

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

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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-



blers from 12 localities within Iberia during the autumn migration period of 2009. We run linear models to analyze the effects of location in Iberia, date, and body size on body mass variation at each migratory flyway (eastern, central and western Iberia). Flight ranges from each site were also calculated. Our results showed that Reed Warblers in Iberia had the necessary fuel needed to arrive in northern Africa but not to tropical Africa. However, body mass patterns varied depending on the geographical region (eastern, central or western Iberia). Date did not affect body mass in central and western Iberia, but in eastern Iberia heavier birds tended to pass later. Thus, the factors shaping body mass of Reed Warblers in Iberia before the sea crossing to Africa seemed to be more complex than just the distance to this geographical barrier, with underlying stopover quality-associated factors possibly playing a relevant role.

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).

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).

Route	Locality (CODE)	Coordinates	Mist nets (m)	Sampling period (freq.)	Captures
E	Viladecans (VILA)	42°18'N, 02°07'E	207	18 Sep–30 Sep (daily)	26
E	Canal Vell (CANA)	40°43'N, 00°44'E	210–240	10 Aug–30 Sep (daily)	304
E	Pego (PEGO)	38° 50'N, 00°07'W	90	10 Aug–30 Sep (daily)	319
C	Jaizubia (JAIZ)	43°21'N, 01°49'W	240	10 Aug–30 Sep (daily)	437
C	El Cruce (CRUC)	42° 01'N, 04°49'W	162	10 Aug–30 Sep (daily)	344
C	Las Minas (MINA)	40°13'N, 03°35'W	138	10 Aug–30 Sep (weekly)	45
C	Arroyo Budi6n (ARRO)	39°03'N, 48°00'W	36	10 Aug–30 Sep (fortnightly)	33
C	Manecorro (MANE)	36°56'N, 06°21'W	252	01 Sep–30 Sep (daily)	28
C	Vejer (VEJE)	36°15'N, 05°58'W	210	10 Aug–30 Sep (weekly)	58
W	Salreu (SALR)	40° 44'N, 08° 33'W	108–120	10 Aug–30 Sep (weekly)	200
W	Taipal (TAIP)	40° 11'N, 08° 41'W	240	10 Aug–14 Sep (weekly)	66
W	Sitio das Fontes-Charito (FONT)	37°10'N, 08°27'W	40–164	10 Aug–30 Sep (weekly)	27

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 (Telleria *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.

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 sympatry at stopover sites during the migration period. Since we were interested in studying true migrants (thus avoiding local birds still moulting 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).

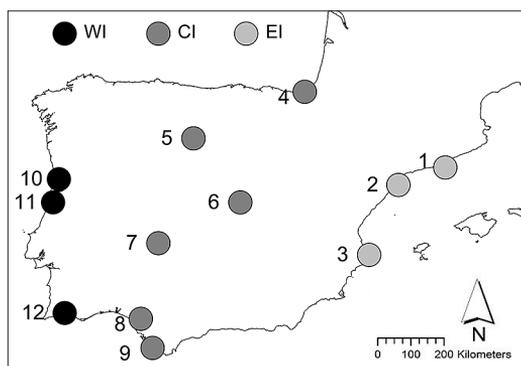


Fig. 1. Sampling localities in Iberia. Eastern Iberia (EI): 1. Viladecans, 2. Canal Vell, 3. Pego; Central Iberia (CI): 4. Jaizubia, 5. El Cruce, 6. Las Minas, 7. Arroyo Budi3n, 8. Manecorro, 9. Vejer; Western Iberia (WI): 10. Salreu, 11. Taipal, 12. Fontes.

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 than 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-

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.

Variable	PC 1	PC 2
Latitude	+0.51	+0.19
Dist(SI)	+0.49	+0.74
Dist(NA)	+0.50	-0.46
Dist(SS)	+0.50	-0.46
Eigenvalue	3.86	0.14
% Variance	96.47	3.45

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 south Iberian coast, northern Africa and tropical Africa (i.e., distance to geographical barriers edges). The PC1 was the only component from the PCA with an eigenvalue > 1, and it explained > 95% of the total variance (Table 2). Higher positive values of PC1 were related to locations situated in more northern latitudes and further from the southern coast of Iberia, the north African coast and tropical Africa. In the construction of linear models we considered both additive and interaction models, including double interactions between the factor "route" and the covariates. We used the small sample sizes' corrected Akaike Information Criterion (AICc) to select the models that best fitted to data (Burnham & Anderson 1998). Models with a difference of AICc < 2 were considered to fit similarly to data. Complementary, we run a linear model on daily number of captures as dependent variable, with route as factor and

both date and latitude as covariates so as to see if the duration of the migratory peak was homogeneous within Iberia.

