Geographic variation in body mass of first-year Reed Warblers *Acrocephalus scirpaceus* in Iberia

Miren Andueza*, Emilio Barba, Jose L. Arroyo, Jordi Feliu, Jaime Gómez, Fernando Jubete, Luis Lozano, Juan S. Monrós, Rubén Moreno-Opo, Júlio M. Neto, Alejandro Onrubia, Paulo Tenreiro, Thijs Valkenburg & Juan Arizaga

On their route to tropical Africa, European trans-Saharan migrants must cross two major geographical barriers, the Mediterranean Sea and the Sahara Desert, which necessitates the accumulation of large fuel loads. While northern Africa is the chief region where most migrants gain fuel for the Sahara crossing, Iberia is a target area to gain fuel before the sea crossing existing between Europe and Africa. Despite the large body of studies approaching the question of fuel accumulation before geographic barriers, it is still poorly known which factors apart from distance to a certain barrier shape the geographical pattern of fuel reserves. To investigate this question in detail we used data of first-year Reed War-
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1. Introduction

Geographic and ecological barriers, such as deserts, oceans or high mountain ranges are important factors in the shaping of bird migration strategies (Moreau 1972), since crossing them implies flying over inhospitable areas, where fuelling is either impossible or almost so. Accordingly, migrants have developed fuelling strategies which allow them to make a successful barrier crossing (Rubolini et al. 2002, Delingat et al. 2008) whilst optimizing fuel accumulation, time and/or the energy expenditure (Alerstam & Lindström 1990, Hedenström & Alerstam 1997, Alerstam et al. 2003).

Afro-tropical European migrants (i.e. European birds that spend the winter in tropical Africa in areas south of the Sahara) must cross two major geographical barriers on their route to Africa from Europe: the Mediterranean sea crossing between Europe and Africa and the Sahara Desert. Although a fraction of migrants may cross the sea by the Strait of Gibraltar (14 km), most migrants are supposed to cross it from a wider area covering the southern coast of Iberia (Moreau 1953, Casement 1966, Bernis 1980, Telleria 1981, Finlayson 1992). Fuelling at sea is impossible and in the Sahara it is only possible if birds find oases en route (Bairlein 1985). Therefore, with the perspective of not finding sufficient feeding possibilities in these zones most small, flapping flight migrants, such as passerines, must accumulate large fuel loads before crossing the barriers (Bairlein 1991, Schaub & Jenni 2000a, Fransson et al. 2005, Yosef & Chernetsov 2005, Fransson et al. 2006, Yohannes et al. 2009).

Depending on species-specific feeding requirements and the availability of suitable habitats expected to be found en route, four general strategies of body mass gain for crossing the Sahara Desert have been reported for European passerines migrating to tropical Africa during the autumn migration period (Schaub & Jenni 2000a): 1) a steady increase in body mass along the route until reaching the northern border of the desert (e.g. Garden Warblers *Sylvia borin*); 2) fuel accumulation well before the Sahara (e.g. Sedge Warblers *Acrocephalus schoenobaenus*); 3) fuel accumulation just in front of the Sahara (e.g. Reed Warblers *Acrocephalus scirpaceus*); and 4) fuelling whilst crossing the Sahara (e.g. Spotted Flycatchers *Muscicapa striata*). In defining these strategies the importance of the sea band (Atlantic/Mediterranean Sea) between Iberia and Africa was not considered. However, sea crossing has been reported to be relevant to the fuel management of migrants (Rubolini et al. 2002).

How body mass of some European long-distance migrant passerines increases before barriers is known on a broad scale, mainly from a continental perspective (Schaub & Jenni 2000a, b, 2001, Rubolini et al. 2002, Yohannes et al. 2009). However, such studies fail to show whether local (i.e., countrywide) variations from the general continental pattern occur, in particular near the edge of geographical barriers. Understanding these small-scale variations is not a trivial matter because the use of a few stopover sites to infer general fuelling strategies might cause bias if these sites are not optimal or if they are not used as true stopover sites (i.e., to gain energy reserves and not only for resting) (Arizaga et al. 2011a).
Situated in south western Europe, Iberia is a converging area for many European passerines moving to or from their wintering areas in western-tropical Africa (Tellería et al. 1999). As a result, Iberia can be considered as a key area for preparation before the sea and the Sahara Desert crossing. Thus, it is an excellent location for the study of fuelling strategies prior to barrier crossing.

