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DEPARTURE DECISIONS OF A MIGRATORY PASSERINE, THE COMMON REED-WARBLER *ACROCEPHALUS SCIRPACEUS*, IN RELATION TO FUEL LOAD AND GEOGRAPHICAL BARRIER PROXIMITY

DECISIONES DE PARTIDA EN UN PASERIFORME MIGRATORIO, EL CARRICERO COMÚN *ACROCEPHALUS SCIRPACEUS,* CON RELACIÓN A LA CARGA DE RESERVAS Y LA PROXIMIDAD A BARRERAS GEOGRÁFICAS

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Summary.—Research on the stopover ecology of migrant birds has examined the role of multiple factors, both intrinsic and extrinsic, on departure decisions. However, a single factor may influence stopover decisions differentially, depending on the relative geographic location of a stopover site within the flyway and the expectation of ecological challenges ahead. For instance, actual fuel load may have a decisive influence on departure decisions before a crossing of major geographical barriers, such as seas or deserts, but may be less important when crossing vast continental areas offering plenty of opportunities to refuel. The aim here was to test whether the relative influence of fuel load on departure decisions of the Common Reed-warbler *Acrocephalus scirpaceus*, a long-distance migrant songbird, varies in relation to proximity to a geographical barrier: the sea expanse between Iberia and Africa. We expected that departure from southern Iberian stopover sites would be highly influenced by fuel load, since migrants would not fly to Africa until they had sufficient fuel to cross the sea. We used Cormack-Jolly-Seber (CJS) models to test for the effect of fuel load on emigration (departure) probability from a number of stopover sites situated in northern and southern Iberia during the autumn migration period. Reed-warblers stopping over for longer than one day were more likely to depart if they were in northern

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Iberia than in southern sites. Moreover, large fuel loads promoted emigration from stopover sites in northern, but not in southern, Iberia. Therefore, we found no evidence supporting the hypothesis that Reed-warblers wait until they acquire large fuel loads before leaving their stopover sites near the edge of the barrier. This study shows that the same parameters may not act in the same way along migration route, in particular in relation to geographical barrier proximity.—Andueza, M., Barba, E., Cuenca, D., Laso, M., Unamuno, E., Unanue, A.,Valkenburg, T., Genovart, M. & Arizaga, J. (2020). Departure decisions of a migratory passerine, the Common Reed-warbler *Acrocephalus scirpaceus*, in relation to fuel load and geographical barrier proximity. *Ardeola*, 67: 15-28.

Key words: *Acrocephalus scirpaceus,* Cormack-Jolly-Seber models, fat, food availability, fuel deposition rate, migration strategies, moult, sea crossing, stopover.

RESUMEN.—La investigación en materia de ecología en puntos de parada migratoria se ha centrado a menudo en el papel de los diversos factores que, bien extrínsecos o intrínsecos, influyen en la decisión de partir. No obstante, un solo factor también puede influir en la decisión de partir de manera diferencial, dependiendo de factores como la localización relativa de los puntos de parada en la ruta migratoria. Así, la carga de reservas podría tener un papel decisivo en la decisión de partir en zonas situadas justo antes del cruce de barreras geográficas importantes, como océanos o desiertos, pero no así en los casos en que la ruta migratoria discurre sobre áreas donde la posibilidad de recargar reservas es amplia. El objetivo de este artículo es comprobar si la influencia de la carga de reservas de carriceros comunes *Acrocephalus scirpaceus* en la decisión de partir de un área de parada migratoria varía según la localización de esta área respecto de la proximidad a una barrera como la franja de océano existente entre Europa y África. Concretamente, se esperaba que la importancia de este factor fuera mayor en el sur de la península ibérica, ya que las aves con pocas reservas no podrían cruzar la franja de océano mencionada. Para ello, se llevaron a cabo modelos de Cormack-Jolly-Seber (CJS) sobre datos obtenidos en varios puntos de parada migratoria, durante el periodo de paso posnupcial, tanto el norte como en el sur de la Península. La probabilidad de partir de la zona de parada en los carriceros del norte fue mayor que en los capturados al sur; además, se vio que la carga de reservas tuvo un efecto positivo en la decisión de partir en las localidades del norte, pero no en las del sur. Por ello, no hallamos evidencias que nos permitan asegurar que la influencia de la carga de reservas en la decisión de partida tuviera un efecto mayor en zonas situadas cerca de barreras geográficas. Nuestro artículo muestra que los mismos factores pueden tener un efecto diferente a lo largo de la ruta migratoria.—Andueza, M., Barba, E., Cuenca, D., Laso, M., Unamuno, E., Unanue, A.,Valkenburg, T., Genovart, M. y Arizaga, J. (2020). Decisiones de partida en un paseriforme migratorio, el carricero común *Acrocephalus scirpaceus,* con relación a la carga de reservas y la proximidad a barreras geográficas. *Ardeola*, 67: 15-28.

