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Connectivity in Reed Warblers *Acrocephalus scirpaceus* between breeding grounds in Europe and autumn stopover sites in Iberia

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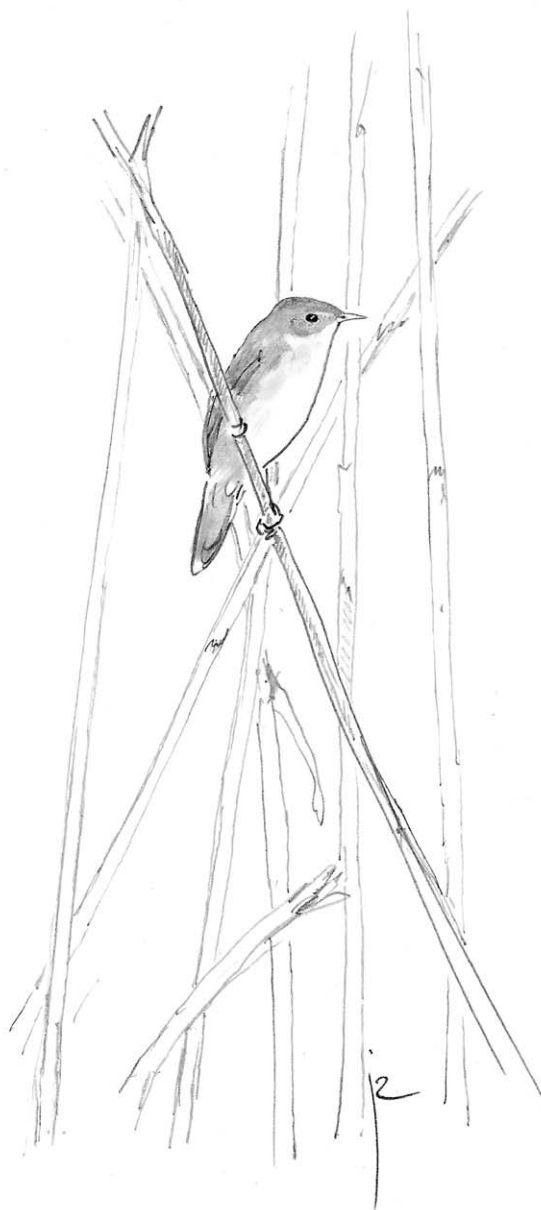
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We determined the degree of connectivity in the Eurasian Reed Warbler *Acrocephalus scirpaceus* between breeding regions in central and northern Europe and stopover sites in Iberia, during the autumn migration. We used both recovery data and wing length analyses to achieve this. Biometric data were obtained during 2009 at 11 sampling localities in Iberia, which we amalgamated into four major migratory areas within the region (Central, Western, Eastern and Southwestern Iberia, hereafter CI, WI, EI, SW). From the EURING database, we selected birds captured at their breeding sites in Europe and recaptured in Iberia during the autumn migration. Reed Warblers passing through WI had shorter wings than those in CI, EI and SW, suggesting that birds in WI migrated shorter distances, a fact also supported by recovery data. Although Reed Warblers showed some population overlap when passing through Iberia, we found that birds passing through EI and CI came from areas further to the east (continental Europe) than those passing through WI (mainly British Isles), thus supporting parallel migration. Reed Warblers tended to converge in south-western Iberia, suggesting an effect of nearby geographical barriers.

Key words: Iberia, migration routes, parallel migration, recoveries, wing length

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The migratory connectivity of a population can be defined as the link between breeding and non-breeding areas and/or as the extent to which different breeding populations mix at the winter quarters (Webster *et al.* 2002, Norris *et al.* 2006). Connectivity patterns affect the degree of adaptation of birds to their non-breeding areas, and their study can provide clues about the evolution of migration and the actual spatio-temporal distribution of birds during the non-breeding period. The study of connectivity has direct conservation implications (Pain *et al.* 2004). This is particularly true in species showing strong connectivity (i.e. when individuals from a population overwinter together in the same area without mixing with others from different populations) as well as in those species which depend on very specific habitats, or have very restricted ecological requirements, such as many wetland species (Atienza *et al.* 2001, Pain *et al.* 2004). Such birds are often particularly vulnerable, as wetlands are especially threatened by human pressure and global climate change (Hartig *et al.* 1997, Airoldi & Beck 2007).