The Reed Warbler *Acrocephalus scirpaceus* is a widespread Palaearctic songbird breeding across most of Europe and overwintering in tropical Africa (Cramp 1992). The species is closely linked with reed beds (*Phragmites australis*) where it feeds on small invertebrates. During the autumn migration, Reed Warblers have been reported to gain the fuel needed to cross the Sahara Desert mainly in northern Africa (Schaub & Jenni 2000a, b, 2001, but see Hilgerloh & Wiltschko 2000). However, crossing the sea band between southern Iberia and Africa may be relevant to the fuel management of Reed Warblers, as has been found for other species in similar circumstances (Rubolini et al. 2002).

In this context, if the main factor determining fuel loads is the distance to the barrier’s edge, we can expect a north–south increase in fuel load in Iberia. However, if another factors, such as the distribution of suitable habitats (Ktitorov et al. 2008, Chernetsov 2013), play a relevant role in the fuel accumulation strategy the accumulation of the reserves needed to cross the sea could occur at sites further north. Previous studies with Reed Warblers used a very low number of sampling sites, mainly in southern Iberia (see Hilgerloh & Wiltschko 2000 and Schaub & Jenni 2000a for further details), so where migrants actually prepare for barrier crossing remains unknown.

Additionally, body mass patterns are also likely to be affected by date (Schaub & Jenni 2000a, b, Maggini et al. 2013). In particular, late migrants have been reported to be more fuel loaded than earlier individuals (Schaub & Jenni 2000a, b). The causes underlying this phenomenon still remain unclear. Late migrants experience higher time-pressure to arrive at their wintering areas, hence they would tend to accumulate more fuel in order to increase their migration speed (Schaub & Jenni 2000a, Bayly 2006). Therefore, we should expect an increase in fuel load with date. Additionally, body mass can change across the season due to population-associated differential passage (Maggini et al. 2013).

The aim of the study was to investigate whether the pattern of Reed Warblers’ body mass variation during autumn migration period in Iberia is shaped just by distance to geographic barriers or by additional parameters.

### Table 1. Characteristics of the sampling localities in Iberia. Captures refer to the number of first-year birds used in analyses (captured on the days considered, with all the necessary data recorded). Each bird has been considered only once (i.e. recaptures have been omitted).

<table>
<thead>
<tr>
<th>Route</th>
<th>Locality (CODE)</th>
<th>Coordinates</th>
<th>Mist nets (m)</th>
<th>Sampling period (freq.)</th>
<th>Captures</th>
</tr>
</thead>
<tbody>
<tr>
<td>E</td>
<td>Viladecans (VILA)</td>
<td>42°18’N, 02°07’E</td>
<td>207</td>
<td>18 Sep–30 Sep (daily)</td>
<td>26</td>
</tr>
<tr>
<td>E</td>
<td>Canal Vell (CANA)</td>
<td>40°43’N, 00°44’E</td>
<td>210–240</td>
<td>10 Aug–30 Sep (daily)</td>
<td>304</td>
</tr>
<tr>
<td>E</td>
<td>Pego (PEGO)</td>
<td>38°50’N, 00°07’W</td>
<td>90</td>
<td>10 Aug–30 Sep (daily)</td>
<td>319</td>
</tr>
<tr>
<td>C</td>
<td>Jaizubia (JAIZ)</td>
<td>43°21’N, 01°49’W</td>
<td>240</td>
<td>10 Aug–30 Sep (daily)</td>
<td>437</td>
</tr>
<tr>
<td>C</td>
<td>El Cruce (CRUC)</td>
<td>42°01’N, 04°49’W</td>
<td>162</td>
<td>10 Aug–30 Sep (daily)</td>
<td>344</td>
</tr>
<tr>
<td>C</td>
<td>Las Minas (MINA)</td>
<td>40°13’N, 03°35’W</td>
<td>138</td>
<td>10 Aug–30 Sep (weekly)</td>
<td>45</td>
</tr>
<tr>
<td>C</td>
<td>Arroyo Budión (ARRO)</td>
<td>39°03’N, 48°00’W</td>
<td>36</td>
<td>10 Aug–30 Sep (fortnightly)</td>
<td>33</td>
</tr>
<tr>
<td>C</td>
<td>Manecorro (MANE)</td>
<td>36°56’N, 06°21’W</td>
<td>252</td>
<td>01 Sep–30 Sep (daily)</td>
<td>28</td>
</tr>
<tr>
<td>C</td>
<td>Vejer (VEJE)</td>
<td>36°15’N, 05°58’W</td>
<td>210</td>
<td>10 Aug–30 Sep (weekly)</td>
<td>58</td>
</tr>
<tr>
<td>W</td>
<td>Salreu (SALR)</td>
<td>40°44’N, 08°33’W</td>
<td>108–120</td>
<td>10 Aug–30 Sep (weekly)</td>
<td>200</td>
</tr>
<tr>
<td>W</td>
<td>Taipal (TAIP)</td>
<td>40°11’N, 08°41’W</td>
<td>240</td>
<td>10 Aug–14 Sep (weekly)</td>
<td>66</td>
</tr>
<tr>
<td>W</td>
<td>Sitio das Fontes-Charito (FONT)</td>
<td>37°10’N, 08°27’W</td>
<td>40–164</td>
<td>10 Aug–30 Sep (weekly)</td>
<td>27</td>
</tr>
</tbody>
</table>
2. Material and methods