Palabras clave: *Acrocephalus scirpaceus,* cruce marino, disponibilidad de alimento, escala, estrategias migratorias, grasa, modelos Cormack-Jolly-Seber, muda, tasa de deposición de combustible.

INTRODUCTION

Migrating birds must often fly over areas, such as oceans or deserts, where there is no chance to land and/or gain fuel (Newton, 2008). Such geographical barriers have promoted the development of strategies for crossing them safely (Alerstam & Lindström, 1990; Lindström & Alerstam, 1992; Dierschke & Delingat, 2001). As a result, migrants must decide when to depart from particular stopover sites, taking into account their species-specific migration strategy and also the particular conditions prevailing at each particular site (Weber *et al.,* 1999; Arizaga *et al*., 2011a; Schmaljohann *et al*., 2011). Research on stopover ecology of migrant birds has dealt with the role of multiple factors, either intrinsic or extrinsic, on departure decisions (Åkesson *et al*., 2002; Schaub *et al*., 2004; Tsvey *et al*., 2007; Andueza *et al*., 2013a). The influence of specific factors driving departure decisions, moreover, can be region- or site-dependent, depending on the relative geographical location of that site and the ecological conditions expected further ahead, including potential fuelling opportunities (Bauer *et al.,* 2008; Schaub *et al.,* 2008). Thus, fuel load is an important consideration for migrants crossing geographical barriers (Schmaljohann *et al.,* 2013; Müller *et al.,* 2018).

Many passerines tend to accumulate large fuel loads before crossing large geographical barriers (Rubolini *et al*., 2002; Fransson *et al.,* 2008; Yohannes *et al*., 2009; Smolinsky *et al*., 2013). In this scenario, the sea crossing between Iberia and Africa is also known to require the accumulation of high fat reserves by a number of passerine species, this mainly at sites close to the south Iberian coast during the post-breeding movements (Hilgerloh & Wiltschko, 2000). In this case, departure from stopovers within this area should be expected to be highly influenced by actual fuel load, since migrants would not fly to Africa until they have acquired sufficiently large fuel reserves. By contrast, fuel might be expected to play a more marginal role in departure decisions made far from the barrier (Andueza *et al.,* 2013a). Alternatively, fuel load may also govern departure decisions from other sites, even if situated inland, especially if food availability is expected to be lower in areas located further south along the route (Bibby & Green, 1981; Schaub & Jenni, 2000b). In this last case, migrants will accumulate the energy reserves needed to cross these geographical barriers at stopover sites that are still distant from the barrier (Biebach, 1990).

Departure decisions from given stopover sites could be also masked by other factors apart from the geographical location of each site. Thus, departure decisions may be associated not with the location of a site in relation to the barrier but to the conditions existing in terms of fuel deposition rate (Schaub *et al*., 2008) or food availability (which itself determines rates of fuel accumulation; Schaub & Jenni, 2000b; Bayly, 2006; Smith & McWilliams, 2010). To some extent, fuel deposition rate can be considered as a site-quality related variable (Grandío, 1999). Analysis of fuel deposition rates at these stopover sites is also relevant in this context (Schaub & Jenni, 2000b).

In bird species in which moult and migration can overlap, it is observed that fuel deposition rates can be compromised until the moult has been completed (Schaub & Jenni, 2000b). Consequently, moulting migrants should have lower rates of fuel accumulation, and may be less likely to depart under given conditions, when compared to those that have finished their moult (Schaub *et al*., 2008).

The aim of this work was to test whether the relative influence of fuel load (controlling for the presence of still moulting birds) on the departure decisions of the Common Reed-warbler *Acrocephalus scirpaceus*, a long-distance migrant songbird, varies in relation to proximity to a geographical barrier: the expanse of sea between Iberia and Africa. For this, we compared departure probability from a number of stopover sites situated in northern and southern Iberia during the autumn migration period, using Cormack-Jolly-Seber (CJS) models.

METHODS

Study species

The Common Reed-warbler is a widespread Palaearctic, trans-Saharan migrant, passerine species, which breeds across most of Europe and overwinters in tropical Africa (Cramp, 1992). The autumn migration period of Reed-warblers in Iberia ranges from mid-July to mid-October (Tellería *et al.,* 1999).

The species is chiefly associated with reed beds *Phragmites* spp., where it feeds opportunistically on invertebrates (Cramp, 1992). Reed-warblers in Europe seem to migrate in short steps, accumulating the reserves required to fly over the Sahara desert mainly in northern Africa (Schaub & Jenni, 2000a). Recent research has provided evidence that the fuel required to pass over the sea band between Europe and Africa need not necessarily be acquired in southern Iberia, but may also be obtained at sites further north (Andueza *et al.,* 2014).

