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Breeding origins and pattern of migration of Bluethroats *Luscinia svecica* wintering from Iberia to Senegal as revealed by stable isotopes

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ABSTRACT

Capsule: Stable isotope analyses reveal some degree of migratory connectivity of Bluethroat populations wintering from Iberia to West Africa.

Aims: To identify the probable breeding origins of Bluethroats wintering from Iberia to Senegal.

Methods: Bluethroat feathers (P1) were sampled from individuals at their wintering areas. These feathers were then analysed for stable H isotopes ($\delta^2\text{H}$). We assigned individual Bluethroats to approximate geographic origin using likelihood-based assignment procedures.

Results: We observed spatial segregation between different Bluethroat populations. At wintering sites north of the Sahara Desert, Bluethroats wintering to the west came from further west origins than those which overwintered to the east. Bluethroats from central-eastern Europe overwintered either within the circum-Mediterranean region or in Senegal. We found no clear evidence supporting a sub-Saharan wintering range for birds breeding in Iberia (*Luscinia svecica azuricollis* subspecies).

Conclusion: North of the Sahara Desert, we found what might be a parallel migration pattern. The apparent lack of *Luscinia svecica namnetum* Bluethroats in Senegal suggests to some extent some kind of leap-frog migration between some *Luscinia svecica cyaneacula* populations and the *L. s. namnetum* subspecies.

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Migratory species can inhabit several widely separated locations over the course of their annual cycle and this has consequences for their effective conservation and limits our understanding of their ecology and evolution (Peach *et al.* 1991, Webster *et al.* 2002, Pain *et al.* 2004, Lok *et al.* 2011). At the population level, strong migratory connectivity occurs when individuals from the same breeding population overwinter together in the same region, distinct from that used by others (e.g. see Zwarts *et al.* 2009). In contrast, weak migratory connectivity implies significant movement from breeding populations to more than one wintering region and vice-versa.

In many cases, ring-recovery data are not sufficient to establish patterns of migratory connectivity when the number of recoveries is low and/or when the recovery rate varies geographically (Korner-Nievergelt *et al.* 2012, Arizaga & Tamayo 2013, Korner-Nievergelt *et al.* 2014). As yet, the use of technologies which directly (e.g. satellite tracking) or indirectly (e.g. light-level-based

geolocators) estimate the geographic position of small migratory birds at various points throughout migration is impractical or requires large sample sizes which are not always easy to collect (Bächler *et al.* 2010, Schmaljohann *et al.* 2012, Tøttrup *et al.* 2012). Alternatively, the use of intrinsic markers such as the stable isotope values of tissues, especially feathers (Hobson & Wassenaar 1997, Chamberlain *et al.* 2000, Yohannes *et al.* 2005, Hobson & Wassenaar 2008) that vary due to the occurrence of isotopic patterns, or 'isoscapes' (West *et al.* 2010), among food webs can occasionally be used to infer approximate origins where tissues were grown. Ideally, the combination of several approaches involving both intrinsic and extrinsic markers will provide the greatest insights.

The Bluethroat (*Luscinia svecica*) is an Holarctic songbird of concern in Europe (Tucker & Heath 2004; Annex I Birds Directive). It breeds from Iberia in Europe, to Alaska and Canada, and spends the winter in southern Europe, Africa or Asia (Collar 2005).

Bluethroats moult at their breeding range (Jenni & Winkler 1994). Of the 11 recognized subspecies, four breed in western and central Europe: *Luscinia svecica cyaneacula* inhabits lowland wetlands from western to eastern Europe (up to southern Russia); *Luscinia svecica namnetum*, breeds on the Atlantic region of France; *Luscinia svecica azuricollis*, found in north-western and central Iberia (Collar 2005); *L. s. svecica*, although breeding mostly in the north and east of Europe, it also occurs at high altitude in several regions in central and eastern Europe (e.g. in the Czech Republic). A recent examination of ring-recovery data for three of these subspecies ringed at their breeding sites in Europe revealed (Arizaga & Tamayo 2013): (1) parallel routes of migration, with Bluethroats breeding in the most easterly regions migrating and wintering the farthest east; (2) a substantial proportion of *L. s. cyaneacula* overwinter in Iberia, suggesting a lack of leap-frog migration; (3) most *L. s. namnetum* apparently overwintering in southwestern Iberia-north-western Africa and (4) the overwintering location of *L. s. azuricollis* remains unknown. However, Arizaga & Tamayo (2013) revealed very few ring-recoveries from Africa, especially from sub-Saharan Africa. This lack of ring-recovery data prevents drawing firm conclusions about migratory connectivity between Africa and Europe. So, in this case, alternative methods, such as the use of intrinsic markers can help us to disentangle these remaining questions (Hobson *et al.* 2004, Hobson *et al.* 2009a, Hobson *et al.* 2012).

