Connectivity patterns and key non–breeding areas of white–throated bluethroat (*Luscinia svecica*) European populations

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Abstract

*Connectivity patterns and key non–breeding areas of white–throated bluethroat (*Luscinia svecica*) European populations.*— Using ring recovery data from the EURING databank, the aims of this study were: (1) to identify the chief migration and wintering areas of white–throated bluethroat European subspecies, *L. s. namnetum*, *L. s. cyanecula* and *L. s. azuricollis*, (2) to evaluate the degree of connectivity between breeding and non–breeding regions and determine the migration patterns of each subspecies, and (3) to evaluate whether recovery data are sufficient to answer the previous questions adequately. Most of the recoveries were obtained during the autumn migration period (n = 155, 68.9%), followed by winter (n = 49, 21.8%) and spring (n = 21, 9.3%). For *L. s. azuricollis*, we did not find any ring recoveries at more than 100 km in autumn or spring, and there were none at all in winter. All analyses thus relate to *L. s. cyanecula* and *L. s. namnetum.* Both subspecies move across a NE–SW axis from their breeding to their wintering areas within the circum–Mediterranean region, mainly in Iberia, following population–specific parallel migration routes. *L. s. namnetum* mainly uses the Atlantic coastal marshes from France to south–western Iberia, where the chief wintering areas are found. *L. s. cyanecula*, however, uses both Atlantic and Mediterranean wetlands in autumn, but only those in the Mediterranean in spring, thus giving rise to a loop–migration pattern. Telescopic migration was demonstrated for *L. s. cyanecula.* Recovery data were insufficient to identify in detail the entire wintering range for all white–throated bluethroat European populations. Technologies such as the use of geolocators will play a relevant role in this scenario.

Key words: EURING databank, Mediterranean region, Migration and wintering, Recovery data, Wetlands.

Resumen

*Patrones de conectividad y principales áreas de invernada de las poblaciones europeas del pechiazul (*Luscinia svecica*).*— Utilizando los datos de recaptura recopilados en la base de datos de EURING, los objetivos del estudio fueron: (1) determinar las principales rutas migratorias y áreas de invernada de las subespecies de pechiazul *L. s. namnetum, L. s. cyanecula* y *L. s. azuricollis*; (2) evaluar el grado de conectividad entre las zonas de reproducción y las áreas de invernada, y determinar los patrones de migración de cada subespecie y (3) evaluar si los datos de recaptura son suficientes para responder adecuadamente a las preguntas anteriores. La mayor parte de las recapturas se obtuvieron durante el período de migración en otoño (n = 155; 68,9%), seguido del invierno (n = 49; 21,8%) y la primavera (n = 21; 9,3%). No se obtuvo ninguna recaptura de *L. s. azuricollis* en más de 100 km en otoño ni en primavera, ni tampoco en todo el invierno. Por consiguiente, todos los análisis hacen referencia a *L. s. cyanecula* y *L. s. namnetum*. Ambas subespecies de desplazan a lo largo de un eje NE–SO desde las zonas de reproducción hasta las zonas de invernada de la región circunmediterránea, principalmente en la península ibérica, y siguen rutas migratorias paralelas que son específicas de cada población. *L. s. namnetum* utiliza principalmente las marismas del Atlántico desde Francia hasta el suroeste de la península ibérica, donde se encuentran las principales zonas de invernada. Sin embargo, *L. s. cyanecula* utiliza los humedales tanto del Atlántico como del Mediterráneo en otoño, pero solo los del Mediterráneo en primavera; en consecuencia, se establece un patrón de migración en bucle. Se demostró que el patrón migratorio de *L. s. cyanecula* es de tipo telescópico. Los datos de recaptura fueron insuficientes para determinar con precisión la distribución invernal de todas las poblaciones europeas de pechiazul. Las tecnologías como la utilización de geolocalizadores desempeñarán una función fundamental en este contexto.

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Introduction

The term connectivity refers to the degree to which breeding and non–breeding areas used by a population of a migrant species are connected (Webster et al., 2002). High or strong connectivity occurs when all/most of the individuals from a population overwinter together in an area well–differentiated from that used by individuals from other populations (Swarth, 1920; Madsen et al., 1999; Chamberlain et al., 2000; Procházka et al., 2008). In contrast, connectivity is weak when individuals from several populations coexist in sympatry in the same wintering area (McGrady et al., 2002). Understanding connectivity patterns provides key clues about the spatio–temporal distribution range of birds during the non–breeding season and it has direct implications on population dynamics (Peach et al., 1991; Baillie & Peach, 1992; Szép, 1995; Newton, 2004) and conservation (Pain et al., 2004; Julliard et al., 2006).