Reed-warblers of all age categories (i.e., adults and first-year birds) perform a partial moult after breeding, which often overlaps with the start of migration to Africa in summer (Jenni & Winkler, 1994). Reed-warblers finish their moult in Europe, i.e. it is not suspended to be resumed in Africa when they reach their wintering sites (Cramp, 1992).

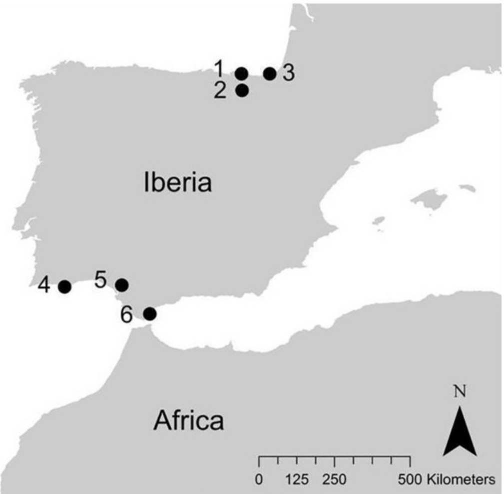

FIG. 1.—Locations of the sampling sites in Iberia. Northern Iberia: 1, Urdaibai (43°.35'N, 02°.66'W). 2, Salburua (42°.86'N, 02°.64'W). 3, Txingudi (43°.35'N, 01°.82'W). Southern Iberia: 4, Faro (37°.02'N, 07°.92'W). 5, Doñana (37°.07'N, 06°.22'W). 6, Guadiaro river mouth (36°.17'N, 05°.17'W).

[Localización de los puntos de muestreo en España y Portugal: norte: 1, Urdaibai (43°.35'N, 02°.66'W). 2, Salburua (42°.86'N, 02°.64'W). 3, Txingudi (43°.35'N, 01°.82'W). Sur: 4, Faro (37°.02'N, 07°.92'W). 5, Doñana (37°.07'N, 06°.22'W). 6, Desembocadura del río Guadiaro (36°.17'N, 05°.17'W).]

Sampling area and data collection

Reed-warblers were captured at six strategically selected sampling localitions (sites) in Iberia (Figure 1): three in northeastern Iberia (Txingudi, Urdaibai and Salburua), located in the Basque region, where the East-Atlantic flyway enters Iberia (Galarza & Tellería, 2003) and three localities in coastal southwestern Iberia (Faro, Doñana and Guadiaro river mouth), where many birds converge before crossing Atlantic waters to North Africa (Andueza *et al.*, 2013b).

The main vegetation at all these sampling sites was reed beds. The sampling period extended from 15th August to 15th September 2012. Daily sampling was carried out at each site using mist nets which remained open for a four-hour period starting at dawn. Once caught, each bird was ringed and aged as either a first-year bird (juvenile; hatched in 2012) or adult (Svensson, 1996). Wing length (±0.5mm, according to method III in Svensson 1996), body mass (±0.1g accuracy) and moult state (moulting/non-moulting) were also recorded. Only juveniles (*n* = 1189) are considered in this paper, given the low number of adults captured. We did not pool both age categories since they might differ in stopover behaviour (e.g., Moore & Yong, 1991; Jakubas *et al.,* 2014).

Fuel deposition rate, fuel load and food availability analyses

Fuel deposition rate was calculated using recaptured birds (*n* = 157), as the weight difference between the first and last capture, divided by the number of days between both capture events (Schaub & Jenni, 2000b). After that, we conducted a Generalized Linear Model (GLM) on fuel deposition rate, considering a linear-link function with Gaussian errors; with region, site nested into region and moult state as factors. Individuals recaptured one day after the first capture were omitted to remove a possible handling effect on fuel deposition rate (Schwilch & Jenni, 2001). Unfortunately, not all stations took the hour of capture into account, so we were not able to include this factor into our models and, therefore, this is an additional source of variation that was not controlled. However, most captures were produced during the first two hours of the morning and therefore a possible effect of this factor on our global results can be considered negligible.