Our aim was to unravel the breeding-ground origins of Bluethroats wintering in Iberia and west Africa to Senegal. We used the stable hydrogen ($\delta^2\text{H}$) isotope ratio of feathers ($\delta^2\text{H}_f$) for our study due to its predictable relationship with $\delta^2\text{H}$ in precipitation, which shows a well described and geographically structured variation that can be used to predict the moult origin areas for birds in Europe (Hobson *et al.* 2004, Hobson *et al.* 2013). In particular, $\delta^2\text{H}$ values decrease from south to north, and also from west to east Europe (Hobson *et al.* 2004).

Material and methods

Sampling sites

This study was carried out across much of the winter distribution range of white-throated Bluethroat populations (*L. s. cyaneacula*, *L. s. namnetum*, *L. s. azuricollis*) in Iberia and Africa (Cramp 1988) (Figure 1). Due to the small sample sizes from Morocco, the data from the two localities in this area

were lumped for the analysis, and considered as a single locality (MO; Table 1).

Data collection

Samples were collected during the winters of 2010/11 and 2011/12 (data from each winter were obtained from December to February of the next year; for details see Table 1). We selected this sampling period to ensure that only wintering Bluethroats were sampled (Cramp 1988).

Bluethroats were captured in wetlands, their typical wintering habitat (Cramp 1988), with either mist nets (normally 16 mm-mesh) or spring traps baited with a mealworm *Tenebrio*. Once caught, Bluethroats were ringed (or the ring was read if the bird had previously been ringed) and their sex and age were determined. Birds were aged as either first-year (birds with some juvenile feathers in the greater coverts and/or tertials) or adults (with no juvenile feathers) (Jenni and Winkler 1994). We then measured wing length (method III by Svensson 1996; 0.5 mm accuracy), and extracted the innermost primary feather (P1) from each wing for the stable isotopes analyses.

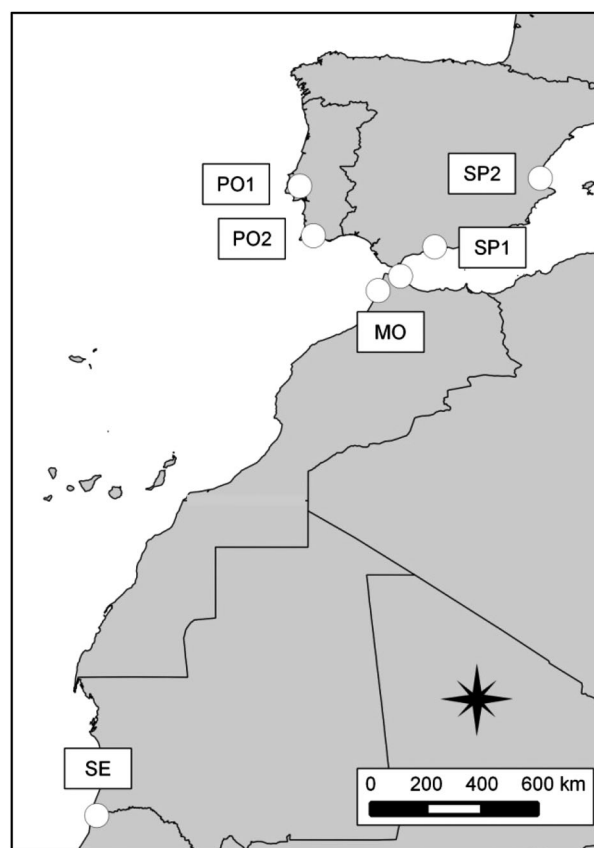


Figure 1. Location of wintering sites where Bluethroats were sampled from Iberia to Senegal. Abbreviations for the sampling localities: SP: Spain; PO: Portugal; MO: Morocco and SE: Senegal.

Table 1. Subspecies assignment for the Bluethroats sampled at each wintering site (*F*: female; *M*: male). Assignments were done using the criteria provided by Neto & Correia (2012). Although Neto & Correia (2012) did not consider the *Luscinia svecica azuricollis* in their paper, the high biometric overlap between *Luscinia svecica cyanecula* and *L. s. azuricollis* allows us to consider that the equation provided by these authors would be valid to separate *Luscinia svecica namnetum* from *L. s. cyanecula*+*L. s. azuricollis*. Site codes: SP: Spain; PO: Portugal; SE: Senegal; MO: Morocco.