Studies on the connectivity patterns of European passerines have targeted mainly Afro–tropical winter quarters (e.g., Hill, 1997; Schäffer et al., 2006; Procházka et al., 2008; Zwarts et al., 2009), while less attention has been paid to the circum–Mediterranean region (although we have exceptions to this rule; e.g., see Newton, 1972; Bairlein, 2001) in spite of its importance as one of the chief wintering areas for several passerine species (Cramp, 1988, 1992; Cramp & Perrins, 1994b, 1994a). The bluethroat (*Luscinia svecica*) is a polytypic Holarctic passerine, breeding from Iberia in West Europe to Alaska and Canada. Two to three white–throated subspecies are recognized as breeding in Europe (Collar, 2005): *L. s. namnetum* breeds in the Atlantic wetlands of France and migrates along the coast of Northern Iberia (Arizaga et al., 2006a) to overwinter mainly in Portugal and Northern Africa (Zucca & Jiguet, 2002); *L. s. cyanecula* breeds from the east of France to Russia, and during the winter it is distributed over a wide geographic area ranging from Southern Europe to tropical Africa (Cramp, 1988); *L. s. azuricollis* breeds only in Iberia, and it is a subspecies well differentiated from the rest, as shown by genetic studies (Johnsen et al., 2006). The winter quarters of *L. s. azuricollis* remain to be discovered (Arizaga et al., 2006b, 2011b). Apart from this general distribution pattern, the degree of connectivity and the identification of key non–breeding areas for these subspecies have not been analysed, in part because the current data come from partial studies carried out in relatively small areas (Tellería et al., 1999; Zucca & Jiguet, 2002; Bønløkke et al., 2006; Spina & Volponi, 2009). Accordingly, there is still a need for a complete overview of how the breeding and non–breeding areas of white–throated European bluethroat populations are connected and where the chief stopover sites during autumn and spring migrations are placed considering a continental or even an inter–continental scale. The compilation of more ring recoveries in recent years could help to fill these gaps in knowledge.

There are normally two main non–breeding longitudinal distribution patterns in migrants: parallel and non–parallel (centrifuge and fan) migrations. If bluethroat populations show parallel migration patterns (indicating strong connectivity between breeding and non–breeding regions), longitudinal geographic location at breeding quarters should be positively correlated with longitudinal geographic location at non–breeding regions, either during the migration period or in winter (e.g., Zwarts et al., 2009). The other patterns would result in no relationship between geographic location at breeding and non–breeding quarters.

Latitudinally, three chief patterns have been identified: leap–frog, chain, and telescopic migrations (Salomonsen, 1955; Newton, 2008). In the case of leap–frog migration, where northern breeders spend the winter in areas further south than those used by southern breeders, latitude of breeding origin should be negatively correlated with latitude of winter quarters. In this case, latitude of breeding origin should also be positively correlated with distance to winter location, as migrants breeding in the north must cover a much longer distance than those that breed further south. In contrast, in the case of chain migration where northern breeders also overwinter in areas further north than southern breeders, the latitude of breeding origin should correlate positively with latitude at winter quarters and not with distance to winter location, since populations occur in winter in the same latitudinal sequence as when occupying their breeding areas. Overall, both patterns will indicate strong connectivity, as each population occupies different wintering quarters. Alternatively, in the case of telescopic migrations, where populations occur in sympatry in the same wintering area, none of these correlations would be expected, but the latitude of breeding origin should be correlated with distance to winter quarters, as migrants coming from more distant regions will have to travel further to reach a sympatric wintering area shared with populations from closer places of origin. In this scenario, connectivity will be weak.

Identifying main wintering areas is basic but insufficient when dealing with migrant species whose fitness could also depend on key sites for stopping–over (Fransson et al., 2005; Julliard et al., 2006). Such key sites can differ seasonally, such as in the case of loop migrations, when the migratory route to reach the winter quarters varies from that used to go to breeding quarters (Berthold, 2001). Within the Africa–European system of bird migrations, migrants in spring tend to displace themselves via routes which are further east than those used during autumn (Bairlein, 2001). This, however, has not been tested for all species and the causes underlying this strategy are still not fully understood.

Using ring recovery data from the EURING databank, our aims here were to evaluate the degree of connectivity between breeding and non–breeding regions, and determine the migration patterns used by each bluethroat subspecies, including the detection of a possible seasonal change in the use of particular routes. For *L. s. azuricollis*, we did not find a single ring recovery at more than 100 km in autumn or spring, and there was norecovery at all in winter. All analyses henceforth will be relative to *L. s. cyanecula* and *L. s. namnetum*.