2.1. Sampling localities

Reed Warblers were captured with mist nets at 12 localities within Iberia during the autumn migration period of 2009 (Table 1, Fig. 1). The sampling frequency ranged from daily to fortnightly at different sites (see Table 1 for details). The vegetation in all localities was composed mainly of reed beds, except in Manecorro, where Mediterranean bushy vegetation (mainly *Pistacea lentiscus*) was abundant, together with a flooded prairie rich in halophytes with scattered tamarisks *Tamarix* spp., willows *Salix* spp. and ash trees *Fraxinus* spp.. Each sampling locality was assigned to one of these three flyways defined in Iberia (Table 1, Fig. 1) (Galarza & Tellería 2003, Navedo et al. 2010, Andueza et al. 2013): Eastern, Central and Western (hereafter, EI, CI, WI).

Each bird was individually ringed and its age determined according to Svensson (1992). Two age categories were identified: first-year birds (birds with fresh juvenile feathers in their wings, hatched in 2009) and adults (with worn feathers in their wings, hatched in 2008 or before). Wing length (± 0.5 mm, according to method III in Svensson 1992) and body mass (± 0.1 g accuracy) were recorded at all the sampling localities.

2.2. Data selection

Reed Warblers are abundant breeders in Iberia (Martí & Moral 2003) and both local and non-local birds occur in sympathy at stopover sites during the migration period. Since we were interested in studying true migrants (thus avoiding local birds still moultng or still at their breeding sites and non-migrating), we selected a sampling period (from 10 August to 30 September) coinciding with the main period of migration (Grandío & Belzunce 1987, Cantos & Tellería 1992), when the proportion of local birds could be expected to be very marginal (negligible) in relation to the bulk of true migrants, and therefore the potential bias caused by including some locals would be small (Schaub & Jenni 2000a). For the analyses, we considered only first-year birds captured during the first 4 h from dawn at each site (except in Fontes, where the birds were captured over a 5 h period).

Ideally, our analyses should have considered body mass at departure, but in the case of migrants captured more than once, we just considered the first capture event to make their data comparable with those birds trapped just once. Furthermore, birds first captured at a ringing station are not always caught the day of arrival (Schaub et al. 2001). Therefore, our sample had a mixture ranging from birds just arrived to birds just about to depart. We assume that a higher mean body mass at a site compared to others is ultimately due to the fact that migrants at that site are more fuel loaded, so likely depart with more fuel that those which would be captured at a site with lower mean fuel loads.

2.3. Statistical analyses

Firstly we conducted a Hierarchical Analysis of Clusters (HAC) in order to quantify the similarity between localities in relation to a size-corrected body mass index consisting of the residuals from a regression of the log-transformed body mass against log-transformed wing length (body size was assessed with wing length; Gosler et al. 1998) of Reed Warblers. For the HAC we used the UPGMA method with a similarity index based on the Euclidean distance between sampling sites. We repeated this HAC for the geographic distance between sampling sites. We conducted a Mantel test between the body mass index and geographic dis-
tances between sites, to check whether body mass depended on the geographic location.