(1) Site code	<i>n</i>	First-year		Adults		Unaged		Subspecies (%)	
		<i>F</i>	<i>M</i>	<i>F</i>	<i>M</i>	<i>F</i>	<i>M</i>	<i>L. s. cyanecula</i>	<i>L. s. namnetum</i>
SP1	10	2	4	0	4	0	0	90.0	10.0
SP2	30	8	10	2	10	0	0	76.7	23.3
PO1	10	0	0	4	2	1	3	0	100
PO2	10	4	2	1	3	0	0	70.0	30.0
SE	12	2	4	2	4	0	0	100	0
MO	7	–	–	–	–	–	–	–	–

We used wing length to assign each bird to a subspecies (*L. s. namnetum* or *L. s. cyanecula* +*L. s. azuricollis*), using the criteria outlined by Neto & Correia (2012). Although Neto & Correia (2012) do not provide specific criteria to identify *L. s. azuricollis*, due to the overlap between *L. s. cyanecula* and *L. s. azuricollis* (Campos *et al.* 2005), the criteria used to assign a bird to *L. s. cyanecula* can be equally applied to assign a bird to *L. s. azuricollis*. Bluethroats were classified as *L. s. namnetum* if wing length was ≤ 72 mm (males) or ≤ 70 mm (females). This classification method is reportedly more accurate than formulae based on Bluethroats caught at their breeding areas (Eybert *et al.* 1999), which have worn plumage (Neto & Correia 2012). We were not able to assign subspecies status of Bluethroats in Morocco due to the lack of biometric data. It is reported, however, that both *L. s. cyanecula* and *L. s. namnetum* overwinter in Morocco (Zucca & Jiguet 2002, Arizaga & Tamayo 2013).

Stable isotopes analyses

We used 0.35 mg of each primary feather for the analyses, relative to the vane near the tip in all cases, hence we were internally consistent. All feathers were cleaned of surface oils using a triple 2:1 chloroform:methanol rinse and prepared for stable hydrogen isotope analysis at Environment Canada, Saskatoon, Canada. The $\delta^2\text{H}$ analyses were carried out using the comparative equilibration approach described by Wassenaar & Hobson (2003) using calibrated keratin-isotope reference materials (Environment Canada caribou hoof standard: -197‰ , commercial keratin: -121.6‰ , khudu horn standard: -54.1‰). Measurements of $\delta^2\text{H}$ were performed on H_2 derived from the high-temperature flash pyrolysis (1350°C) of the feathers with a HEKAtech HT-O AnalyzerTM linked to an Elementar IsoprimeTM continuous-flow isotope-ratio mass spectrometer. All $\delta^2\text{H}$ values were given in delta notation, in units per mil (‰), and

normalized on the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation scale. Within-run ($n = 5$) replicates of keratin standards typically yielded variance (sd) of 2‰.

Statistical analyses

We tested for between-site variation in $\delta^2\text{H}_f$ using robust regression with the ‘MASS’ package (Venables & Ripley 2002) within the R statistical computing environment (R Core Team 2014).

We assigned individual Bluethroats to approximate geographic origin using likelihood-based assignment procedures. To that end, the GIS-based isoscape of the amount-weighted, mean annual $\delta^2\text{H}$ in precipitation (Bowen *et al.* 2005), was converted into a predicted $\delta^2\text{H}_f$ isoscape using the transfer function reported in Procházka *et al.* (2013). The resulting feather isoscape was further restricted to fall solely within the known breeding range of *L. s. cyanecula*, *L. s. namnetum* and *L. s. azuricollis* (digitized from the European Bird Census Council) using a Spatial AnalystTM ‘extract values by mask’ operation in ArcGIS version 10.1 (ESRI, Redlands, CA). The resulting isoscape was then converted to ASCII raster format for all subsequent analyses.