The connectivity patterns of European passerines have been the target of several studies that have chiefly focused on the location of wintering grounds (Pain *et al.* 2004, Procházka *et al.* 2008). It remains largely unknown, however, whether connectivity is maintained between breeding and stopover sites during migration. Population-specific travel (migratory) directions and the use of population-specific key stopover places are likely to be among the chief factors that determine connectivity during the migration period.

The existence of migratory divides between western and eastern Europe (e.g. Helbig 1996, Pulido 2007) results in European populations of several bird species having different migratory directions. Thus, western populations migrate following a southwest axis in autumn, whereas eastern populations migrate following a southeast axis (e.g. Schlenker 1988, Bensch *et al.* 2006, Procházka *et al.* 2008, Reichlin *et al.* 2009). In this context, high connectivity between breeding and stopover grounds is expected if the divide is strongly marked and hence there is no overlap between western and eastern populations.

On a smaller scale, in populations using a main migratory direction a positive relationship between the geographic location of breeding and stopover areas can be expected. This connectivity could evolve when migrants follow the most direct routes during migration, saving time and reducing the energy cost (Alerstam 1990a; Newton 2008). In other words, if connectivity is strong, migrants breeding in regions further east should pass through regions which are

further east than those used by migrants breeding in regions further west.

Iberia is a region of passage for several European Afro-tropical migrants (Tellería *et al.* 1999), therefore it is a suitable area for the investigation of the existence of population-specific stopover or passage regions. The particular geographic position of Iberia allows us to consider, for analytical purposes, three major regions of passage: (1) Central Iberia (CI), entering through the western edge of the Pyrenees (Galarza & Tellería 2003) and heading south following a south-west axis of migration; (2) Western Iberia (WI), entering Iberia through the north coast and flying parallel to the Atlantic coast until reaching southern Portugal, following a southern axis of migration; (3) Eastern Iberia (EI), entering Iberia through the eastern edge of the Pyrenees and continuing south following a south-west axis along the Mediterranean coast. Migrants passing through CI and WI and, to a lesser extent, EI, should be expected, owing to their main migration axes, to converge in southwestern Iberia (SW), as reported by Cantos (1998).

Due to aerodynamics (Norberg 1990), flight morphology is co-adapted with migratory behaviour: wings are more pointed and longer and the tail shorter with increasing distances of migration (Pérez-Tris *et al.* 1999, Calmaestra & Moreno 2001). These adaptations are observed at both a inter- (Mönkkönen 1995, Calmaestra & Moreno 2001) and intra-specific level (Copete *et al.* 1999, Pérez-Tris *et al.* 1999, García-Peiró 2003, Chernetsov 2004, Förschler & Bairlein 2010). As a result, these biometric differences can be used to assess the origin of migrants, or at least, to distinguish different populations (i.e. Chandler & Mulvihill 1990, García-Peiró 2003, Fiedler 2005, Arizaga *et al.* 2006).

In this study, we investigate whether species with a marked migratory divide in Europe also show connectivity on a smaller scale, testing whether migrants use parallel routes between their breeding and stopover areas. With this goal, we used both recovery and morphology data of Reed Warbler *Acrocephalus scirpaceus*, captured in Iberia during the autumn migration period. Our hypothesis is that if this species, which presents a high connectivity between breeding and wintering areas (Procházka *et al.* 2008), also maintains a strong connectivity during migration, on a smaller scale, a positive relationship should be expected between its longitude of origin and capture in Iberia, resulting in parallel migration of different populations within the region. Also, biometric differences are expected within Iberia, with birds originating from further away, which therefore cover longer distances, presenting longer and more pointed wings.