Secondly, we ran Generalized Linear Models (with a linear-link function) to determine the relevance of several factors on Reed Warblers’ body mass pattern in Iberia. In particular we considered as dependent variable the size-corrected body mass index (as described above) and route (EI, CI, WI) as a factor. Date and “location” of capture in Iberia were included as covariates. The covariate “location” was the first principal component (PC1) of a Principal Component Analysis (PCA) on latitude of capture in Iberia, shortest distance to the geographical barrier’s edges: distance to south Iberian coast [Dist(SI)], to north African coast [Dist(NA)] and to the south of the Sahara [Dist(SS)]. All the variables were correlated with the factor loadings of the PC1.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>+0.51</td>
<td>+0.19</td>
</tr>
<tr>
<td>Dist(SI)</td>
<td>+0.49</td>
<td>+0.74</td>
</tr>
<tr>
<td>Dist(NA)</td>
<td>+0.50</td>
<td>–0.46</td>
</tr>
<tr>
<td>Dist(SS)</td>
<td>+0.50</td>
<td>–0.46</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>3.86</td>
<td>0.14</td>
</tr>
<tr>
<td>% Variance</td>
<td>96.47</td>
<td>3.45</td>
</tr>
</tbody>
</table>

Finally, we estimated the potential flight ranges for both the entire sample and the 25% heaviest birds fraction from each site, since these birds would be those likely about to depart (Ellegren & Fransson 1992, Arizaga et al. 2011b). We considered for the calculations an intermittent strategy (Schmaljohann et al. 2007). In particular, we considered that migrants fly for a period of 10 h from 20.00 to 06.00 (night) and rest during the day for 14 h (Salewski et al. 2010). For each bird, we calculated the number of flying and resting hours before they would have consumed their fuel store (i.e., until reaching their lean body mass), assuming a body mass loss of 1%/h during the flight (Hussell & Lambert 1980, Kvist et al. 1998) and 0.5% / h during the diurnal resting (Meijer et al. 1994). The duration of the resting period on the day of capture was considered to be 8 h, starting at 12.00, when sampling ended. Knowing the flying period of each individual assuming this intermittent strategy, the potential flight ranges were then calculated multiplying the flying hours by the flight speed of passerines under still air as in Delingat et al. (2008). We calculated the minimum potential flight ranges considering a flight speed of 40 km/h (Bruderer & Boldt 2001).

To estimate lean body mass we selected Reed Warblers without any visible fat content and ran a linear regression on body mass with wing length as an independent variable. There is evidence from analyses of recovery data and wing length within Iberia (Andueza et al. 2013) that during migration different European populations converge in Iberia and segregate in different regions according to their origin, resulting in a geographical morphology variation. Hence the relationship between body mass and wing length is expected to vary between sites. Consequently, we obtained a different equation at each site for estimating $m_0$. For sites without fatless birds (Fontes and Viladecans), the equation of the nearest site was used. Manecorro and Vejer had less than 10 individuals each, so, owing to their proximity, we pooled both sites into a single equation.

All analyses were carried out using SPSS 15.0, except the Hierarchical Analysis of Clusters, which was done with PAST.

Table 2. Factor loadings of the two Principal Components from a Principal Component Analysis on the latitude of capture in Iberia and the shortest distances to the geographical barrier’s edges: distance to south Iberian coast [Dist(SI)], to north African coast [Dist(NA)] and to the south of the Sahara [Dist(SS)]. All the variables were correlated with the factor loadings of the PC1.
3. Results

Overall, we captured 1887 first-year Reed Warblers (each bird considered only once) with their body mass and wing length recorded. The number of first-year Reed Warblers captured per site ranged from 26 (Viladecans) to 437 (Jaizubia). Mean body mass ± SE for the complete data set was 10.9 ± 0.03 g \((n = 1887)\), and ranged from 10.0 ± 0.1 g (Salreu, \(n = 200\)) to 11.8 ± 0.3 g (Fontes, \(n = 27\)) (Fig. 2). The 25% heaviest fraction of birds, the most likely to be ready to depart, had a mean body mass of 12.7 g ± 0.1 g \((n = 462)\), ranging from 11.3 ± 0.1 g (Salreu, \(n = 50\)) to 14.2 ± 0.5 g (Fontes, \(n = 6\)) (Fig. 2).