We used normal probability density functions to assess the likelihood that any cell (pixel) within the $\delta^2\text{H}_f$ isoscape represented a potential origin for an individual by comparing the observed $\delta^2\text{H}_f$ value with those predicted by the $\delta^2\text{H}_f$ isoscape (Hobson *et al.* 2009b). The normal probability density functions were parameterized by treating the isoscape predicted $\delta^2\text{H}_f$ value at each cell as the mean and variance was estimated based upon the sd of the residuals (10.7‰) from the transfer function reported in Procházka *et al.* (2013). Following Wunder (2007, 2010), each individual was assigned to its most likely moult origin area by selecting the isoscape pixels associated with the upper 67% of probabilities (consistent with 2:1 odds of being correct versus incorrect) and classifying these as

likely (1) origin for the sample, while all others were classified as unlikely (0) resulting in one binary surface per individual. We then summed the individual surfaces to depict the geographic distribution of origin of all individuals within a given sampling location following Hobson *et al.* (2009b).

All assignments were completed using scripts from Van Wilgenburg & Hobson (2011) which employ functions for the 'raster' package (Hijmans & Van Etten 2012) within the R (v. 3.1.1) statistical computing environment (R Core Team 2014).

Results

Overall, $\delta^2\text{H}_f$ values did not vary between sex classes, but varied between age classes, and there was no significant interaction between the two factors (Bluethroats of unknown age omitted; Sex: $F_{1,63} = 0.710$, $P = 0.403$; Age: $F_{1,63} = 4.373$, $P = 0.041$; Sex \times Age: $F_{1,63} = 0.103$, $P = 0.750$). Adults showed slightly higher isotopic values (mean \pm sd = $-62.5 \pm 22.1\text{‰}$, $n = 31$) than first-year birds ($-76.4 \pm 28.6\text{‰}$, $n = 36$).

Wintering Bluethroats showed significant variation in $\delta^2\text{H}_f$ among sampling sites ($F_{6,72} = 436.2$, $P < 0.001$). Samples collected in Morocco and Portugal were the most enriched in ^2H (Figure 2), with the most enriched samples coming from Morocco (mean \pm sd: $-45.0 \pm$

7.7‰) and the most depleted ones in ^2H coming from Senegal ($-90.6 \pm 11.1\text{‰}$) and Spain (SP1 $-90.8 \pm 14.4\text{‰}$; and SP2 $-74.0 \pm 13.7\text{‰}$).

Consistent with between-site variation in $\delta^2\text{H}_f$ (Figure 2), our assignment model placed Bluethroats to different origins depending on winter location (Figure 3). Bluethroats captured in Spain mostly came from central and eastern Europe, but the Bluethroats caught at SP1 were isotopically consistent with likely origins further to the east than those from SP2. Bluethroats wintering in Portugal and Morocco were mostly assigned to likely origin regions in western France and Iberia, with only a few birds being potentially consistent with origins in central and eastern Europe (Figure 3). Finally, Bluethroats caught in Senegal were isotopically consistent with likely origins over central-eastern Europe.

Based on biometrics, the proportion of *L. s. namnetum* ranged from 100% in one of the Portuguese sites to 0% in Senegal (Table 1). In the rest of the sites the proportion of *L. s. namnetum* was always $\leq 30\%$. Overall, we found no significant correlation between $\delta^2\text{H}_f$ values and wing length ($r = -0.179$, $P = 0.135$, $n = 71$). Similarly, Bluethroats classified as *L. s. namnetum* did not show different mean isotopic signatures than *L. s. cyanecula* ($t = 0.943$, $df = 69$, $P = 0.349$).

Discussion

Bluethroats wintering from Iberia to Senegal showed substantial between-site variation in $\delta^2\text{H}_f$, with the lowest values reported in Bluethroats wintering in Senegal, and the highest detected in Morocco. This variation was significant and supports wintering spatial segregation between populations of different origin.

Within Iberia, apparently one of the chief wintering areas for *L. s. cyanecula* and *L. s. namnetum* (Arizaga & Tamayo 2013), Bluethroats caught to the east were also more likely to come from further east in Europe than those wintering in regions further to the west. As in a previous study using ring-recovery data (Arizaga & Tamayo 2013), this result supports a population-specific longitudinal distribution within Iberia in winter parallel to that existing on the breeding quarters. This spatial pattern is similar to that found for other passerines birds during the autumn migration period in Iberia (Andueza *et al.* 2013), or during the winter period in the Sahel (Zwarts *et al.* 2009). Thus, Bluethroats seem to minimize migration distance and use the most direct routes between their breeding and non-breeding areas, at least for the fraction spending the winter within the western circum-Mediterranean region.