METHODS

Study species

Reed Warblers have a wide geographic distribution, breeding in much of Europe and overwintering in tropical Africa (Cramp 1992). This species is a suitable model to study the degree of connectivity between breeding and stopover regions in Iberia since Reed Warblers are common migrants passing through the area en route to their wintering areas (Tellería *et al.* 1999). In this study we considered birds likely to be true stopping-over migrants (i.e. accumulating fuel) and also birds which merely land and resume their migration the next day. Aiming to identify the origin of migrants passing through specific regions, rather than detecting the potential use of Iberia, we did not make a distinction by passage time.

Sampling sites and field data

Reed Warblers were captured with mist nets at 11 localities in Iberia during the autumn migration period of 2009 (Figure 1). Each locality was assigned to one of the migratory regions in Iberia (CI, WI, EI, SW) (Figure 1). Data were collected from 15 July to 15 October and mist nets were open with a variable frequency, ranging between daily and fortnightly, during a period of 4–6 h starting at dawn. The vegetation in all localities was composed mainly of Reed *Phragmites australis* beds.

Each bird was individually ringed and its age determined as either first-year (birds with fresh juvenile feathers in their wings, hatched in 2009) or adult (with worn feathers in their wings, hatched in 2008 or before) following Svensson (1998). Wing length (± 0.5 mm, according to method III in Svensson 1998) was recorded at all sampling localities. Additionally, primary feathers length (± 0.5 mm; P1 to P9, numbered from innermost to outermost) were measured at 4 of 11 sites (TAIP, JAIZ, CANA, PEGO).

Biometric analyses

Wing morphology is known to have evolved with migratory behaviour, wing pointedness being a good indicator of migratory distances (Lockwood *et al.* 1998). The C_2 index, as defined by Lockwood *et al.* (1998) is a commonly used wingtip shape index to describe wing pointedness. Negative values represent more pointed wings, whilst positive values indicate a more rounded shape. In our data set, only wing length was available at all sampling sites, so we used this measure as an indicator of wing pointedness, since wing length was negatively correlated with the C_2 index value at all the sites where primary feather length was

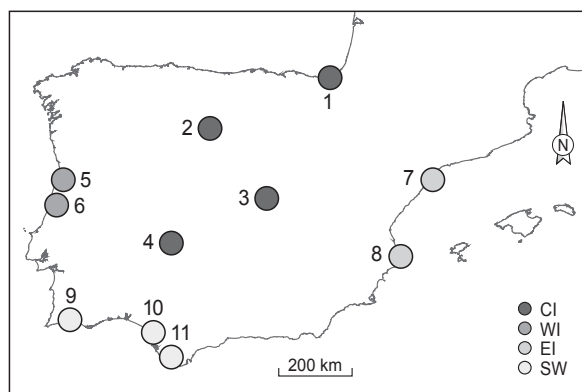


Figure 1. Sampling localities in the Iberian Peninsula. Central Iberia (CI): 1 = Jaizubia (JAIZ); 2 = El Cruce (CRUC); 3 = Las Minas (MINA); 4 = Arroyo Budi3n (ARRO). Western Iberia (WI): 5 = Salreu (SALR); 6 = Taipal (TAIP). Eastern Iberia (EI): 7 = Canal Vell (CANA); 8 = Pego (PEGO). Southwestern Iberia (SW): 9 = S3tio das Fontes-Charito (FONT); 10 = Manecorro (MANE); 11 = Vejer (VEJE).

recorded (total of birds: $r = -0.238$, $P < 0.001$, $n = 1319$; first-year birds: $r = -0.356$, $P < 0.001$, $n = 890$; adults: $r = -0.159$, $P < 0.001$, $n = 429$).