The HAC revealed two clusters of localities in relation to Reed Warblers’ size-corrected body mass index (Fig. 3). Such clusters, however, were not correlated with the geographic distance between localities (Mantel test: \(r = -0.039, P = 0.592\)), suggesting that body mass was independent of geographic location in Iberia and the distance between sampling sites.

We tested 7 linear models overall. Only one model was observed to fit the data better than the rest: the one including the interactions between route and date and route and location of capture in Iberia (Table 3). Both interaction terms were significant although the principal effect of date was not (Table 4). Body mass tended to increase in WI towards the south but to decrease in EI (Fig. 4), whilst remaining unchanged in CI. Moreover, body mass tended to increase with date in EI, whereas in CI and WI remained constant as season progressed (Fig. 4). The daily number of captures varied between routes (Wald \(\chi^2 = 18.441, P < 0.001\)) and the interaction of latitude with date was significant (Wald \(\chi^2 = 6.417, P = 0.011\)). Later in the season captures tended to decrease in northern latitudes and increased towards the south \((B_{\text{latitude} \times \text{date}} = -0.032)\).

Potential flight ranges from each site revealed that, on average, Reed Warblers stopping over at southern Iberian sites (Vejer, Manecorro and Fontes) could reach the north African coast without further refuelling (Table 5). The south of the Sahara Desert could not be reached from any site in Iberia on average (Table 5), and none of the Reed Warblers had enough fuel to do so. The 25% fraction of heaviest birds could reach north Africa.
from sites further north, such as Canal Vell, Pego, Arroyo Budión and Las Minas (Table 5).

4. Discussion

Average body masses of first-year Reed Warblers captured in Iberia during the autumn migration period were low, especially when compared to values obtained in other works in southern Iberia (Peiro 1995, Schaub & Jenni 2000a, Hilgerloh & Wiltischko 2000) or in northern Europe (Chernetsov 1999, Schaub & Jenni 2000a). Reed Warblers have been reported to show high year to year variations in body condition even near the edge of geographical barriers (Yosef & Chernetsov 2005). Although this may explain the discrepancy between our results, which included a single season, and other previous works, it is also possible that heavy birds were underrepresented in our data, given their lower mobility (Bairlein 1987, Titov 1999, 94 ORNIS FENNICA Vol. 91, 2014

Table 3. The 7 linear models applied to investigate the effect of route, date and latitude on the body mass index of Reed Warblers captured in Iberia during the autumn migration period. The models are ranked according their AICc values (small sample sizes' corrected Akaike Information Criterion). ∆AICc is the difference in AICc in relation to the most parsimonious model.

<table>
<thead>
<tr>
<th>Model</th>
<th>Effects included</th>
<th>AICc</th>
<th>∆AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Route, Location, Date, Route × Location, Route × Date</td>
<td>-6083.13</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>Route, Location, Route × Location</td>
<td>-6036.93</td>
<td>46.20</td>
</tr>
<tr>
<td>3</td>
<td>Route, Date, Route × Date</td>
<td>-6001.14</td>
<td>81.99</td>
</tr>
<tr>
<td>4</td>
<td>Route, Location, Date</td>
<td>-5997.13</td>
<td>85.99</td>
</tr>
<tr>
<td>5</td>
<td>Route, Date</td>
<td>-5994.92</td>
<td>88.20</td>
</tr>
<tr>
<td>6</td>
<td>Route</td>
<td>-5965.68</td>
<td>117.45</td>
</tr>
<tr>
<td>7</td>
<td>Route, Location</td>
<td>-5965.60</td>
<td>117.53</td>
</tr>
</tbody>
</table>

Table 4. Wald $\chi^2$ values for each effect of the best model (model 1 in Table 2) explaining body mass variation of Reed Warblers stopping over in Iberia during the autumn migration period.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Wald $\chi^2$</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Route</td>
<td>22.733</td>
<td>3</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Location</td>
<td>1.051</td>
<td>1</td>
<td>0.305</td>
</tr>
<tr>
<td>Date</td>
<td>25.939</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Route × Location</td>
<td>84.692</td>
<td>2</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Route × Date</td>
<td>8.256</td>
<td>2</td>
<td>0.016</td>
</tr>
</tbody>
</table>

Table 5. Mean potential flight ranges in km (± SE) of Reed Warblers from each sampling site in Iberia assuming an intermittent flying strategy. Flight ranges are reported for the entire sample (Range 100%) and for the 25% heaviest fraction of birds (Range 25%). Additionally, we indicate the shortest distance (in km) from each site to the south Iberian coast (S Iberia), north African coast (N Africa), and southern border of the Sahara (S Sahara).