Material and methods

Data collection

The data used in this study were obtained from the EURING databank (ring recoveries of bluethroats ringed from 1926 to 2009). We only used data of blue-throats ringed in their breeding areas and recaptured during the autumn or spring migrations or during the winter, or *vice versa*. In the cases where the number of recoveries per bird and period were > 1 (*e.g.*, a bird recaptured three times at the same stopover site during the autumn migration period), we only consi-dered one of the recoveries. If such recoveries were obtained at different locations, then the most distant location was considered for the analysis. When a single bird was recovered in different periods (*e.g.*, a bird is recaptured during the autumn migration period and also during the winter period), a recovery per period was considered (*i.e.* in the last case two recoveries were considered, one breeding–autumn, and the other breeding–winter). This resulted in a sample of 833 recoveries. The phenological periods were defined as follows (based on Cramp, 1988): breeding (May–Jul), autumn (Aug–Nov), winter (Dec–Feb), spring (Mar–Apr). From the 833 recoveries we considered the following for the analyses: (1) recovery data obtained at > 100 km from breeding site for the recoveries made in autumn and spring; (2) all the recoveries made during winter. We differentiated these periods because birds captured during the autumn or spring migration period could still be at (autumn) or have already arrived at (spring) their breeding sites, so these birds do not reflect the true geographic po-sition during migration period. In contrast, bluethroats captured during the winter are truly wintering birds; in this case we cannot reject having resident bluethroat populations/individuals, which move a null or negligible distance. Some bluethroats captured in winter could be birds in active migration.

Subspecies were identified using the areas where ring recoveries were obtained during the breeding period. Thus, bluethroats breeding in the Atlantic wet-lands of France from Arcachon to Mont St. Michel were considered as *L. s. namnetum* (Zucca & Jiguet 2002), bluethroats breeding in Iberia as *L. s. azuricollis,* and the rest as *L. s. cynaecula* (Cramp, 1988).

Statistical analyses

Simple linear correlations were used to test whether the location (longitude and latitude) of bluethroats at their breeding areas was correlated with the location at their non–breeding areas during autumn, winter and spring. Similarly, correlations were also used to test a positive relationship of breeding origin location with distance to winter quarters.

We used 95% kernel polygons to identify the main non–breeding quarters of *L. s. cyanecula*, us-ing ArcGIS 9.2 ESRI. This analysis was carried out only on *L. s. cyanecula* since sample sizes for the other subspecies were too small to allow us to build these polygons.

Table 1. Number of recoveries of bluethroats of *L. s. namnetum* and *L. s. cyanecula* subspecies between breeding and non–breeding periods. (Source: EURING databank.)

Tabla 1. Número de recapturas de las subespecies de pechiazul L. s. namnetum *y* L. s. cyanecula *entre los períodos reproductivos y los no reproductivos. (Fuente: base de datos EURING.)*

Period	All recoveries	Recoveries > 100 km
Autumn	470	155 (33.0%)
Winter	49	48 (98.0%)
Spring	184	21 (11.4%)

We used circular statistics to analyze the spatial distribution of recovery data. All angles were calcu-lated from breeding to non–breeding (autumn, winter or spring) location. We used a Watson–Williams *F*–test to test between–period variations in mean migratory axis of recoveries plus a Mardia–Watson–Wheeler test to assess differences in spatial distribution pattern between periods (Arizaga et al., 2010b).

Circular statistics were carried out using Oriana 3.0 software. SPSS software was used for the remaining statistical analyses. All means are given ± SE.

Results

Overall, we obtained a data set with most recoveries made during the autumn migration period ($n = 155$, 68.9%), followed by winter ($n = 49$, 21.8%) and spring ($n = 21$, 9.3%) (table 1). Most of the recoveries during the autumn and spring migrations were obtained at less than 100 km from breeding sites (table 1), thus indicating that many recoveries from this period were birds still remaining (autumn) or already present (spring) in their breeding areas. In contrast, during the winter, only one bird was recaptured at less than 100 km from its breeding location (table 1), indicating that most blue-throats left their breeding areas to spend this period in more distant regions (mean: 1,517.2 ± 86.3 km).