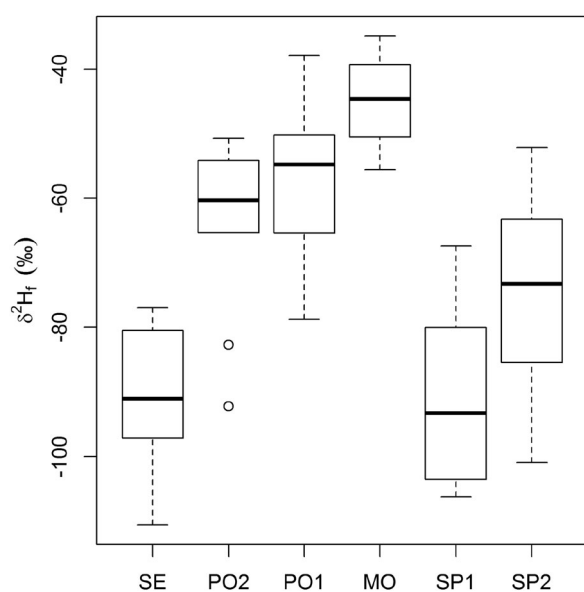


Figure 2. Variation in $\delta^2\text{H}$ of feathers obtained from Bluethroats wintering in Senegal (SE: $n = 12$), Portugal (PO1: $n = 10$; PO2: $n = 10$), Morocco (MO: $n = 7$) and Spain (SP1: $n = 9$; SP2: $n = 30$) corresponding to those sites depicted in Figure 1. Sites are sorted from westernmost (left) to easternmost (right). Boxes depict the 25th–75th percentile (interquartile) range of the data and the horizontal line within each box is the median. Whiskers extend 1.5 times beyond the interquartile range; circles denote outliers.