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.

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 \pm 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 ± 0.1 g ($n = 462$), ranging from 11.3 ± 0.1 g (Salreu, $n = 50$) to 14.2 ± 0.5 (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,

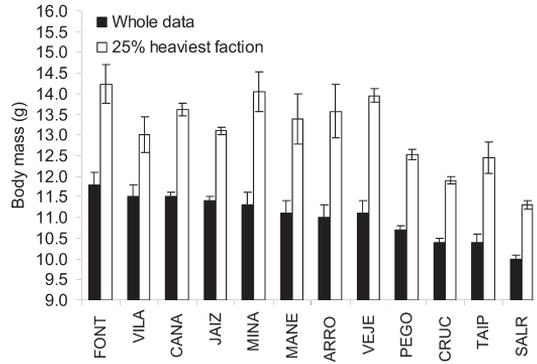


Fig. 2. Mean body mass (weight) \pm SE of Reed Warblers for the entire sample, and the 25% heaviest birds fraction at each locality.

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

Fig. 3. Cluster showing the distance (km) between sites (left) and diagram obtained from a Hierarchical Analysis of Clusters showing the Euclidean distance between localities in relation to size-corrected body mass of Reed Warblers (right).

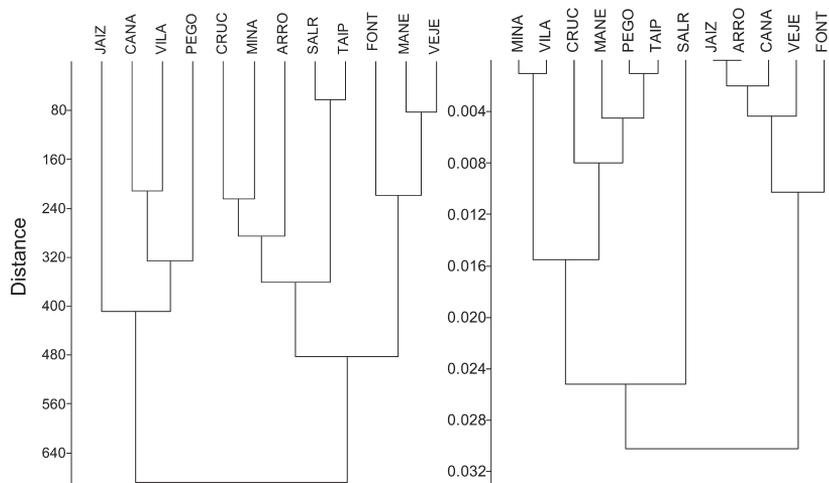


Table 3. The 7 linear models applied to investigate the effect of route, date and latitude on the body mass index of Reed Warblers captured in Iberia during the autumn migration period. The models are ranked according their AICc values (small sample sizes' corrected Akaike Information Criterion). Δ AICc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

Model	Effects included	AICc	Δ AICc
1	Route, Location, Date, Route \times Location, Route \times Date	-6083.13	0.00
2	Route, Location, Route \times Location	-6036.93	46.20
3	Route, Date, Route \times Date	-6001.14	81.99
4	Route, Location, Date	-5997.13	85.99
5	Route, Date	-5994.92	88.20
6	Route	-5965.68	117.45
7	Route, Location	-5965.60	117.53

from sites further north, such as Canal Vell, Pego, Arroyo Budi3n 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 & Wiltshcko 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

Table 4. Wald χ^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.

Effect	Wald χ^2	df	P
Route	22.733	3	< 0.001
Location	1.051	1	0.305
Date	25.939	1	< 0.001
Route \times Location	84.692	2	< 0.001
Route \times Date	8.256	2	0.016

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,

Table 5. Mean potential flight ranges in km (\pm 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).