The distribution (longitude and latitude) of bluethroats during the non–breeding period was positively cor-related with their distribution range during the breed-ing period (table 2). Longitudinally, we observed that bluethroats from regions further east also appeared further east outside the breeding and *vice versa*, either in autumn, winter (with *r* coefficients > 0.6) or, especially, in spring (*r* > 0.8; table 2), thus support-ing parallel migration patterns, more marked during the spring migration period. Furthermore, bluethroats from regions further east appeared in areas further north both in autumn and spring, although this might

Table 2. Linear correlations used to test the relationship between breeding and non–breeding geographic distribution of *L. s. namnetum* and *L. s. cyanecula* bluethroats. Recoveries obtained at less than 100 km during the autumn and spring migration periods were excluded to avoid considering birds still in their breeding areas.

Tabla 2. Correlaciones lineales utilizadas para comprobar la relación entre la distribución geográfica de los períodos reproductivo y no reproductivo de las subespecies de pechiazul L. s. namnetum *y* L. s. cyanecula. *Para no incluir las aves que aún permanecían en sus zonas reproductivas, se excluyeron las recapturas obtenidas a menos de 100 km durante los períodos de migración de otoño y primavera.*

Period	n	Breeding latitude		Breeding longitude	
		r	*p*	r	*p*
All subspecies					
Non–breeding latitude					
Autumn	155	+0.289	**< 0.001**	+0.250	**0.002**
Winter	49	–0.258	0.074	+0.234	0.105
Spring	21	+0.337	0.135	+0.702	**< 0.001**
Non–breeding longitude					
Autumn	155	+0.187	**0.020**	+0.686	**< 0.001**
Winter	49	–0.040	0.784	+0.659	**< 0.001**
Spring	21	+0.184	0.424	+0.877	**< 0.001**
L. s. namnetum					
Non–breeding latitude					
Autumn	31	+0.380	**0.035**	–0.249	0.177
Winter	6	–0.416	0.413	+0.405	0.426
Spring	2	–	–	–	–
Non–breeding longitude					
Autumn	31	+0.155	+0.406	–0.008	0.966
Winter	6	+0.432	+0.393	–0.419	0.409
Spring	2	–	–	–	–
L. s. cyanecula					
Non–breeding latitude					
Autumn	124	+0.315	**< 0.001**	+0.299	**0.001**
Winter	43	–0.269	0.081	+0.359	**0.018**
Spring	19	+0.239	0.325	+0.683	**0.001**
Non–breeding longitude					
Autumn	124	–0.045	0.617	+0.663	**< 0.001**
Winter	43	–0.340	**0.026**	+0.601	**< 0.001**
Spring	19	–0.155	0.526	+0.846	**< 0.001**

just be due to the fact that northern breeders also tended to breed further east ($r = 0.261$, $p < 0.001$, $n = 224$). Considering the two subspecies separately, such patterns were confirmed only for *L. s. cyanecula* (table 2). Latitudinally, bluethroats breeding further north were also located in areas further north, and east, in autumn, but not in winter or spring (table 2). This pattern was maintained when the two subspecies were considered separately.