<table>
<thead>
<tr>
<th>Site</th>
<th>Range 100%</th>
<th>Range 25%</th>
<th>S Iberia</th>
<th>N Africa</th>
<th>S Sahara</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fontes</td>
<td>431 ± 62</td>
<td>811 ± 91</td>
<td>7</td>
<td>275</td>
<td>1,775</td>
</tr>
<tr>
<td>Vejer</td>
<td>420 ± 47</td>
<td>875 ± 52</td>
<td>8</td>
<td>52</td>
<td>1,552</td>
</tr>
<tr>
<td>Canal Vell</td>
<td>332 ± 16</td>
<td>701 ± 26</td>
<td>509</td>
<td>469</td>
<td>1,968</td>
</tr>
<tr>
<td>Viladecans</td>
<td>302 ± 44</td>
<td>533 ± 84</td>
<td>626</td>
<td>521</td>
<td>2,021</td>
</tr>
<tr>
<td>Taipal</td>
<td>252 ± 33</td>
<td>579 ± 66</td>
<td>339</td>
<td>545</td>
<td>2,045</td>
</tr>
<tr>
<td>Manecorro</td>
<td>223 ± 61</td>
<td>669 ± 125</td>
<td>11</td>
<td>136</td>
<td>1,636</td>
</tr>
<tr>
<td>Las Minas</td>
<td>275 ± 46</td>
<td>688 ± 78</td>
<td>385</td>
<td>501</td>
<td>2,001</td>
</tr>
<tr>
<td>Jaizubia</td>
<td>224 ± 11</td>
<td>520 ± 16</td>
<td>725</td>
<td>802</td>
<td>2,303</td>
</tr>
<tr>
<td>Arroyo Budión</td>
<td>206 ± 53</td>
<td>590 ± 120</td>
<td>225</td>
<td>348</td>
<td>1,848</td>
</tr>
<tr>
<td>Pego</td>
<td>187 ± 13</td>
<td>508 ± 24</td>
<td>292</td>
<td>282</td>
<td>1,782</td>
</tr>
<tr>
<td>El Cruce</td>
<td>152 ± 10</td>
<td>393 ± 17</td>
<td>590</td>
<td>678</td>
<td>2,178</td>
</tr>
<tr>
<td>Salreu</td>
<td>152 ± 13</td>
<td>390 ± 23</td>
<td>401</td>
<td>596</td>
<td>2,095</td>
</tr>
</tbody>
</table>
We found that the north-south body mass variation in Iberia was not homogeneous, as it varied between migratory flyways, suggesting that, when descending to a more regional scale, Reed Warblers’ fuelling strategy is flexible and can be shaped by other factors apart from just distance to the barrier’s edge. Thus, Reed Warblers passing through EI tended to be more fuel loaded at sites located further north and further from the barrier’s edge, whereas the opposite was observed in WI. In CI, some southern sites were found to record higher mean body masses, but some northern sites showed similar values (i.e. Jaizubia and Vejer).

Furthermore, in southern Iberia birds at sites which were very close together were observed to have very different values (i.e. Manecorro and Vejer). Such differences may be due to differences in habitat quality (Ktitov et al. 2008, Chernetsov 2013).

Thus, at a site where reed beds were not the dominant vegetation (Manecorro), body masses were lower than at nearby stations with abundant reed beds. Therefore, at a relatively local scale, the distribution of suitable habitats probably shapes body mass patterns across different routes of migration (Moore & Aborn 2000, Fransson et al. 2008, Chernetsov 2013). Consequently (or alternatively), our findings may be related to a different sea crossing preparation of the Reed Warblers passing through each migratory flyway in Iberia. In WI, Reed Warblers seem to accumulate an amount of fuel required to just reach a close (one-day flight) next stopover site, except in the south, where they would increase their energy stores to reach the north of Africa (Weber et al. 1998). In EI, however, Reed Warblers seem to preferably gain fuel at reed beds located further from south Iberian coast, in northern latitudes (maybe given the lack of suitable reed beds in southeastern Iberia).