The quantity of invertebrates within the reed beds was used as a surrogate of food availability. To assess this, we followed Poulin *et al.* (2002), sweeping the reed beds 500 times, with a 30-cm insect net along a single transect parallel with the net lines. During each sweep the vegetation was struck from the bottom upwards, with the net wing at an angle of about 45º. This method allowed us to sample a broad range of invertebrates, chiefly arthropods, the main prey of Reed-warblers (Poulin & Lefebvre, 1997). The sampling was carried out in the two-hour period before dusk. Each site was sampled every ten days (three times overall), starting on 21st August. At Urdaibai and Salburua the first sampling event was missed for logistical reasons. The invertebrates were stored in 70% ethanol. Reed-warblers mostly take prey 1-20mm long (Bibby & Thomas, 1985). Therefore, we selected prey within this size range to estimate food availability. We obtained the dry weight (±0.01g accuracy) of each sample after a drying it for 24 hours at 50ºC. We compared food availability between regions and sites using non-parametric tests. We also tested whether the fuel deposition rate was correlated with food availability using a Spearman correlation test ($n = 6$ sites).

We also explored to what extent fuel load varied between the two regions. Fuel load was assessed using residual values from a linear regression of body mass on wing length (Schulte-Hostedde *et al.,* 2005). We conducted a GLM based on using a linear link-function with Gaussian errors; with region, site nested into region and moult state as control fixed factors. We ran the GLM twice for first and last captures, respectively. All analyses were made with SPSS v. 15.0.

Capture-recapture models

Departure decisions were modeled using CJS models. We considered that survival (ϕ) of a bird from one day to the next at a stopover site being the probability of remaining at that stopover site (Schaub *et al.,* 2001), then the emigration (i.e., departure) probability (ε) is $1-\phi$.

Before starting to run and select models, we assessed the fit of our data to CJS assumptions. We used a goodness-of-fit (GOF) test with U-CARE software (Choquet *et al.,* 2009). We did not detect global over-dispersion or trap-dependence ($P > 0.05$), but we detected ($P < 0.05$) the presence of transients (i.e. birds that stayed less than one day at each site). To control for the presence of transients, we used an age-dependent structure in all the models (e.g. Pradel *et al.,* 1997; Salewski *et al.,* 2007).

We were not able to separate migrants and local birds properly using wing length (as suggested in Bibby & Green, 1981) due to the high overlap between the two in Iberia (M. Andueza, pers. obs.). Reed-warblers show some overlap between their summer moult (when a number of body feathers are replaced) and the first stages of their autumn migration (Schaub & Jenni, 2000a). This moult affects birds at their breeding sites (local breeding birds) and at the first stopover sites during the autumn migration period (migrants). Thus, although our sampling was carried out in a period when the local birds can be acceptably considered to be a small minority relative to the bulk of migrants passing through Iberia (Cantos, 1998), we could not fully exclude the presence of local birds, which would be likely to have a different behaviour than the migrant fraction (Schaub & Jenni, 2000a). Considering moulting and non-moulting Reed-warblers in our models may in part allow us to control for the presence of these local birds.

With this structure, we calculated two local survival rates, ϕ_1 (i.e., survival from t to $t+1$, where t is the capture day; this rate includes both transients and non-transients), and ϕ_2, (daily survival after the second day; this rate only includes non-transients, i.e. migrants that stay in the area for longer than one day). The proportion of transients is calculated as: $\tau = 1\text{-}(\phi_1/\phi_2)$. Apart from estimating ϕ_1 and ϕ_2 (or ε_1 and ε_2), we tested for the effect of several factors on departure probability: moult state (moulting/non-moulting,