Site	Range 100%	Range 25%	S Iberia	N Africa	S Sahara
Fontes	431 \pm 62	811 \pm 91	7	275	1,775
Vejer	420 \pm 47	875 \pm 52	8	52	1,552
Canal Vell	332 \pm 16	701 \pm 26	509	469	1,968
Viladecans	302 \pm 44	533 \pm 84	626	521	2,021
Taipal	252 \pm 33	579 \pm 66	339	545	2,045
Manecorro	223 \pm 61	669 \pm 125	11	136	1,636
Las Minas	275 \pm 46	688 \pm 78	385	501	2,001
Jaizubia	224 \pm 11	520 \pm 16	725	802	2,303
Arroyo Budi3n	206 \pm 53	590 \pm 120	225	348	1,848
Pego	187 \pm 13	508 \pm 24	292	282	1,782
El Cruce	152 \pm 10	393 \pm 17	590	678	2,178
Salreu	152 \pm 13	390 \pm 23	401	596	2,095

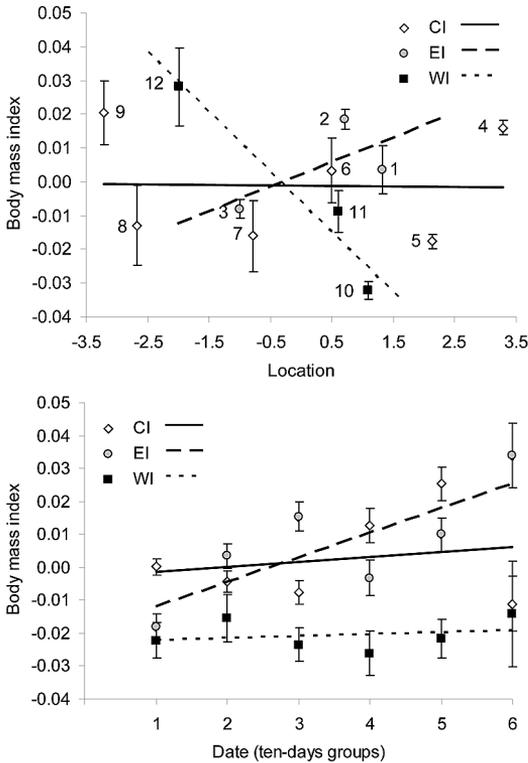


Fig. 4. Variation in Reed Warblers size-corrected body mass index (Mean \pm SE) depending on the location (above) and date (below) in eastern (EI: 1. Viladecans, 2. Canal Vell, 3. Pego), central (CI: 4. Jaizubia, 5. El Cruce, 6. Las Minas, 7. Arroyo Budi3n, 8. Manecorro, 9. Vejer) and western Iberia (WI: 10. Salreu, 11. Taipal, 12. Fontes). The variable date is shown as groups of ten sampling days.

Chernetsov 2006) and thus their lower capture probability.

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 (Kitorov *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 region 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 & Wiltschko 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 luscinoides*) 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 overfly 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 rytikerttusten ruumiinpainon maantieteellinen vaihtelu Iberian niemimaalla

Eurooppalaiset Saharan eteläpuolelle talveksi muuttavat linnut joutuvat ylittämään kaksi suurta maantieteellistä estettä, Välimeren ja Saharan aavikon, mikä vaatii huomattavasti vararavintoa. Suurin osa muuttajista kartuttaa vararavintoa Saharan ylittämistä varten Pohjois-Afrikassa, mutta Afrikkaan siirtymistä varten vararavintoa kerätään Iberian niemimaalla. Vaikka useat tutkimukset ovat selvittäneet vararavinnon karttumista ennen maantieteellisten esteiden ylittämistä, tunnetaan silti huonosti mitkä seikat etäisyyden lisäksi vaikuttavat vararavinnon kertymisen maantieteelliseen jakaumaan.

Tätä kysymystä selvittääksemme tutkimme ensimmäisen kalenterivuoden syysmuutolla olevia rytikerttusia 12 paikassa Iberian niemimaalla vuonna 2009. Tutkimme lineaaristen mallien avulla paikan, ajoituksen ja linnun koon yhteyttä painon vaihteluun eri muuttoreiteillä (Iberian niemimaan itä-, keski- ja länsiosia). Lisäksi laskettiin lentomatkojen kantamat kultakin paikalta.

Tuloksemme osoittivat, että rytikerttusilla on Iberian niemimaalla riittävästi vararavintoa muuttaa Pohjois-Afrikkaan, mutta ei Saharan eteläpuoleiseen Afrikkaan. Ruumiinpainon jakauma vaihteli kuitenkin maantieteellisestä alueesta riippuen (itä-, keski- ja länsiosia). Ajoitus ei vaikuttanut linnun painoon keskimmaisella tai läntisellä muuttoreitillä, mutta itäisellä muuttoreitillä painavimmat linnut muuttivat keskimäärin myöhemmin. Näin ollen ennen meren ylitystä Iberian niemimaalla rytikerttusten painon kertymiseen näyttävät vaikuttavan muutkin tekijät kuin ainoastaan etäisyys maantieteelliseen esteeseen. Levähdyspaikkojen laadulla voi mahdollisesti olla tärkeä rooli painon kertymisessä.