Southern sites would act more as resting sites instead of true fuelling ones and as a result body mass decreases from north to south along this route, since the distance to northern Africa (with target stopover sites that would be used to gain fuel before the Sahara crossing) is shortened. Also, a fraction of Reed Warblers could cross the Mediterranean directly from reed beds further north without needing to reach the southern Iberia coast before “jumping” to Africa. We have no data to determine departure direction from these two sites to support this hypothesis.

In EI, body mass increased with date, as expected according to other works (Schaub & Jenni 2000a, Bayly 2006). However, in the rest of Iberia, body masses remained constant as season progressed. Differences in body mass change with date between flyways can be associated to a differential passage of European populations in Iberia (Maggini et al. 2013, Andueza et al. 2013). Thus, in CI and WI populations with similar body masses would pass during the whole migration period, whereas populations in EI would present different fuel loads. Moreover, the use of the sites within routes was not homogeneous during all the study period, as Reed Warblers were more abun-
dant in southern sites than in northern ones later in the season.

The estimation of flight ranges showed that birds could reach the north-African coast only from southern Iberia. If we consider the 25% heaviest birds, hence focusing on those birds more likely to be about to depart, then those from EI could also reach the north of Africa. Thus, fuel accumulation before the Sahara Desert may happen in northern Africa, as concluded by Schaub & Jenni (2000a). A number of authors have pointed out the importance of this area as a key fuelling area between tropical Africa and Europe (e.g., Maggini & Bairlein 2011). Moreover, the sea crossing between Iberia and Africa could demand extra fuel accumulation (a safety strategy) as the flight ranges observed, especially in southern Iberia, exceeded the north of Africa. However, our findings seem to contradict previous estimations where Reed Warblers were described as being able to make a non-refuelling flight from northern Iberia to northern Africa (Arizaga et al. 2011b), and from southern Iberia to tropical Africa (Hilgerloh & Wiltshcko 2000).

In these cases flight ranges were calculated assuming a faster airspeed (60 km/h) and a non-stop flying strategy, without regarding the important energetic costs of diurnal stopovers (Wikelski et al. 2003). Our results are similar to what was found for first-year Savi’s Warblers (Locustella luscinioides) in Portugal (Neto et al. 2008). However, real flight ranges could be higher because we used here fuel loads of first captures at ringing stations, which would be lower than departure fuel loads. Estimations were made considering still air conditions, but migrants usually select the best (or the least worse) wind conditions to perform their migratory flights (e.g. Weber & Hedenström 2000, Dänhardt & Lindström 2001, Tsvey et al. 2007, Morganti et al. 2011). Hence, depending on the frequency of favourable wind conditions during the migratory period (tailwinds vs. headwinds), real flight ranges could be increased or decreased. Moreover, adult birds would probably have longer flight ranges (Woodrey & Moore 1997), because fuel loads in adult birds are commonly higher than in first-year birds (Merom et al. 1999, Heise & Moore 2003, Arizaga & Barba 2009).

Although fuel load of migrants before barriers crossing has been the target goal of several studies (e.g. Fransson et al. 2006, 2008, Delingat et al. 2008, Yohannes et al. 2009), its geographical variation at a more local scale in the proximities of a geographical barrier has not been studied in detail. We have highlighted that the fuelling strategy of Reed Warblers in Iberia before the sea and the Sahara Desert crossing is consistent with that described by Schaub & Jenni (2000a), as Iberia is not used to gain the large fuel loads that would be required to reach tropical Africa without further refuelling. Additionally, we have reported how sea crossing constitutes an energetically demanding challenge for Reed Warblers, which must accumulate relatively important fuel reserves to overly it. However, the factors shaping fuel storage are more than just the distance to the geographical barrier, in this particular case distance to the Atlantic or the Mediterranean Sea, and there may be underlying geographical or stopover quality-associated factors, revealing that a higher degree of landscape complexity in the fuelling strategy of Reed Warblers in relation to barrier crossing exists (Ktitorov et al. 2008).

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Nuorten rytkerttusten ruumiinpainon maantieteellinen vaihtelu Iberian niemimaalla


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