The distance from breeding to winter quarters was positively correlated to breeding latitude (latitude: $r = 0.612$, $p < 0.001$; longitude: $r = –0.049$, $p = 0.738$, $n = 49$), indicating that bluethroats breeding in northern regions migrated a longer distance than those from areas further south. The breeding latitude was not correlated with the winter latitude (table 2), so bluethroats breeding in areas further north did not overwinter further to the south than those breeding
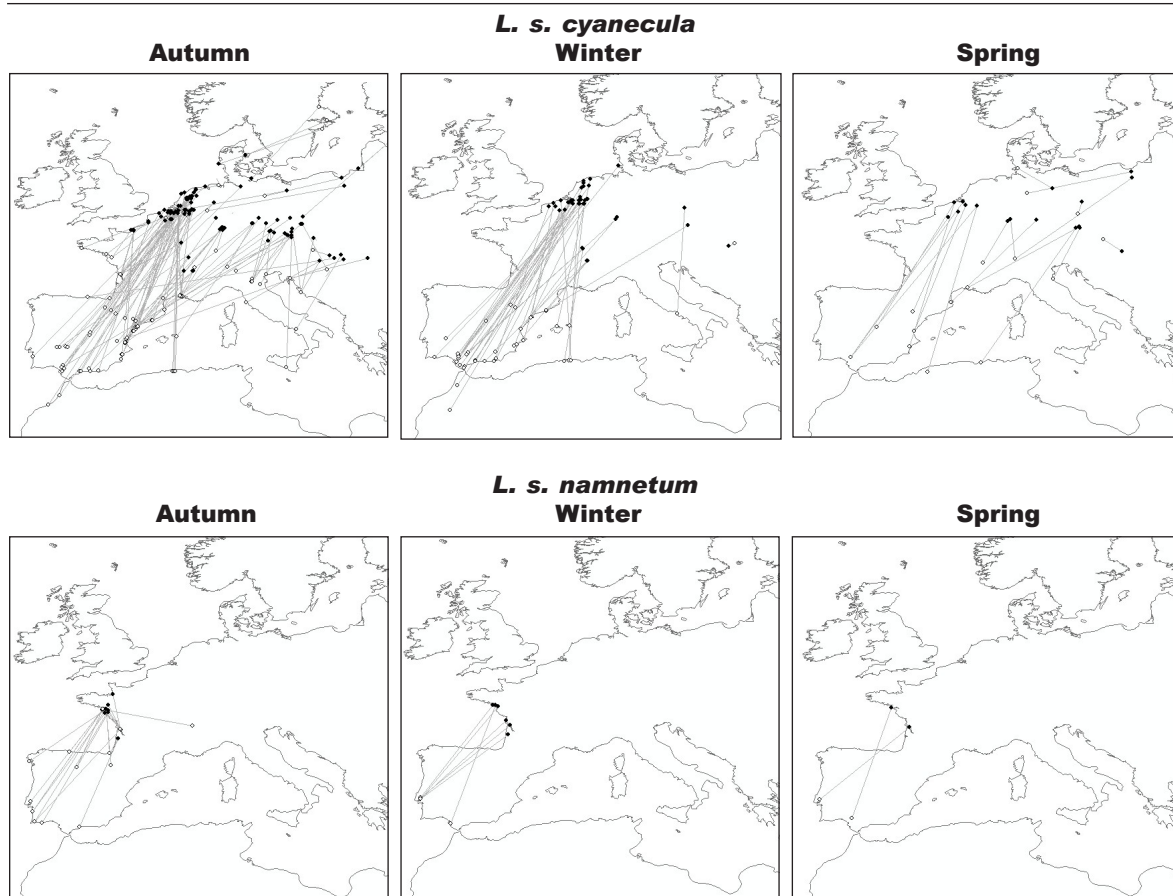
L. s. cyanecula

| Autumn | Winter | Spring |

L. s. namnetum

| Autumn | Winter | Spring |

Fig. 1. Recoveries of *L. s. cyanecula* and *L. s. namnetum* captured / recaptured during the breeding period and recaptured/captured during the non–breeding period in autumn, winter, and spring. Sample sizes are shown in table 2. In *L. s. cyanecula*, we have not shown the single winter relating to a bird ringed in The Netherlands and recaptured in Senegal.

Fig. 1. Recapturas de L. s. cyanecula *y* L. s. namnetum *capturadas / recapturadas durante el período reproductor y recapturadas/capturadas durante el período no reproductor en otoño, invierno y primavera. Los tamaños muestrales se indican en la tabla 2. En* L. s. cyanecula *no hemos mostrado la única recaptura de invierno de un ave que se anilló en los Países Bajos y se recapturó en Senegal.*

in areas further south. Only a single recovery was found south of the Sahara and this was a bird ringed in The Netherlands.

Most winter recoveries (*n* = 39, equivalent to 79.6%) appeared in Iberia, both in the case of *L. s. namnetum* (100%) and *L. s. cyanecula* (76.7%) (fig. 1). *L. s. namnetum* was concentrated in areas within south–western Iberia whereas *L. s. cyanecula* tended to overwinter in south–eastern and eastern Iberia. There were also additional recoveries of this subspecies in northern Africa (Morocco). In both subspecies bluethroats mostly overwintered in coastal regions, especially on the Mediterranean and southern Atlantic coasts of Iberia (fig. 1).

The small sample sizes obtained for *L. s. namnetum* preclude us from making a firm conclusion with regard