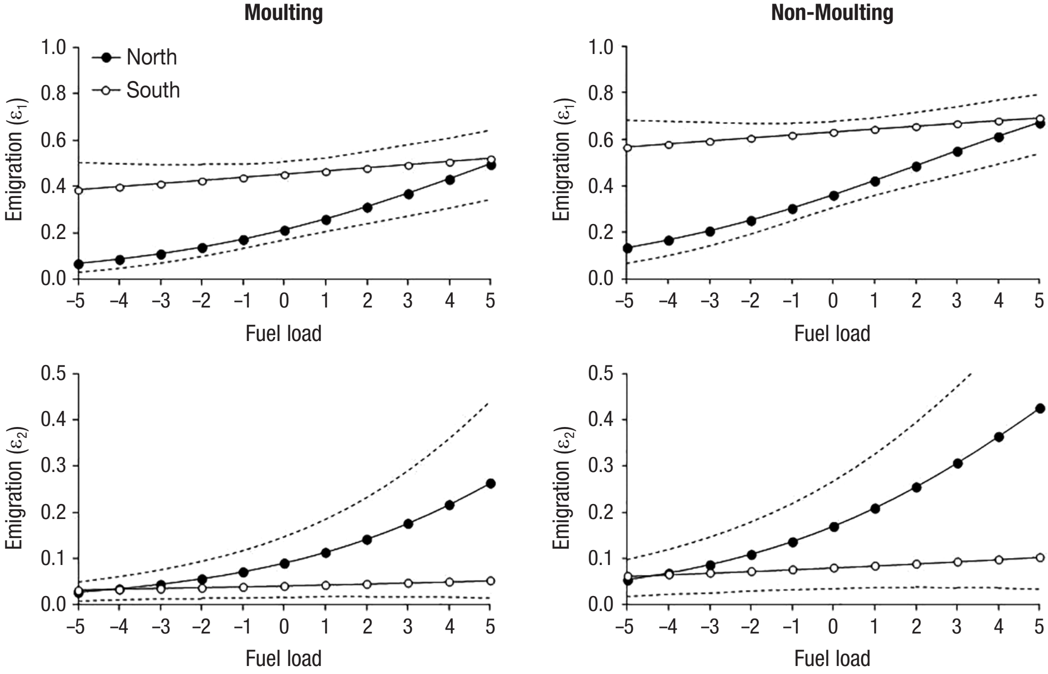

FIG. 2.—Mean (±95% confidence intervals; dashed lines) first-day after capture (ε_1) and non-transient (ε_2) emigration probabilities of moulting and non-moulting Reed-warblers caught in northern and southern Iberia during their autumn migration in relation to their fuel loads. Values obtained from model one in Table 2.

[Media (± intervalo de confianza al 95%; sólo mostramos los límites más altos y bajos para obtener una figura más clara) de la probabilidad de emigración para el primer día tras la primera captura (ε_1*) o en días posteriores (*ε_2*) de carriceros comunes mudando o no mudando, capturados tanto en el norte como en el sur de la península ibérica durante el paso migratorio posnupcial, en relación con la carga de reservas. Valores calculados a partir del modelo 1 de la Tabla 2.]*

a binary variable), region (northern/southern Iberia; a binary variable) and fuel load (an individual-associated linear variable). We tested for the effect of each single factor and all the possible combinations, either additive or with interactions, avoiding over-parameterised models.

We also tested whether recapture probability was constant (p), time-dependent [p(t)] or site-dependent [p(site)], across the study period.

CJS models were run using MARK software (White & Burnham, 1999). Small sample size-corrected Akaike values (AICc) were used to rank and select those models that best fitted the data (Burnham & Anderson, 1998). Two models were considered to have the same support if they differed in less than two AICc units (Burnham and Anderson, 1998). Within a given model, a particular variable (or factor) was considered to have a significant effect on ε if "zero" was not included within the 95% confidence interval (95% CI) of its B-parameter.

RESULTS

Overall, we captured 1,189 first-year Reed-warblers (northern Iberia, $n = 607$; southern Iberia, $n = 582$; see Table 1 for details). Moulting Reed-warblers were more abundant in southern Iberia than in northern Iberia ($\chi^2 = 115.066$, $P < 0.001$; Table 1).

Recapture probability seemed to be site dependent; hence we fixed p(site) to test for the effect on ε_1 and ε_2. Two models were observed to fit our data better than the rest (Table 2), and they all considered an effect of the region, moult state and fuel load on both ε_1 and ε_2 (Table 2). When looking at these first two models we observed that the different independent variables had similar effects on both ε_1 and ε_2. Therefore, we focused on Model 1 to see the relationship among all these variables and ε_1 and ε_2 in detail (Figure 2). Overall, Reed-warblers with more fuel tended to be more likely to depart. Focusing on ε_1, Reed-warblers from southern Iberia were more likely to depart than those

TABLE 1

Number of captures of first-year Reed-warblers, within-site recaptures and moulting Reed-warblers, and median date of passage at each sampling site. The mean (±SE) food availability (dry weight, in g) for the sampling events (500 sweeps) at each sampling site is also shown.
[Número de capturas de carriceros comunes juveniles, autorrecuperaciones y fecha mediana de paso en cada uno de los sitios de muestreo. Se indica, además, el valor medio (±SE) de la disponibilidad de alimento (peso seco, en g) estimada para cada sitio.]

	Northern Iberia			**Southern Iberia**		
Site	Txingudi	Salburua	Urdaibai	Faro	Guadiaro	Doñana
No. of captures	237	309	61	246	62	274
No. of recaptures	46 (19.3%)	15 (4.9%)	20 (32.8%)	43 (17.5%)	10 (16.1%)	29 (10.6%)
No. of moulting birds	36 (15.1%)	18 (5.8%)	0 (0%)	60 (24.4%)	14 (22.6%)	149 (54.4%)
Median passage date	23 Aug	01 Sep	29 Aug	30 Aug	26 Aug	25 Aug
Food availability (g)	0.51 ± 0.19	0.88 ± 0.21	0.89 ± 0.03	0.23 ± 0.09	1.06 ± 0.26	0.51 ± 0.19

from northern Iberia for given fuel loads. Focusing on ε_2, however, we observed that Reed-warblers from southern Iberia were less likely to depart than those from northern Iberia, especially for high fuel load values. So, overall, we observed that, for the fraction of Reed-warblers stopping over at each site (i.e. transients excluded), departure probability increased with increasing fuel load values in northern Iberia but not in southern

Table 2

CJS models used to model departure probabilities from northern and southern Iberia. Abbreviations: ε_1: initial (first-captures) departure probability; ε_2: departure probability of non-transients; *p*: recapture probability; AICc: corrected Akaike's Information Criterion; ΔAICc: difference in AIC values of each model from the first model; np = number of parameters. Factors: r, region; m, moult state; f, fuel load; t, time-dependent.

