age and sex effects were removed, wing pointedness significantly varied among subspecies ($F_{2,249} = 14.3$, $P < 0.001$), with a Tukey-B test revealing that *namnetum* subspecies showed a relatively more rounded wing that the other two groups (Table 1, Fig. 1A). The *namnetum* subspe-

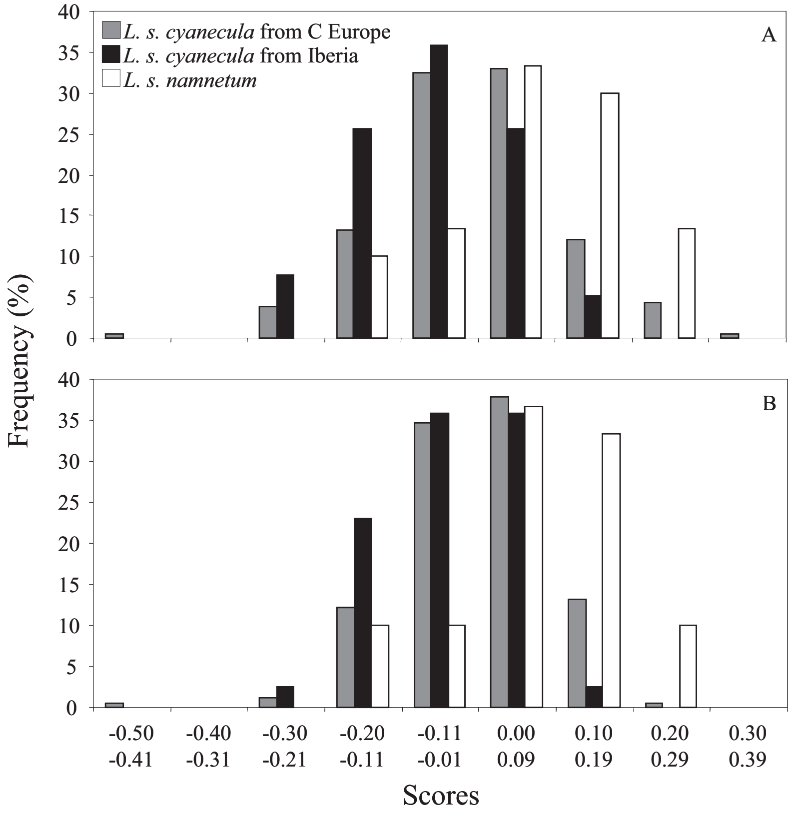

Fig. 1. Frequencies (%) of distribution of C_2 (A) and C_3 (B) scores of 3 populations of Bluethroats from W Europe: *L. s. namnetum* (n = 31), *L. s. cyanecula* from C Europe (n = 181) and *L. s. cyanecula* from Iberia (n = 39).

Table 2. Sample size (n, number of individuals), mean values (± SE, in mm) of primary lengths, and wing length in three populations of Bluethroats. Primaries (P) are numbered from outermost (P1) to innermost (P8) (most-distal primary is omitted). For wing length, results derived from Tukey-B tests are shown (groups between which no significant differences were found are shown with the same superscripts).

	Population		
	L. s. namnetum (W France)	*L. s. cyanecula* (C Europe)	*L. s. cyanecula* (Iberia)
n	31	182	39
P1	46.0 ± 0.4	50.4 ± 0.2	53.3 ± 0.2
P2	51.6 ± 0.4	56.2 ± 0.2	58.9 ± 0.3
P3	52.5 ± 0.4	57.0 ± 0.2	59.7 ± 0.3
P4	52.9 ± 0.4	57.1 ± 0.2	59.3 ± 0.3
P5	51.9 ± 0.3	55.7 ± 0.2	57.8 ± 0.3
P6	50.0 ± 0.3	53.9 ± 0.2	55.9 ± 0.2
P7	48.9 ± 0.3	52.7 ± 0.2	54.8 ± 0.2
P8	48.2 ± 0.3	51.8 ± 0.2	54.2 ± 0.2
Wing length	67.9^{a} ± 0.4	73.9^{b} ± 0.2	75.4^{b} ± 0.3