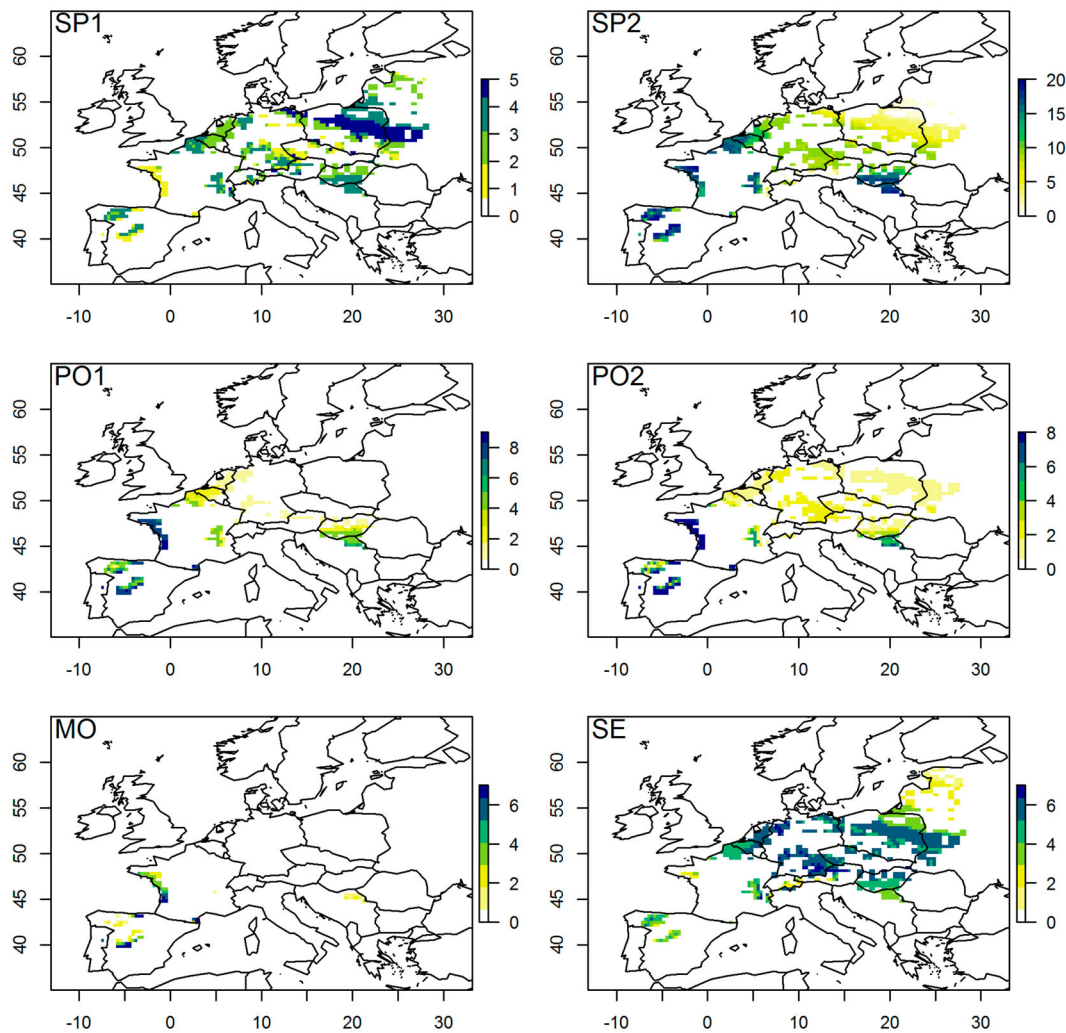


Figure 3. Assessment of the potential origin breeding quarters of Bluethroats caught at a number of wintering places from Iberia to Senegal. Wintering site codes as shown in Table 1. Legends refer to number of individual Bluethroats assigned to each pixel with a 2:1 odds ratio (see Methods).

Between 30% and 100% of the Bluethroats caught in Iberia belonged to the *L. s. namnetum* subspecies. Our isotopic assignments to origins were largely consistent with the breeding distribution of this subspecies (i.e. in the Atlantic region of France; Cramp 1988, Zucca & Jiguet 2002), especially if we take into account the results from Portugal. We note that a number of Bluethroats sampled in eastern Iberia (SP2) were consistent with origins in western France. Previous morphometric studies suggest that *L. s. namnetum* is very rare in eastern Iberia (Arizaga *et al.* 2006a). Isotopically, the breeding quarters in western and eastern France have similar values (Hobson *et al.* 2004), but the Bluethroats breeding in western France belong to *L. s. namnetum* and the ones from eastern France to *L. s. cyanecula* (Zucca & Jiguet 2002). For this reason, assignment to subspecies helped us to clarify ambiguous assignments based on the isotope approach. In contrast, the

assignment of some birds from Portugal to origins located in central-eastern Europe also suggests the occurrence of some *L. s. cyanecula* Bluethroats wintering in westernmost Iberia, a result consistent with other studies based on morphometric data (Correia & Neto 2013).

Wing length- and shape-based biometric analyses suggested that Bluethroats breeding in Iberia might spend the winter in tropical Africa (Arizaga *et al.* 2006b), but this was not supported by the isotopic analyses. According to our model, some birds spending the winter in Iberia very likely originated from Iberia. Again, however, our model could not separate potential origins in western France from Iberia, so this result must be considered very cautiously.

Birds from Senegal showed isotopic values similar to those found in Spain, supporting a further north/eastern origin than Bluethroats wintering in Portugal

or Morocco. This result is also consistent with biometric data assigning these birds to the *L. s. cyaneacula* subspecies. Bluethroats caught in Morocco were largely assigned similar origins to those sampled in Portugal, with the exception that a few individuals from Portugal were potentially consistent with central and eastern Europe. Although subspecies of these birds in Morocco were not identified, previous work has shown that at least some might be *L. s. namnetum* (Zucca & Jiguet 2002), although *L. s. cyaneacula* also winter within the region (Arizaga & Tamayo 2013). Morocco, chiefly western Morocco along coastal Atlantic marshes (Arizaga & Tamayo 2013), might host a subspecies assemblage similar to Portugal. Our results support this pattern, and also agree with previous studies that also suggested this pattern (Zucca & Jiguet 2002; Correia & Neto 2013).

Also interesting is the fact that some populations that overwinter in Iberia or Africa were assessed to breed in areas of central-eastern Europe (these birds would belong to the subspecies *L. s. cyaneacula*), whilst at the same time it is reported that *L. s. svecica* birds from these origin areas overwinter in Asia (Lislevand *et al.* 2015). Thus, central-eastern Europe is a geographic region where birds (or subspecies) with different migratory behaviour breed in close proximity.

In conclusion, $\delta^2\text{H}_f$ measurements support spatial segregation among different Bluethroat populations in Europe. North of the Sahara Desert, we found what might be a parallel migration pattern with Bluethroats wintering to the west having natal origins from further west than those wintering to the east. Birds wintering in Senegal were more likely to originate from central-eastern Europe, indicating some kind of leap-frog migration, at least of some *L. s. cyaneacula* populations in relation to *L. s. namnetum*. We found no clear evidence supporting a sub-Saharan wintering range for birds breeding in Iberia (*L. s. azuricollis* subspecies).

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