References

- Alerstam, T. & Lindström, Å. 1990: Optimal migration: the relative importance of time, energy and safety. — In *Bird Migration: Physiology and Ecophysiology* (ed. E. Gwinner): 352–367. Springer, Berlin.
- Alerstam, T., Hedenström, A. & Åkesson, S. 2003: Long-distance migration: evolution and determinants. — *Oikos* 103: 247–260.
- Andueza, M., Barba, E., Arroyo, J.L., Feliu, J., Greño, J.L., Jubete, F., Lozano, L., Monrós, J.S., Moreno-Opo, R., Neto, J.M., Onrubia, A., Tenreiro, P., Valkenburg, T., Zumalacárregui, C., González, C., Herrero, A. & Arizaga, J. 2013: Connectivity patterns in Reed Warblers *Acrocephalus scirpaceus* between breeding grounds in Europe and stopover sites in Iberia during autumn migration. — *Ardea* 101: 133–140.
- Arizaga, J. & Barba, E. 2009: Fuel load and flight ranges of blackcaps *Sylvia atricapilla* in northern Iberia during autumn and spring migrations. — *Current Zoology* 55: 401–440.
- Arizaga, J., Arroyo, J.L., Rodríguez, R., Martínez, A., San-Martín, I. & Sallett, Á. 2011a: Do Blackcaps *Sylvia atricapilla* stopping over at a locality from Southern Iberia refuel for crossing the Sahara? — *Ardeola* 58: 71–85.
- Arizaga, J., Sánchez, J.M., Díez, E., Cuadrado, J.F., Asenjo, I., Mendiburu, A., Jauregi, J.I., Herrero, A., Elsegui, Z., Aranguren, I., Andueza, M. & Alonso, D. 2011b: Fuel load and potential flight ranges of passerine birds migrating through the western edge of the Pyrenees. — *Acta Ornithologica* 46: 19–28.
- Bairlein, F. 1985: Body weights and fat deposition of paleo-arctic passerine migrants in the Central Sahara. — *Oecologia* 66: 141–146.
- Bairlein, F. 1987: The migratory strategy of the Garden Warbler: a survey of field and laboratory data. — *Ringling & Migration* 8: 59–72.
- Bairlein, F. 1991: Body mass of Garden Warblers (*Sylvia borin*) on migration: a review of field data. — *Vogelwarte* 36: 48–61.
- Bayly, N.J. 2006: Optimality in avian migratory fuelling behaviour: a study of a trans-Saharan migrant. — *Animal Behaviour* 71: 173–182.
- Bernis, F. 1980: La migración de las aves en el estrecho de Gibraltar. Vol. 1. Aves planeadoras. — Universidad Complutense de Madrid, Madrid. (In Spanish)
- Burnham, K.P. & Anderson, D.R. 1998: Model selection and inference. A practical information theoretic approach. — 1st edn. Springer-Verlag, New York.
- Bruderer, B. & Boldt, A. 2001: Flight characteristics of birds: I. Radar measurements of speeds. — *Ibis* 143: 178–204.
- Cantos, F.J. & Tellería, J.L. 1994: Stopover site fidelity of four migrant warblers in the Iberian Peninsula. — *Journal of Avian Biology* 25: 131–134.
- Casement, M.B. 1966: Migration across the Mediterranean observed by radar. — *Ibis* 108: 461–491.
- Cramp, S. 1992: Handbook of the Birds of Europe, the Middle East and North Africa, Vol. 6. — Oxford Univ. Press, Oxford.
- Chernetsov, N. 1999: Timing of spring migration, body condition, and fat score in local and passage populations of the Reed Warbler *Acrocephalus scirpaceus* on the Courish Spit. — *Avian Ecology & Behaviour* 2: 75–88.