to the possible use of different routes in autumn and spring (table 2; fig. 1), but this was not the case for *L. s. cyanecula* (table 2; fig. 1). In this subspecies, during autumn, we observed a high number of recoveries on both the Atlantic and the Mediterranean coasts, especially in France and in the east of Iberia (fig. 2). Sites with particularly high concentrations of recoveries were the Arcachon bay area and the Ebro basin and delta, together with the Mediterranean wetlands from La Camargue in France, and Doñana and its surroundings in Iberia (fig. 2). In spring, however, not a single recovery was obtained on the Atlantic side apart from the Doñana and surrounding areas. The remainder were all related to the Mediterranean. As in autumn, bluethroats in spring mainly used the wetlands existing from Doñana to La Camargue (fig. 2).
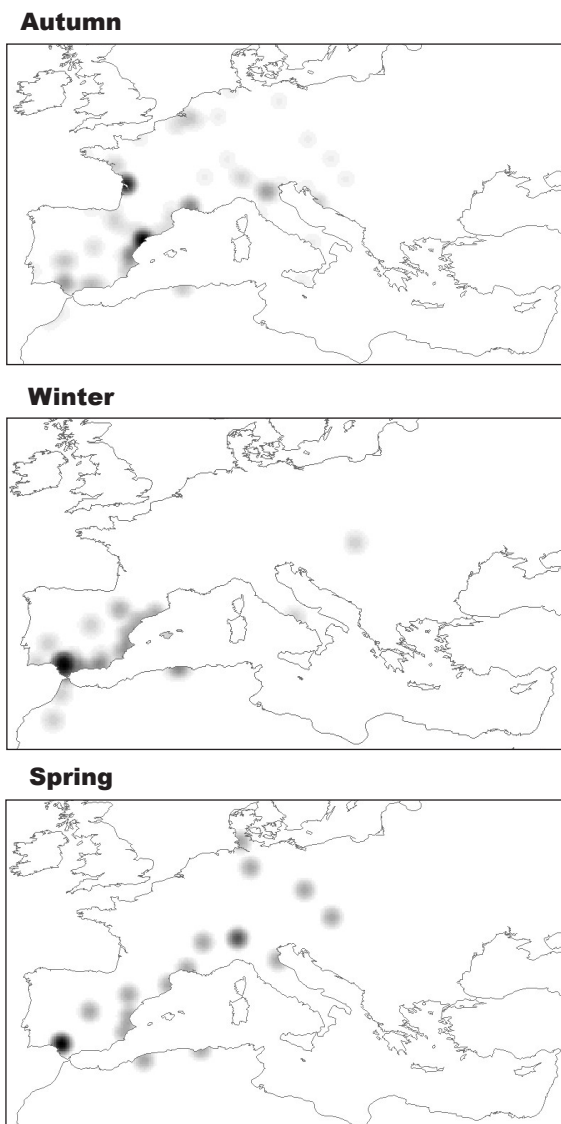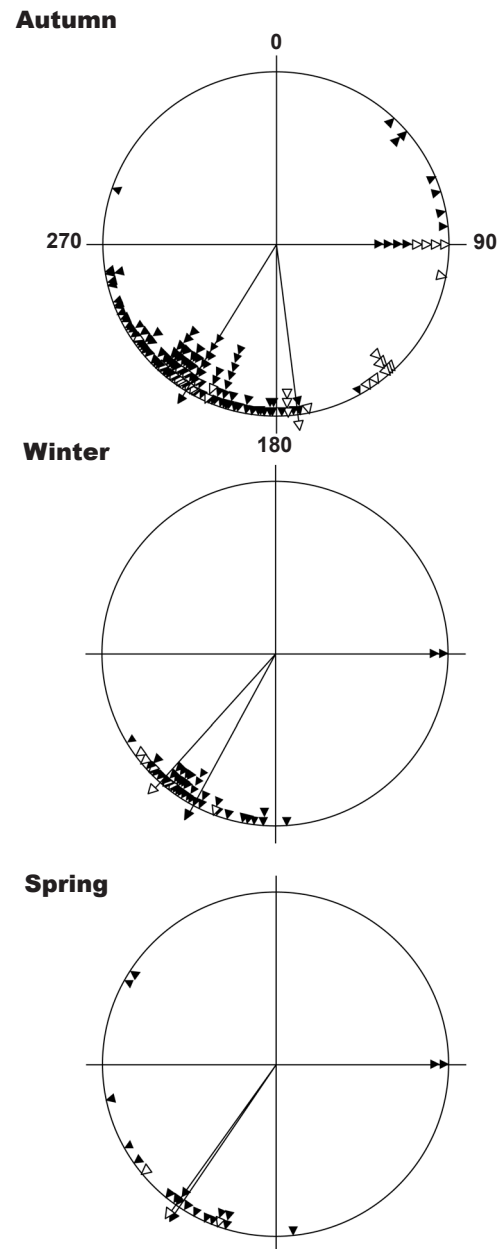
Autumn

Winter

Spring

Fig. 2. 95% kernel polygons obtained from recovery data of *L. s. cyanecula* between breeding and non–breeding regions in autumn, winter and spring.

Fig. 2. Funciones de kernel al 95% obtenidas a partir de los datos de recaptura de L. s. cyanecula *entre las regiones reproductivas y no reproductivas en otoño, invierno y primavera.*

Autumn

Winter

Spring

△ *L. s. namnetum*
▲ *L. s. cyanecula*

Fig. 3. Row data and mean migratory direction of bluethroats captured during the non–breeding period at a distance of more than 100 km from breeding localities. Angles established from breeding to non–breeding localities.