[Modelos CJS utilizados para modelizar la probabilidad de migración en el norte y sur de la península ibérica. Abreviaciones: ε_1*: probabilidad de partir (migración) al día siguiente de la primera captura;* ε_2*: probabilidad de partir dos o más días después de la primera captura (aves no transeúntes); p, probabilidad de recaptura; AICc, Criterio de Información de Akaike corregido para muestras pequeñas; ΔAICc: diferencia AICc con relación al primer modelo; np = número de parámetros. Factores: r, región; m, estado de muda; f, fuel; t, modelo tiempo-dependiente.]*

Model	AICc	ΔAICc	AICc Weight	np
1. ε_1(r×f+m), ε_2(r×f+m), *p*(site)	2306.49	0.00	0.26	13
2. ε_1(r+m+f), ε_2(r+m+f), *p*(site)	2307.19	0.71	0.18	12
3. ε_1(m+site), ε_2(m+site), *p*(site)	2310.87	4.39	0.03	16
4. ε_1(r×f+m), ε_2, *p*(site)	2312.43	5.95	0.01	12
5. ε_1(r+m), ε_2(r+m), *p*(site)	2312.59	6.11	0.01	11
6. ε_1(r+m+f), ε_2, *p*(site)	2319.42	12.94	0.00	10
7. ε_1(m), ε_2, *p*(site)	2321.56	15.07	0.00	10
8. ε_1(r+f), ε_2, *p*(site)	2338.99	32.50	0.00	9
9. ε_1(r+m+f), ε_2(r+m+f), *p*(t)	2342.07	35.58	0.00	37
10. ε_1, ε_2, *p*(site)	2357.63	51.15	0.00	8
11. ε_1(r+m), ε_2(r+m), *p*(t)	2360.23	53.74	0.00	36
12. ε_1(r×f+m), ε_2(r×f+m), *p*	2365.92	59.43	0.00	8
13. ε_1(m), ε_2, *p*(t)	2371.73	65.24	0.00	34
14. ε_1(m+f), ε_2(m+f), *p*(t)	2372.27	65.79	0.00	36
15. ε_1(m), ε_2(m), *p*	2373.31	66.82	0.00	35
16. ε_1(r+m+f), ε_2(r+m+f), *p*	2375.65	69.16	0.00	6
17. ε(t), *p*(site)	2391.08	84.60	0.00	37
18. ε(t×site), *p*(site)	2671.26	364.77	0.00	191

Iberia. The difference between moulting and non-moulting Reed-warblers was weak, with non-moulting Reed-warblers having slightly higher emigration values for given fuel loads in each region (Figure 2).

The fuel deposition rate did not differ between the two regions (northern and southern Iberia), although it varied among sites and in relation to the moult state (Region, $F_{1,140} = 0.001$, $P = 0.972$; Moult State, $F_{1,140} = 6.418$, $P = 0.012$; Site (Region), $F_{4,140} = 2.591$, $P = 0.039$; Region × Moult State, $F_{1,140} = 0.717$, $P = 0.398$; Table 3).

Fuel load of first-captured birds varied among sites and in relation to the moult state, but not between northern and southern Iberia (Region, Wald $\chi^2 = 0.380$, $P = 0.538$; Moult State, Wald $\chi^2 = 41.004$, $P < 0.001$; Site (Region), Wald $\chi^2 = 116.450$, $P < 0.001$; Region × Moult State, Wald $\chi^2 = 3.430$, $P = 0.064$; Table 3). The same result was obtained when considering fuel load at last capture of

TABLE 3

Mean (±SE) fuel deposition rate (g/d; excluding those birds recaptured on the following day to their first capture) and fuel load (residual values from a weight-wing length linear regression) of Reed-warblers at each region and sampling site, for moulting and non-moulting birds. Sample sizes are shown (*n*). *[Tasa de deposición de fuel (media ±SE; unidades en g/d; se excluyen las aves que fueron recapturadas el día después de la primera captura) y 'fuel' (residuales provenientes de la regresión peso-longitud alar) en carriceros comunes capturadas en cada una de las dos regiones de estudio. Se muestra, además, el tamaño muestral (n).]*