To check whether there were morphological variations between migratory regions, we conducted a GLM on wing length with age (first-year birds, adults) and region (CI, WI, EI, SW) as factors. Localities were nested into regions, as indicated in Figure 1, and they were included in the models as a random factor. Apparently, we would not be able to separate migrants and local birds using wing length (as suggested in Bibby & Green 1981), due to the high overlap observed (M. Andueza, pers. obs.). Therefore, in order to minimize a local birds' effect, we selected Reed Warbler data collected during the peak of migration (presumably with a higher proportion of migrants in relation to local birds). The migration peak differed between age classes (Bibby & Green 1981, Cramp 1992). To identify it for each age category, we used data from sites with daily trapping sessions and a sufficiently high number of captures, selecting the date frame with higher number of daily captures for each age. Thus, we determined that the main period of passage lasted from 10 August to 30 September for first-year Reed Warblers, and from 1 August to 30 September for adults.

As a complement, we also compared the proportion of age classes in the four migratory regions using the χ^2 test (applying Yate's correction) on contingency tables, to test for a differential use of regions depending on age, and hence whether connectivity patterns differed between juveniles and adults.

Recovery data analyses

Data on Reed Warblers captured at their breeding areas outside Iberia (from May to the end of June; Cramp 1992) and in Iberia during the autumn migration period (from July to October) were obtained from the EURING data bank ($n = 210$).

To test the prediction that parallel migration of the European populations between their breeding grounds and Iberian stopover areas occurs depending on their origin, we conducted a stepwise linear regression on location in Iberia (longitude) with origin in Europe (latitude and longitude) as predictor variables, using the EURING recovery data set.

To check whether possible biometric (wing length) differences between migratory regions in Iberia (CI, WI, EI, SW) could be explained by differences in both the origin of migrants passing through them, and the distance covered from their breeding sites in Europe, we selected those birds recaptured in each migratory region (CI, WI, EI, SW) from the EURING data set. Particularly, we considered those birds captured within a 100 km-radius area of each of the sampling localities belonging to each migratory region. We ran two analyses: 1) ANOVAs to see if birds' origin (latitude and longitude) differed between the four sampling areas; 2)

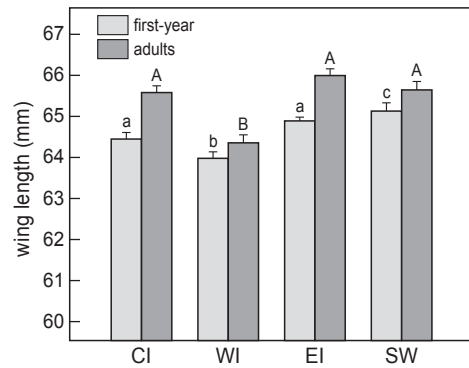


Figure 2. Wing length (mean \pm SE) of Reed Warblers for each age class and region. Different letters between regions indicate significant differences.

an ANCOVA to compare the distance covered from breeding areas amongst regions, including birds' capture locations in Iberia (longitude and latitude) as covariates, so as to remove the effect (heterogeneity) of capture location in Iberia on distance from origin.

For all analyses, each bird was considered only once at each site in order to avoid pseudoreplication. The software SPSS v. 15.0 was used for statistics. We give mean values \pm SE.

RESULTS

A total of 3073 different Reed Warblers were captured, of which 2103 (68.4%) were first-year birds and the rest adults. Age ratios varied between regions ($\chi^2 = 19.11$, $P < 0.001$), with the lowest proportion of first-year birds being found in SW (61.2%), followed by CI (67.5%), WI (71.5%) and EI (72.1%) (Table 1).

Wing length varied between routes and ages, with the interaction between both factors being significant (Table 2). For first-year birds, Reed Warblers passing through WI had significantly shorter wings than those passing through other regions, whilst those in SW had significantly longer wings (Figure 2). For adults, birds in WI also showed shorter wings but there was no difference between the other three regions (Figure 2). For all regions, first-year birds had shorter wings than adults (Figure 2).

The longitude of capture in Iberia was interrelated with coordinates of origin (GLM, B-parameters: latitude: $B = -0.35$, $P < 0.001$; longitude: $B = 0.20$, $P < 0.001$; $n = 105$). Hence, the European breeding sites of Reed Warblers recaptured in more eastern locations in Iberia were located further east and south than

Table 1. Percentages of first-year Reed Warblers by region (indicated between brackets) pairwise compared by χ^2 tests. CI: Central Iberia; WI: Western Iberia; EI: Eastern Iberia, SW: Southwestern Iberia.