- Chernetsov, N. 2006: Habitat selection by nocturnal passerine migrants en route: mechanisms and results. — *Journal of Ornithology* 147: 185–191.
- Chernetsov, N. 2013: Body mass of European Robins *Erithacus rubecula* at migratory stopovers is strongly habitat-related. — *Avian Ecology & Behaviour* 23: 15–21.
- Dänhart, J. & Lindström, Å. 2001: Optimal departure decisions of songbird from an experimental stopover site and the significance of weather. — *Animal Behaviour* 62: 235–243.
- Delingat, J., Bairlein, F. & Hedenström, A. 2008: Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). — *Behavioral Ecology & Sociobiology* 62: 1069–1078.
- Ellegren, H. & Fransson, T. 1992: Fat loads and estimated flight-ranges in four *Sylvia* species analysed during autumn migration at Gotland, South-East Sweden. — *Ringing & Migration* 13: 1–12.
- Finlayson, J.C. 1992: *Birds of the Straits of Gibraltar*. — Academic Press, London.
- Fransson, T., Jakobsson, S. & Kullberg, C. 2005: Nonrandom distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover sites. — *Journal of Avian Biology* 36: 6–11.
- Fransson, T., Jakobsson, S., Kullberg, C., Mellroth, R. & Pettersson, T. 2006: Fuelling in front of the Sahara desert in autumn—an overview of Swedish field studies of migratory birds in the eastern Mediterranean. — *Ornis Svecica* 16: 74–83.
- Fransson, T., Barboutis, C., Mellroth, R. & Akriotis, T. 2008: When and where to fuel before crossing the Sahara desert—extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*. — *Journal of Avian Biology* 39: 133–138.
- Galarza, A. & Tellería, J.L. 2003: Linking processes: effects of migratory routes on the distribution of abundance of wintering passerines. — *Animal Biodiversity & Conservation* 26: 19–27.
- Grandío, J.M. & Belzunce, J.A. 1987: The autumn migration of *Acrocephalus* warblers and other reed passerines in the Valley of Jaizubia (Guipuzcoa). — *Munibe* 39: 81–94.
- Gosler, A.G., Greenwood, J.J.D., Baker, J.K. & Davidson, N.C. 1998: The field determination of body size and condition in passerines: a report to the British Ringing Committee. — *Bird Study* 45: 92–103.
- Hedenström, A. & Alerstam, T. 1997: Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. — *Journal of Theoretical Biology* 189: 227–234.
- Heise, C.D. & Moore, F.R. 2003: Age-related differences in foraging efficiency, molt, and fat deposition of Grey Catbirds prior to autumn migration. — *The Condor* 105: 496–504.
- Hilgerloh, G. & Wiltshko, W. 2000: Autumn fat load and flight range of passerine long-distance migrants in southwestern Spain and northwestern Morocco. — *Ardeola* 47: 259–263.
- Hussell, D.J.T. & Lambert, A.B. 1980: New estimates of weight loss in birds during nocturnal migration. — *The Auk* 97: 547–558.
- Ktitorov, P., Bairlein, F. & Dubinin, M. 2008: The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. — *Landscape Ecology* 23: 169–179.
- Kvist, A., Klaasen, M. & Lindström, Å. 1998: Energy expenditure in relation to flight speed: what is the power of mass loss rate estimates? — *Journal of Avian Biology* 29: 485–498.
- Maggini, I. & Bairlein, F. 2011: Body condition and stopover of trans-Saharan spring migrant passerines caught at a site in southern Morocco. — *Ringing & Migration* 26: 31–37.
- Maggini, I., Spina, F., Voigt, C.C., Ferri, A. & Bairlein, F. 2013: Differential migration and body condition in Northern Wheatears (*Oenanthe oenanthe*) at a Mediterranean spring stopover site. — *Journal of Ornithology* 154: 321–328.
- Martí, R. & Moral, J.C. 2003: *Atlas de las Aves Reproductoras de España*. — Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid. (In Spanish)
- Meijer T., Möhring F.J. & Trillmich F.J. 1994: Annual and daily variation and body mass of starlings *Sturnus vulgaris*. — *Journal of Avian Biology* 25: 98–104.
- Merom, K., McCleery, R. & Yom-Tov, Y. 1999: Age-related changes in wing-length and body mass in the Reed Warbler *Acrocephalus scirpaceus* and Clamorous Reed Warbler *A. stentoreus*. — *Bird Study* 46: 249–255.
- Moore, F.R. & Aborn, D. 2000: Mechanisms of *en route* habitat selection: How do migrants make habitat decisions during stopover? — *Studies in Avian Biology* 20: 34–42.
- Moreau, R.E. 1953: Migration in the Mediterranean area. — *Ibis* 95: 329–364
- Moreau, R.E. 1972: *The palearctic-African bird migration systems*. — Academic Press, New York.
- Morganti, M., Mellone, U., Bogliani, G., Saino, N., Ferri, A., Spina, F. & Rubolini, D. 2011: Flexible tuning of departure decisions in response to weather in black redstarts *Phoenicurus ochruros* migrating across the Mediterranean Sea. — *Journal of Avian Biology* 42: 323–334.
- Navedo, J.G., Masero, J.A., Overdijk, O., Orizaola, G. & Sánchez-Guzmán J.M. 2010: Assessing the role of multiple environmental factors on Eurasian Spoonbill departure decisions from stopover sites. — *Ardea* 98: 3–12.
- Neto, J.M., Encarnação, V., Fearon, P. & Gosler A.G. 2008: Autumn migration of Savi's Warblers *Locustella luscinioides* in Portugal: differences in timing, fuel deposition rate and non-stop flight range between the age classes. — *Bird Study* 55: 78–85.
- Peiro, I.G. 1995: Patterns of abundance, body-mass dynam-