cies tended to have relatively longer P4, whilst in *cyanecula* P3 tended to be longer, so the longest primary was in a less distal position in *namnetum* (Table 2). Wing convexity also varied among the three groups ($F_{2,249}$ = 13.1, $P < 0.001$), with *namnetum* subspecies having a relatively more convex wing than *cyanecula* from both C Europe and Iberia (Table 1, Fig. 1B).

Wing length, overall, varied in relation to sex and age (sex: $F_{1,248}$ = 41.3, P < 0.001; age: $F_{1,248}$ = 12.4, P = 0.001; interaction: $F_{1,248}$ = 0.001, P = 0.98), with males having longer wings than females (74.5 ± 0.2, n = 167; 71.3 ± 0.3, n = 85, respectively), as well as adults than young birds (74.8 ± 0.4, n = 65; 72.9 ± 0.2, n = 187, respectively). Wing length (once the sex and age effects were removed) also varied among the three groups, with *namnetum* showing shorter wings ($F_{2,249}$ = 139.2, $P < 0.001$) than *cyanecula* from both C Europe and Iberia (Table 2).

4. Discussion

4.1. Differences between populations

Aerodynamics associated with flight predicts that long-distance migrants have a relatively more pointed and concave wing (Lockwood *et al.* 1998). As expected, significant differences on wingtip shape indices were observed among the three population groups here compared, with *namnetum* having a relatively more rounded wing than *cyanecula* (both from C Europe and Iberia), as well as a more convex wing. It might be partially explained due to the fact that in *namnetum* the longest primary has a less distal position than in *cyanecula*, which in birds in general is related to more rounded wing shapes (Lockwood *et al.* 1998), as well as to more convex ones. Thus, overall, these results might be attributable to different migration distances of populations of Bluethroats in W Europe. This result suggests a rapid evolutionary speed with which migration pressure can act on wing morphology, since the divergence of populations of Bluethroats is very recent (Questiau *et al.* 1998), based on analyses of mitochondrial DNA (for further details see also Egbert & Belthoff 2003).

Because *namnetum* birds are short-distance migrants (Zucca & Jiguet 2002, Collar 2005), a more rounded wing, which allows higher manoeuvrability and hence the ability to reduce the risk to be predated, is expected to give them some advantages (in terms of survival) over other wing morphologies. In contrast, a significantly more pointed wing in *cyanecula* from both C Europe and Iberia supports a wingtip shape adapted to a more energy efficient flight (for further details see Norberg 1989), and typically found in long-distance migrants (Mönkkönen 1995). Indeed, populations of Bluethroats from C Europe show longer migration distances than those from W France (Cramp 1988, Collar 2005). In contrast, wintering areas of birds breeding in Iberia are unknown, due to the lack of recaptures (Hernández *et al.* 2003) and the high similarity with Bluethroats from C Europe (Cramp 1988, Campos *et al.* 2005), which makes it impossible to distinguish between the two *cyanecula* groups we considered here in their wintering areas. Our results may support that Bluethroats from Iberia were long-distance migrants, as a consequence of their pointed and concave wings, as we observed in *cyanecula* from C Europe. Future studies with stable isotopes or other techniques might be of particular relevance to know the biogeography of Bluethroats from W Europe, particularly for the populations from Iberia, for which the knowledge of where their wintering area is found might be of particular relevance to plan efficient conservation policies.