Fig. 3. Datos no elaborados y dirección media de la migración de los pechiazules capturados durante el período no reproductor a una distancia de más de 100 km de las localidades de reproducción. Ángulos establecidos desde las localidades reproductivas y a las no reproductivas.

Overall, bluethroats moved along a NE–SW axis between their breeding and non–breeding areas, without significant differences between periods (Watson Williams test: $F_{2,221}$ = 0.698, p = 0.499; mean vector: 206.9 ± 2.7º, n = 224; data considered here: movements > 100 km). However, dispersion of data differed between periods (Mardia test: W = 11.936, p = 0.018). In particular, recovery data from winter were less dispersed than during autumn and almost

significantly less than during spring (pairwise comparisons: autumn–winter, $W = 10.803$, $p = 0.005$; autumn–spring, $W = 0.416$, $p = 0.812$; winter–spring: $W = 5.087$, $p = 0.079$; fig. 3). By subspecies, the migratory direction was observed to differ subspecifically in autumn (Watson Williams test: $F_{1,153} = 19.224$, $p < 0.001$; L. s. namnetum, $n = 31$; L. s. cyanecula, $n = 124$), but not in winter ($F_{1,46} = 1.655$, $p = 0.205$; L. s. namnetum, $n = 6$; L. s. cyanecula, $n = 42$) or spring ($F_{1,19} = 0.002$, $p = 0.965$; L. s. namnetum, $n = 2$; L. s. cyanecula, $n = 19$; fig. 3). The small sample sizes for L. s. namnetum in winter and spring should be noted, however.

Discussion

We used ring recovery data from the EURING databank to identify the main migration and wintering areas of white–throated bluethroat subspecies breeding in Europe, and also to understand the connectivity patterns between breeding and non–breeding grounds of each subspecies. Of the three white–throated bluethroat subspecies with recovery data available in the EURING databank, we only obtained valuable data for two of them: L. s. namnetum and L. s. cyanecula.

Most L. s. namnetum recoveries were spread across the Atlantic coasts of France and Iberia, thus confirming that this subspecies uses a very specific, narrow corridor to move from its breeding area on the Atlantic side of France to its wintering area on the south–western coast of Iberia (Zucca & Jiguet, 2002). Outside this Atlantic scenario, L. s. namnetum should be regarded as a rarity (Arizaga et al., 2006a). If we consider L. s. cyanecula, it seems to move across broad fronts, although some degree of connectivity between breeding and non–breeding grounds exists. The clearest, most marked result was that L. s. cyanecula bluethroats breeding further east were also located in regions further east during the autumn migration period, winter and spring. This result highlights the occurrence of parallel routes of migration among L. s. cyanecula populations, so that migrants breeding in adjacent places follow the same (SW in this case) main direction but do not exhibit high overlap, as has already been shown for other species in Europe (Imboden, 1974; Bairlein, 2001). Particularly marked was the connectivity between breeding and non–breeding grounds in spring, with a correlation coefficient > 0.8, as compared to autumn and winter, with r values > 0.6. This result suggests that migrants use more direct, probably more population–specific routes in spring than in autumn, and that the overlap that they exhibit at their wintering areas is less marked in spring.

In autumn, both subspecies were mainly concentrated in coastal marshes, both on the Atlantic (Arcachon, Doñana) and on the Mediterranean coasts (from the east of Iberia to La Camargue, and also around Venice). This suggests that these wetlands could play a key role for the conservation of both L. s. namnetum and L. s. cyanecula subspecies. A possible drawback in relation to this result is a possible geographic bias in sampling (ringing) effort. If this effort is higher at

the large, main marshes with apparent good habitats, then this result must be considered cautiously, and we cannot fully reject the possibility that some inland humid zones could also be r elevant for bluethroats.

The number of recoveries during the spring migration period was very low, so we should be cautious about making a firm conclusion with regard to this period. This is especially applicable to L. s. namnetum, for which there were only two recoveries in this period.. In the case of L. s. cyanecula, where autumn recoveries were obtained both on the Atlantic and the Mediterranean coasts, in spring the recoveries all had a Mediterranean–biased distribution, suggesting loop–migration. A reason commonly suggested is that using more direct routes allows migrants to reach their breeding areas faster, which is crucial in terms of fitness as it has breeding consequences (Kokko, 1999). Alternative hypotheses are the wind–assistance and the food provisioning hypotheses. The wind–assistance hypothesis states that migrants will gain advantage by migrating over areas that provide greater tail wind assistance or have weaker head wind. If the dominant wind varies seasonally and regionally, then migrants will use different routes depending on the season, and thus will show loop–migration. The food provisioning hypothesis states that migrants would use routes that provide a more abundant food supply. When this supply varies seasonally and regionally, loop–migration is expected.