	Fuel deposition rate (g/day)		**Fuel load at first capture (residual values)**		**Fuel load at last capture (residual values)**	
Localities	**Non-moulting**	**Moulting**	**Non-moulting**	**Moulting**	**Non-moulting**	**Moulting**
Northern Iberia	+0.08 ± 0.04 (*n* = 65)	−0.04 ± 0.05 (*n* = 14)	+0.28 ± 0.06 (*n* = 529)	−0.14 ± 0.13 (*n* = 56)	+0.46 ± 0.19 (*n* = 65)	−0.54 ± 0.18 (*n* = 14)
Txingudi	+0.12 ± 0.06 (*n* = 25)	−0.07 ± 0.05 (*n* = 13)	+0.80 ± 0.10 (*n* = 198)	−0.05 ± 0.15 (*n* = 40)	+0.93 ± 0.30 (*n* = 25)	−0.57 ± 0.19 (*n* = 13)
Salburua	−0.08 ± 0.05 (*n* = 21)	0.20 (*n* = 1)	+0.01 ± 0.09 (*n* = 293)	−0.36 ± 0.23 (*n* = 16)	−0.33 ± 0.25 (*n* = 21)	−0.19 (*n* = 1)
Urdaibai	+0.12 ± 0.05 (*n* = 19)	—	−0.15 ± 0.13 (*n* = 61)	—	+0.19 ± 0.27 (*n* = 19)	—
Southern Iberia	+0.05 ± 0.03 (*n* = 39)	−0.01 ± 0.01 (*n* = 39)	−0.07 ± 0.08 (*n* = 376)	−0.58 ± 0.05 (*n* = 203)	+0.07 ± 0.21 (*n* = 39)	−0.62 ± 0.11 (*n* = 39)
Faro	+0.10 ± 0.05 (*n* = 21)	−0.03 ± 0.02 (*n* = 20)	+0.12 ± 0.12 (*n* = 188)	−0.59 ± 0.10 (*n* = 58)	+0.38 ± 0.34 (*n* = 21)	−0.64 ± 0.19 (*n* = 20)
Guadiaro	−0.13 ± 0.10 (*n* = 6)	−0.07 ± 0.05 (*n* = 4)	+0.31 ± 0.25 (*n* = 49)	−0.10 ± 0.26 (*n* = 13)	−0.58 ± 0.44 (*n* = 6)	−0.31 ± 0.09 (*n* = 4)
Doñana	+0.05 ± 0.02 (*n* = 12)	+0.02 ± 0.02 (*n* = 15)	−0.45 ± 0.07 (*n* = 142)	−0.63 ± 0.06 (*n* = 132)	−0.14 ± 0.21 (*n* = 12)	−0.68 ± 0.16 (*n* = 15)

recaptured birds (Region, Wald $\chi^2 = 0.017$, $P = 0.896$; Moult State, Wald $\chi^2 = 20.306$, $P < 0.001$; Site (Region), Wald $\chi^2 = 11.582$, $P = 0.021$; Region × Moult State, Wald $\chi^2 = 2.102$, $P = 0.147$; Table 3).

Mean invertebrate biomass was similar between regions (M-W test: $U = 3.500$, $P = 0.658$; northern Iberia: 0.63 ± 0.13 g/500 sweeps; southern Iberia: 0.60 ± 0.16 g/500 sweeps), and also among sites (K-W test: $\chi^2 = 10.500$, $P = 0.062$) (Table 1). Mean fuel deposition rate at each site was not correlated with food availability ($r = -0.421$; $P = 0.226$; $n = 6$), including when moulting and non-moulting Reed-warblers were considered separately (non-moulting: $r = -0.397$; $P = 0.436$; $n = 6$; moulting: $r = -0.500$; $P = 0.500$; $n = 4$).

DISCUSSION

According to CJS models, departure probability (i.e. emigration) of first-year Reed-warblers from stopover sites situated in northern and southern Iberia varied in relation to the region (i.e. distance from the sea barrier between Iberia and Africa), moult state (moulting or non-moulting) and fuel load. Reed-warblers captured in northern and southern Iberia belong to populations following a similar migratory direction (Andueza *et al.,* 2013b). Therefore, between-region variations should be linked to the birds' geographical location in relation to the barrier and not to the fact that they belong to populations with presumably different migration strategies.