	EI (72.1%)	CI (67.5%)	WI (71.5%)
CI (67.5%)	$\chi^2 = 5.050$ $P = 0.025$		
WI (71.5%)	$\chi^2 = 0.029$ $P = 0.866$	$\chi^2 = 2.073$ $P = 0.150$	
SW (61.2%)	$\chi^2 = 16.346$ $P < 0.001$	$\chi^2 = 5.807$ $P = 0.016$	$\chi^2 = 9.972$ $P = 0.002$

Table 2. Effects of region, locality and age (adults, first-year birds) on the wing length of Reed Warblers during autumn migration in Iberia. Localities were nested within regions (Central, Western, Eastern, Southwestern).

Factor	SS	df	F	p
Region	406.21	3	0.84	0.514
Age	6500129.7	1	59859.39	<0.001
Locality(Region)	785.88	7	19.19	<0.001
Region \times Age	66.67	3	3.60	0.013

those of birds recaptured further west. Particularly, Reed Warblers from the British Isles migrated through western Iberia, with no recoveries found in the Mediterranean façade, whereas birds from the continent migrated through more eastern regions, although they covered most of the area (Figure 3).

When comparing the average longitude of origin of recaptures at each Iberian migrating region, we found that birds passing through EI and CI had more eastern origins than those from WI and SW ($F_{4,77} = 11.35$, $P < 0.001$) (Figure 4). Significant differences between regions were also found in latitude of origin ($F_{4,77} = 6158.08$, $P < 0.001$). Although *a posteriori* tests did not detect significant differences, birds from EI tended to have a more southern origin (Figure 4). Also, the distance to the breeding areas (once the effect of covariates, latitude and longitude of capture in Iberia, was removed from the variable distance to origin) differed between regions ($F_{4,77} = 1.22$, $P < 0.001$). Although *a posteriori* tests did not show significant

differences, birds passing through EI and CI tended to come from more distant origins than those in WI and SW (Figure 4).

Finally, recovery data showed a high concentration of Reed Warblers in some areas, especially in southwest Iberia, but also on the western edge of the Pyrenees and some zones in eastern and central Iberia (Figure 5).

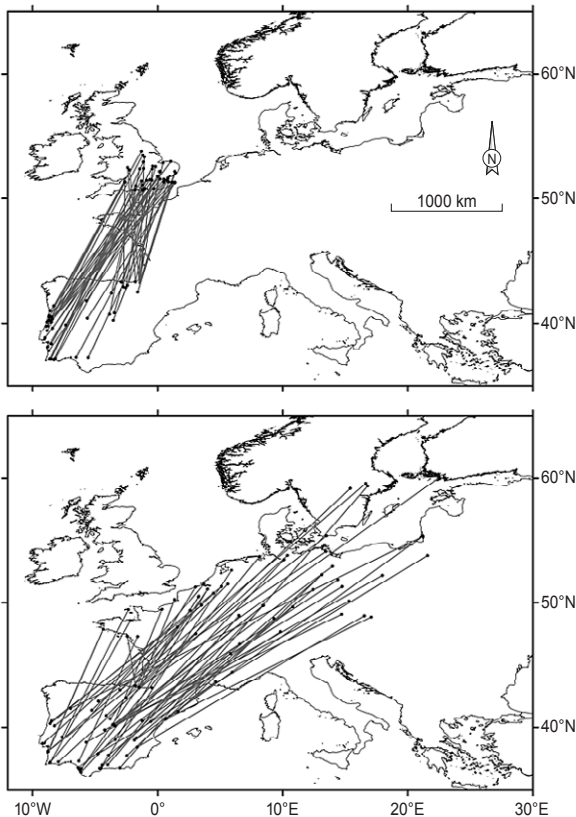


Figure 3. Recoveries of Reed Warblers captured/recaptured in Europe during the breeding period (upper panel = Britain and lower panel = continental Europe) and recaptured/captured in Iberia during the autumn migration.