We further observed that wing length was longer in *cyanecula* populations (both from C Europe and Iberia). In contrast to wingtip shape indices, wing length is a size-affected record (indeed, it is sometimes considered to be a good estimate of body size [Gosler *et al.* 1998]). Although commonly associated with migration behaviour, wing length could in our case also reflect differences in body size between the populations, rather than strictly an adaptation to migration, with *cyanecula* subspecies (both from C Europe and Iberia) having a larger size than *namnetum* (Cramp 1988). Birds from C Iberia were captured around six months later than those captured in Fuenterrabía and Villafranca, and the plumage of the former was therefore possibly more abraded than that of the latter. Hence, it remains possible that Bluethroats from Iberia have an even longer mean wing than *cyanecula* from C Europe.

4.2. Differences between sex and age classes

Bluethroat wingtip shape indices are different between the sexes, with the wings of males being more pointed, as well as more concave. These results could suggest that male Bluethroats migrate longer distances than females. However, data on recaptures from abroad in Iberia suggest that females overwinter further south than males (Hernández *et al.* 2003). Alternatively, more pointed and concave wings would allow males to maintain higher flight speeds, and therefore allows them to reach their wintering areas (or their breeding areas, in spring) earlier than females. Early arrival, especially in spring, would be advantageous to males (for further details see Cristol *et al.* 1999). However, in a recent work on wingform and its relationship with flight, Swaddle & Lockwood (2003) observed that in Starlings (*Sturnus vulgaris*) wing morphology was not correlated to flapping-flight speeds. In addition, Ellegren (1990) observed in populations from Sweden that the total migratory speed was best explained by stopover length as well as fuel load, rather than by the speed with which an individual covers a particular distance during flight. The pattern of wingtip shape in male Bluethroats can also be associated to flight during song display (Cramp 1988), as has been documented in other small birds (e.g. Borrás *et al.* 1998). Further study into this pattern is needed.

Peiró (1997) observed no difference in a population of migrating and wintering *cyanecula* Bluethroats in SE Iberia. However, Peiró (1997) used data derived from a PCA on distances of primaries to the wing tip (corrected size effect, according to Senar *et al.* 1994). Thus, these results might suggest that either PCA on primary feathers (e.g. Senar *et al.* 1994, Mönkkönen 1995) is less suitable than SCCA (Lockwood *et al.* 1998) to detect variations of wing morphology. In addition, measuring distances of primaries to the wing tip may accumulate more error than measuring the lengths of primary feathers, and may thus be less suitable for showing small variations in wingtip shape.

We found a lack of differences in wing morphology between age classes, which is in contrast to data on other small European migrants. In Blackcaps (*Sylvia atricapilla*) wing shape in juveniles is reported to be more rounded than in adults (Perez-Tris & Tellería 2001). Possibly, migration in Bluethroats is a strong selective pressure which favours similar shaped wings in all age classes, but further studies are needed to verify this hypothesis.

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Sinirinnan siiven morfologia saattaa heijastella alalajien eroavaa muuttokäyttäytymistä

Pitkän matkan muuttolintujen siivet ovat teräväkärkisemmät ja koverammat kuin lyhyitä matkoja muuttavien lintujen. Tällaisten siipien oletetaan minimoivan lentämisen energiankulutuksen. Tutkimalla siipien morfologian vaihtelua populaatioiden välillä voidaan saada tietoja joidenkin populaatioiden vielä tuntemattomista talvehtimisalueista. Analysoimme kolmen sinirinta populaation siipien muodon vaihtelua Länsi-Euroopassa. Kaikkien näiden populaatioiden muuttomatkat ovat erilaiset ja ne talvehtivat eri paikoissa. Siiven terävyyden mittana käytettiin C2-siivenkärki-indeksiä ja koveruuden mittana C3-siivenkärki-indeksiä (Lockwood *et al.* 1998). Koirailla oli terävimmät ja koverimmat siivet. Alalajilla *namnetum* oli pyöreämmät ja vähemmän koverat siivet sekä lyhyempi muuttomatka kuin *cyanecula*lla. Keski-Euroopan ja Espanjan *cyanecula*-populaatioiden siipien muodossa ei havaittu eroja. Tämä viittaa siihen, että Espanjan sinirintapopulaatio on myös pitkän matkan muuttaja.

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