Moulting Reed-warblers were more abundant in southern Iberia than in northern Iberia. This result may be related to the existence of latitudinal phenological differences, with first-year Reed-warblers in southern Iberia starting their summer moult later than in northern Iberia, following a similar pattern to that observed between northern and southern Europe (Cramp, 1992). Additionally, the presence of the sea area between Iberia and Africa may result in an accumulative effect in southern Iberia, especially of those birds that are still moulting or performing post-fledging dispersal movements and are not yet ready to cross the sea to Africa (Bulyuk *et al.,* 2000). It is notable that moulting birds had lower ε_1 and ε_2 values than non-moulting Reed-warblers. Moulting birds also had lower (even negative) fuel deposition rates. Thus, overall, it may be assumed that moulting Reed-warblers (probably) comprise a high proportion of local birds or even some active migrants (as also reported by Schaub & Jenni, 2000b) that however still show different stopover behaviour when compared with non-moulting fraction birds. Hereafter, we largely focus on these last birds since they are more likely to be true migrants (*sensu* birds in active migration).

The proportion of transients was higher in southern Iberia (i.e. the region situated closer to the barrier) than in northern Iberia. This regional difference may be due to various reasons that require further investigation. Here, we can do no more than propose some plausible explanations: 1) Near the edge of the sea barrier the need to accumulate fuel is presumably high. Hence birds experiencing even slightly lower than expected fuel deposition rates may leave these southern sites shortly after arrival (Alerstam & Lindström, 1990); 2) The accumulation of many Reed-warblers in southwestern Iberia (Andueza *et al.,* 2013b) may lead to high intra-specific competition, resulting in higher transience (Senar & Metcalfe, 1988; Moore & Yong, 1991); 3) Some first-year Reed-warblers may attain sufficient fuel load to reach the north African coast at sites further north (Andueza *et al.,* 2014). Hence they could fly to Africa without needing to stage in southern Iberia for some days to gain fuel. Although the first two hypotheses cannot be rejected, the last one is also supported by our own data.

In a previous study we found that the potential flight ranges of Reed-warblers caught at Txingudi, in northern Iberia, were sufficient to reach North Africa without needing further refuelling (Arizaga *et al.,* 2011b). Thus, some Reed-warblers stopping over in southern Iberia should have sufficient fuel to continue to Africa, making one-day stopovers more likely.

Overall, Reed-warblers with more fuel were more likely to depart than those with lower fuel, although in southern Iberia this effect was rather weak, indicating that this factor did not operate in the same way in the two regions. This result allows us to reject the hypothesis that departure from stopovers in southern Iberia (i.e. before crossing the sea to Africa) is highly influenced by actual fuel load. Reed-warblers in southern Iberia may wait for other cues (a tailwind perhaps) to depart, hence using their actual fuel load (which may be either low or high) to reach North Africa. The shortest distance from our Iberian sampling localities to Africa is only 16km (< 400km for the most southwestern locality in Portugal) and, possibly, given favourable winds, Reed-warblers may cross the sea barrier without needing very large fuel loads. In this case, some birds would need to gain sufficient weight in northern Africa to overfly over the Sahara to tropical Africa (Schaub & Jenni, 2000a). The conservation of the Moroccan coastal wetlands would be critical, in this scenario.

Reed-warblers stopping over for more than one day in southern Iberia did not gain fuel at a faster rate and did not have a higher mean fuel load than those in northern Iberia. Accordingly, we obtained no evidence supporting the hypothesis that Reed-warblers in southern Iberia wait to gain more fuel before departing to cross the sea between Iberia and Africa, as observed in other passerine birds at similar barrier crossings (Schaub *et al.*, 2008; Goymann *et al.*, 2010; Smolinsky *et al.*, 2013). Instead, this sea barrier might force a stay in southern Iberia for those migrating first-year birds that may experience difficulties in accumulating fuel or, alternatively, which might be more sensitive to other factors, such as wind direction, that may also be important to departure decisions, especially at the edge of geographical barriers (Åkesson *et al.,* 2002; Arizaga *et al.*, 2011a).

Mean site-associated fuel deposition rates were not correlated with food availability and showed no obvious differences between northern and southern Iberia. Therefore, it is possible that the differential use of northern and southern sites in terms of departure decisions was not caused by food availability, or not solely due to this factor (Ktitorov *et al.*, 2008). As stated before, other conditions operating near the edge of a geographical barrier, such as predator pressure, competition or prevailing meteorological conditions, may be important (Carpenter *et al.*, 1993; Schmaljohann & Dierschke, 2005; Schmaljohann & Naef-Daenzer, 2011; Bulyuk & Tsvey, 2013; Nilsson *et al.*, 2019).

In conclusion, CJS models show that first-year Reed-warblers stopping over for longer than one day are more likely to depart if they are in northern Iberia than in southern sites located close to the sea area between Iberia and Africa. Moreover, increasing fuel load promotes emigration from given stopover sites in northern Iberia, but not in southern Iberia. Therefore, we found no evidence to suggest that Reed-warblers wait to attain high fuel loads before departing their stopover sites near the edge of a geographical barrier.

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