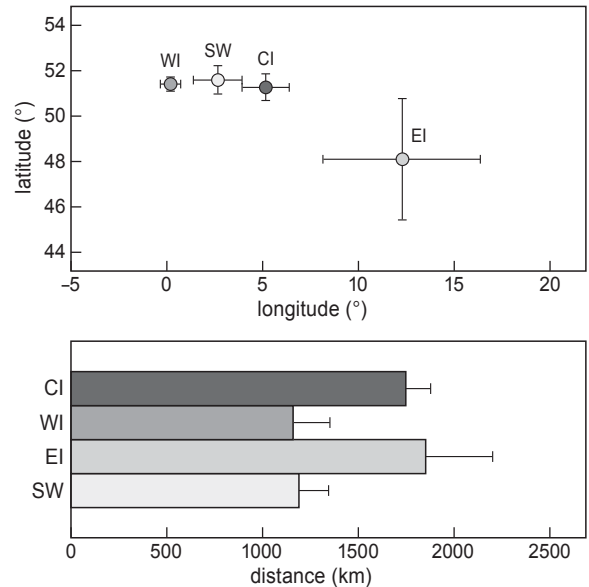


Figure 4. Mean \pm SE geographic origin and distance from breeding sites (independent of the effect of capture location in Iberia) of Reed Warblers captured at each migratory region in Iberia (CI: $n = 34$; WI: $n = 17$; EI: $n = 4$; SW: $n = 22$). For each region, the recoveries of Reed Warblers within a 100-km radius area around each sampling site were considered.

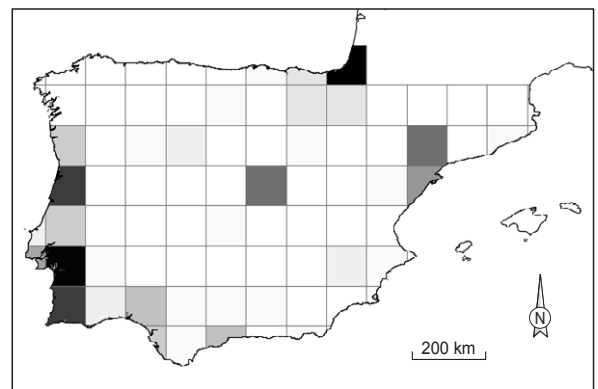


Figure 5. Density of Reed Warblers expressed as number of recoveries/square. Darker squares indicate higher densities, ranging from 0 to 90 recoveries/square.

DISCUSSION

The need for fuelling before the Mediterranean Sea and the Sahara desert may lead migrants to stop over in key sites and, accordingly, show a higher philopatry in Iberia than elsewhere (Cantos & Tellería 1994). In this context, studying the connectivity between breeding and stopover sites is of great importance in understanding the spatio-temporal distribution patterns of European bird populations during migration, as well as in identifying target stopover sites, which is crucial from a conservation standpoint.

The Reed Warblers passing through more eastern regions in Iberia during autumn came from breeding sites further to the east and south, whilst those passing through more western Iberian zones came from breeding areas further west and north. For example, birds breeding in the United Kingdom or Ireland passed mainly through WI and no recoveries were found in EI, [see Wernham *et al.* (2002) for further details]. This result agrees with the prediction that the different European populations of Reed Warblers tend to migrate in parallel flyways between their breeding and stopover areas according to their origin, following the shortest routes. Procházka *et al.* (2008) concluded that Reed Warblers breeding in Europe show high connectivity in their wintering areas south of the Sahara Desert. Hence, their geographic distribution in Africa during the winter is a mirror image of their distribution in Europe during the breeding period.