Most recoveries in winter (ca. 80%) appeared in Iberia, thus revealing the relevance of this area for the conservation of bluethroats (L. s. namnetum and L. s. cyanecula) in Europe. Other Mediterranean peninsulas, such as Italy (not Greece, where we found no recoveries), did not seem to be important wintering regions for the studied bluethroat populations. This conclusion agrees with previous research (Spina & Volponi, 2009). Especially relevant was the southern half of Iberia, with both the Atlantic and the Mediterranean coasts being utilized.

Apart from the Mediterranean marshes in eastern Iberia (Peiró, 1997) and some Andalusian wetlands in the south–east which had been reported to host bluethroats in winter (Cortés et al., 2002), we discovered high concentrations within the Atlantic wetlands of Doñana and Bahía de Cádiz. It is of note that this was the area with the highest densities of wintering L. s. cyanecula in Europe, as revealed by ring recovery data. Again, as we have said previously, the identification of these key sites must be regarded with some caution because we have no data on a possible bias in sampling effort. The Ebro Valley, in northern Iberia, was pointed out in the past as being a chief corridor for the bluethroat during migration period (Hernández et al., 2003), but was not considered to be a main wintering area (Arizaga et al., 2010a). In our study the Ebro Valley (or more specifically part of it) appeared as a relatively important wintering area. Some Moroccan wetlands also appeared to host a relatively high number of bluethroats during the winter. Interestingly, although biometric analyses have shown that L. s. namnetum overwinter in Morocco (Zucca & Jiguet, 2002), no recoveries of this subspecies have

been obtained for the Maghreb. In part this is likely due to the low ringing effort carried out in Morocco as opposed to Iberia. Future campaigns in Morocco will be capital to clarify whether the main wintering area of the *L. s. namnetum* subspecies is Portugal or the Atlantic wetlands of Morocco.

The distribution of recoveries at winter quarters did not correlate with the distribution at breeding quarters, thus not supporting the leap–frog and chain migration strategies. Conversely, telescopic migration was evidenced, with a high overlap between populations from different origin latitudes within their wintering areas. The distance from breeding to winter quarters correlated positively with breeding latitude, thus adding further support to this theory. This result, however, may be biased due to the lack of recoveries in tropical Africa. The single recovery obtained in this region was from a bird ringed in The Netherlands, one of the most northern breeding places for the *L. s. cyanecula* subspecies (Cramp, 1988). Future studies using other methods, such as stable isotopes analyses (Pain et al., 2004) and/or the use of geo–locators (Bächler et al., 2010) will clarify whether *L. s. cyanecula* populations demonstrate a telescopic migration strategy.

Recovery data were insufficient to identify in detail the entire wintering range for all white–throated bluethroat European populations. Paradigmatic examples of this were the lack of recovery data from bluethroats breeding in Iberia (*L. s. azuricollis*), and also the lack of recoveries in the Sahelian non–breeding areas, where only one recovery (from an individual ringed in The Netherlands) was obtained. Morphological studies lend support to the hypothesis that bluethroats breeding in Iberia are long–distance migrants that probably overwinter in tropical Africa (Arizaga et al., 2006b). Additionally, the mean wing length of bluethroats captured in Senegal during the winter (Arizaga et al., 2011a) approached that reported for the Iberian population (Arizaga et al., 2011b). The difficulty to find/obtain recoveries in Africa may explain why the wintering area of this subspecies remains still unknown. Moreover, as the number of bluethroats ringed as breeders in Iberia is small (*ca.* less than 1,000 individuals from 2000 to 2010; J. García, per. com.), the chances of obtaining recoveries outside their breeding areas are low given the low recapture rates of ringed passerines.

In conclusion, European populations of white–throated bluethroat (belonging to *L. s. namnetum* and *L. s. cyanecula* subspecies) move on a NE–SW axis from their breeding areas to their wintering areas within the circum–Mediterranean region, mainly in Iberia, following population–specific parallel migration routes . *L. s. namnetum* mainly uses the Atlantic coastal marshes from France to south–western Iberia, where the chief wintering areas are found, whilst *L. s. cyanecula* uses both the Atlantic and the Mediterranean wetlands in autumn but only the Mediterranean wetlands in spring, thus giving rise to a loop–migration pattern. Nothing is yet known, however, about the Afro–tropical winter grounds on a population scale, or about the *L. s. azuricollis* subspecies breeding in Iberia.

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