- mics and habitat use of the reed warbler *Acrocephalus scirpaceus* in two reedbeds of south-eastern Spain. — Ringing and Migration 16: 100–108.
- Rubolini, D., Gardiazabal, A., Pilastro, A. & Spina, F. 2002: Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. — Journal of Avian Biology 33: 15–22.
- Salewski, V., Schmaljohann, H. & Lietchi, F. 2010: Spring passerine migrants stopping over in the Sahara are not fall-outs. — Journal of Ornithology 151: 371–378.
- Schaub, M. & Jenni, L. 2000a: Body mass of six long-distance migrant passerine species along the autumn migration route. — Journal für Ornithologie 141: 441–460.
- Schaub, M. & Jenni, L. 2000b: Fuel deposition of three passerine bird species along the migratory route. — Oecologia 122: 306–317.
- Schaub, M. & Jenni, L. 2001: Variation of fuelling rates among sites, days and individuals in migrating passerine birds. — Functional Ecology 15: 584–594.
- Schaub, M., Pradel, R., Jenni, L. & Lebreton, J.D. 2001: Migrating birds stopover longer than usually thought: an improved capture-recapture analysis. — Ecology 3: 852–859.
- Schmaljohann, H., Liechti, F. & Bruderer, B. 2007: Songbird migration across the Sahara: the non-stop hypothesis rejected! — Proceedings of the Royal Society B 274: 736–739.
- Svensson, L. 1992: Identification guide to European passerines. — 4th edn. L. Svensson, Stockholm.
- Tellería, J.L. 1981: La migración de las aves en el estrecho de Gibraltar. Vol 2. Aves no planeadoras. — Universidad Complutense, Madrid. (In Spanish)
- Tellería, J.L., Asensio, B. & Díaz, M. 1999: Aves Ibéricas. II. Paseriformes. — J.M. Reyero Editor, Madrid. (In Spanish)
- Titov, N. 1999: Fat level and temporal pattern of diurnal movements of Robins (*Erithacus rubecula*) at an autumn stopover site. — Avian Ecology & Behaviour 2: 89–99.
- Tsvey, A., Bulyuk, V.N. & Kosarev, V. 2007: Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. — Behavioral Ecology & Sociobiology 61: 1665–1674.
- Weber, T.P. & Hedenström, A. 2000: Optimal stopover decisions under wind influence: the effects of correlated winds. — Journal of Theoretical Biology 205: 95–104.
- Weber, T.P., Ens, B.J. & Houston, A.I. 1998: Optimal avian migration: A dynamic model of fuel stores and site use. — Evolutionary Ecology 12: 377–401.
- Wikelski, M., Tarlow, E.M., Raim, A., Diehl, R.H., Larkin, R.P. & Visser, G.H. 2003: Costs of migration in free-flying songbirds. — Nature 423: 704.
- Woodrey, M.S. & Moore, F.R. 1997: Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. — The Auk 114: 695–707.
- Yohannes, E., Biebach, H., Nikolaus, G. & Pearson, D.J. 2009: Passerine migration strategies and body mass variation along geographic sectors across East Africa, the Middle East and the Arabian Peninsula. — Journal of Ornithology 150: 369–381.
- Yosef, R. & Chernetsov, N. 2005: Longer is fatter: body mass changes of migrant reed warblers (*Acrocephalus scirpaceus*) staging at Eilat, Israel. — Ostrich 76: 142–147.