Although connectivity between breeding regions in Europe and passage regions in Iberia exists, the degree of this was found to be relatively low. Less than 20% ($R^2 = 0.177$) of the variance was associated with the geographic distribution of Reed Warblers in Iberia. In part this apparently weak connectivity may be due to the particular geographic conditions of southern Europe. The fact that the sea crossing is longer through the central Mediterranean than via its western edge probably forces many migrants to disperse to the latter area. This gives rise to a funnel effect in Iberia (i.e. population overlapping), larger than that which would be expected if such a geographic obstacle did not exist (Galarza & Tellería 2003). This is supported by the high concentrations of Reed Warblers detected in southwest Iberia, probably due to the effect of nearby geographic barriers (Newton 2008), namely the Atlantic Ocean and the Sahara Desert. Our results support the idea that Reed Warblers tend to cross this desert along the Atlantic coast, where conditions are more favourable than in central Saharan zones (Hilgerloh 1990, Cramp 1992). Hence, in order to facilitate this, the different

populations within Iberia converge towards southwest. Moreover, first-year birds show more variation in migratory direction (Fransson & Stolt 2005), so adults should theoretically show stronger connectivity. However, our sample size was too small to run detailed analyses considering both age categories separately.

Although Reed Warblers from East Europe have been reported to migrate towards Africa following a southeast route of migration (Cramp 1992, Berthold 2001, Procházka *et al.* 2008), we observed that a fraction of this population migrates through a southwest axis, thus flying to Africa *via* Iberia. This suggests the presence in East Europe of a fraction of Reed Warblers with a genetically determined southwest direction of migration (c.f. Helbig 1996, Pulido 2007).

Reed Warblers from western Europe fly over a shorter distance to arrive in Iberia, *en route* to Africa in autumn, than those from eastern Europe. As a consequence of this they were predicted to have a less marked long-distance-like morphology. Our analyses on wing length between regions agreed with this hypothesis, with birds in WI (coming from closer regions, mainly Britain) showing significantly shorter wings than those captured in the other three regions (coming from more distant origins, mainly continental Europe). However, the lack of difference in wing length between CI and EI suggests that biometric differences exist between British birds and the other European populations, but not between the latter. Moreover, we also observed that, in first-year birds, the longest wings were found in SW. These results would support an influx of Reed Warblers of eastern origin, which may converge in southwestern Iberia before crossing the sea to Africa (Cantos 1998), without stopping at northern Iberian sites. In adults, however, we did not find this pattern and the wing length of SW birds did not differ from that of birds from CI and EI. We are unable to give an explanation for this difference between age classes.

In SW a lower proportion of first-year birds in relation to adults was observed. First-year birds show more scattered migratory directions than adults (Alerstam 1990b; Fransson & Stolt 2005) and due to their inexperience do not always follow the optimal migratory direction, which in our study case would be through a southwestern axis in Iberia. So, in this scenario, a fraction of juveniles would cross the sea to Africa by eastern southern sites. Additionally, the proportion of adults could be increased by migrants that do not stopover in Iberia until reaching its southwestern corner, where they prepare for barrier crossing (Cantos 1998, Schaub & Jenni 2000).

In conclusion, we showed that Reed Warblers have a population distribution during autumn migration within Iberia consistent with the hypothesis that migrants maintain a moderate degree of connectivity between their breeding and stopover sites in this region. However, although population segregation occurs (i.e. British and continental Reed Warblers), a certain degree of overlapping exists, probably due to a barrier crossing effect.

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SAMENVATTING

In hoeverre mengen vogels van verschillende herkomst zich tijdens de trek, of blijft er op de trek een scheiding bestaan tussen de verschillende broedpopulaties? Deze vraag werd onderzocht voor Kleine Karekieten *Acrocephalus scirpaceus* die in het najaar door Spanje en Portugal trekken. Er werden op elf plekken karekieten gevangen. Die plekken werden in vier geografische gebieden gegroepeerd: Midden, West, Oost en Zuidwest. Kleine Karekieten die in het westen werden gevangen, hadden kortere vleugels dan de vogels van elders. Dat wijst erop dat de vogels die in het westen van het Iberisch Schiereiland doortrekken een kortere afstand overbruggen tijdens de trek dan de vogels uit de andere gebieden. Dit werd bevestigd door ringgegevens. De vogels die door het oosten en midden van Spanje doortrokken, waren overwegend afkomstig van het vasteland van Europa, terwijl de vogels in het westen vooral van de Britse eilanden kwamen. Dit wijst erop dat de verschillende broedpopulaties trekroutes hebben die parallel aan elkaar lopen. In het zuidwesten van het Iberisch Schiereiland mengden de verschillende populaties zich, wat heel goed een stuwingseffect kan zijn langs de Spaanse en Portugese zuidkust. (JP)

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Appendix 1. Characteristics of the sampling localities in Iberia (WI, Western Iberia; CI, Central Iberia; EI, Eastern Iberia; SW, Southwestern Iberia). Sampling frequency indicates the minimum sampling frequency; sampling effort, metres of mist nets; and sampling duration, the number of hours since dawn. RW (Reed Warbler) shows the number of captures of first-year birds/adults during the period considered for analyses. Locality abbreviations: TAIP, Taipal; SALR, Salreu; JAIZ, Jaizubia; CRUC, El Cruce; MINA, Las Minas; ARRO, Arroyo Budi3n; CANA, Canal Vell; PEGO, Pego; MANE, Manecorro; VEJE, Vejer; FONT, Charito-S3tio das Fontes.

Region	Locality	Coord.	Sampling period	Sampling frequency	Sampling duration (h)	Sampling effort (m)	RW
WI	TAIP	40° 11'N, 08° 41'W	04 Aug/ 12 Sep	Weekly	5	240	70/71
WI	SALR	40° 44'N, 08° 33'W	03 Jul/30 Sep	Weekly	5	108–120	223/46
CI	JAIZ	43° 21'N, 01° 49'W	15 Jul/15 Oct	Daily	4	240	445/286
CI	CRUC	42° 01'N, 04° 49'W	15 Jul/15 Oct	Daily	4	162	349/59
CI	MINA	40° 13'N, 03° 35'W	04 Jul/30 Oct	Weekly	4	138	48/53
CI	ARRO	39° 03'N, 48° 00'W	12 Jul/25 Oct	Fortnightly	4	36	35/24
EI	CANA	40° 43'N, 00° 44'E	4 Aug/30 Nov	Daily	4	240–210	302/114
EI	PEGO	38° 50'N, 00° 07'W	1 Aug/1 Oct	Daily	6	90	349/138
SW	MANE	36° 56'N, 06° 21'W	1 Sep/ 31 Oct	Daily	4	252	28/23
SW	VEJE	36° 15'N, 05° 58'W	10 Jul/27 Oct	Weekly	4	210	59/76
SW	FONT	37° 10'N, 08° 27'W	09 Aug/30 Sep	Weekly	2–14.5	40–164	195/80

Appendix 2. Mean (SE) number of daily captures during the study period standardised for 4 h and 100 m of nets for Reed Warblers (RW) at each site and region. Abbreviations as in Appendix 1.

Site	RW	
	First-year	Adults
TAIP	10.0 (3.4)	13.5 (3.0)
SALR	21.0 (1.9)	5.8 (1.3)
Total WI	17.46 (2.0)	5.7 (1.2)
JAIZ	9.1 (1.4)	7.8 (2.0)
CRUC	10.6 (1.1)	2.4 (0.5)
MINA	5.0 (0.8)	4.7 (1.5)
ARRO	19.4 (4.7)	11.1 (3.7)
Total CI	4.4 (0.4)	1.7 (0.3)
CANA	6.5 (1.1)	3.3 (7.2)
PEGO	12.7 (1.5)	6.7 (1.1)
Total EI	7.9 (0.9)	4.7 (0.8)
MANE	0.4 (0.1)	0.3 (0.1)
VEJE	2.6 (0.7)	3.0 (0.7)
FONT	3.9 (1.1)	2.2 (0.7)
Total SW	2.1 (0.5)	1.5 (0.3)