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## Identifying the winter grounds of the recently described Barbary Reed Warbler (*Acrocephalus baeticatus ambiguus*)

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The Iberian and North African populations of reed warblers have been recently described as a separate taxon, *ambiguus*, forming a sister clade to the Sahelian subspecies *minor* of African Reed Warbler *Acrocephalus baeticatus*. While the breeding range of *ambiguus* has been identified, the migration strategy of its populations remained unknown. We deployed geolocators and sampled the innermost primary from breeding adults in Spain for stable hydrogen ( $\delta^2\text{H}$ ) analyses and also analysed stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes in feathers collected in two reed warbler taxa (*A. scirpaceus* and *A. baeticatus ambiguus*) in Morocco, to identify the moulting and wintering sites of these populations. Ring recoveries, geocator tracks and probabilistic assignments to origin from  $\delta^2\text{H}$  values indicate that Spanish *ambiguus* likely moult south of the Sahara and winter in West Africa, probably from Mauretania to southern Mali and Ivory Coast. Moroccan *ambiguus*, however, undergo the post-breeding moult north of the Sahara, and possibly then migrate to West Africa. With other populations of *ambiguus* breeding from Algeria to Libya and likely wintering further east in the Sahelian belt, the Barbary Reed Warbler can therefore be considered as a trans-Saharan migrant, with a post-breeding moult strategy variable between populations, and likely structured according to the breeding latitude.

**Key words:** deuterium, carbon-13, nitrogen-15, geocator, ring recovery, stable isotopes, trans-Saharan migrant

Advances in molecular sequencing and population genetics regularly reveal cryptic species that largely differ genetically despite morphological similarities (Pavlova *et al.* 2008, Toews & Irwin 2008, Collinson *et al.* 2017). One challenge is thereafter to update or acquire knowledge on the ecology of each taxon. Compared to their European counterparts, *Acrocephalus* reed warblers breeding in Iberia and North Africa display distinct biometrics and plumage characteristics (Jiguet *et al.* 2010, Hering & Winkler 2010), and are genetically closer to the African Reed Warblers *Acrocephalus baeticatus* (Hering *et al.* 2009), forming a sister clade to all sub-Saharan populations breeding across the Sahel (subspecies *minor*, Olsson *et al.* 2016). They have been recognized as a distinct subspecies, *Acrocephalus baeticatus ambiguus* (Olsson *et al.* 2016). With a breeding distribution ranging from Iberia and western Morocco to coastal Libya (Hering *et al.* 2009, 2010; Olsson *et al.* 2016), closely matching the African distribution of the Barbary Partridge, we propose to name this taxon the Barbary Reed Warbler.

The Eurasian Reed Warbler *Acrocephalus scirpaceus* is one of the most studied migrant passerines in Europe, with hundreds of thousands of individuals ringed each year, and numerous ring recoveries informing migratory connectivity (Procházka *et al.* 2008, 2017). However, ring recoveries do not necessarily relate to birds of known breeding origin, as many individuals are ringed along their migration routes, or even as non-local transients during the breeding season (Clavel *et al.* 2008). As a consequence, any reed warbler ringed in Iberia in May, June or July might be either a local breeding *ambiguus* or a late/early migrant *scirpaceus*. Without information on phenotype, genotype or definite breeding status, the taxonomic status of such warblers cannot be definitively assessed. Therefore, to identify the wintering grounds of *ambiguus*, it is not necessarily prudent to use winter recovery data of birds ringed in Iberia or North Africa during the breeding season. Nevertheless, there are a few winter records along the Senegal River of birds ringed during the breeding period within breeding populations located at mid-latitudes in Spain and Portugal (around 40°N; Procházka *et al.* 2008), and so of birds presumably belonging to *ambiguus*. To summarize, the migration strategy and wintering grounds of the Barbary Reed Warbler are still unknown and remain to be documented.

Archival light-level geolocators are useful to determine the migration routes and wintering grounds of small songbirds, and have been used previously on *scirpaceus* reed warblers (Procházka *et al.* 2017). Stable isotopes in winter grown feathers can also be effective in identifying African moulting grounds of long-distance migrant songbirds (Hobson & Wassenaar 2019). Because reed warblers undergo a complete post-breeding moult occurring after arrival on the wintering grounds after autumn migration (Dowsett-Lemaire & Dowsett 1987, Svensson 1992, Demongin 2013), individuals returning to the breeding grounds in spring wear winter-grown feathers that can be sampled to analyse stable isotopes to determine African moulting grounds. However, adults moulting some primary feathers in late summer are not common but some occur in Spain (Svensson 1992), and Jiguet *et al.* (2010) reported numerous adult *ambiguus* actively moulting their remiges in Morocco at the end of August.

As a consequence, we do not know whether *ambiguus* moult on the breeding or on the wintering grounds, or whether this depends on individual strategies or breeding location.

Most Moroccan adult *ambiguus* undergo the post-breeding complete moult on the breeding grounds, with many adults moulting simultaneously most primaries by early September (Jiguet *et al.* 2010, Amezian *et al.* 2010). By taking a species' moult pattern and tissue-specific isotopic discrimination and elemental turnover rates into account, we can infer the breeding or wintering origin of individuals from the stable isotope signatures if the birds use isotopically distinct areas, which is the case for Eurasian Reed Warblers breeding in Europe (Procházka *et al.* 2008). For example,  $\delta^{13}\text{C}_f$  values in reed warbler feathers moulted south of the Sahara indicate a xeric biome dominated by C4 plants and differed significantly from those in feathers of first-year birds grown at known breeding sites indicating a C3-dominated biome (Procházka *et al.* 2008).

In order to unravel the key elements of the moult and migration ecology of *ambiguus* reed warblers, we deployed light loggers and sampled winter-grown feathers to analyse stable hydrogen isotopes ( $\delta^2\text{H}_f$ ) in breeding adults captured in Catalunya and Andalucía, Spain. We also analysed feather stable carbon ( $\delta^{13}\text{C}_f$ ) and nitrogen ( $\delta^{15}\text{N}_f$ ) isotopes of *ambiguus* individuals captured in Morocco either in June (local breeding birds) or in September (juveniles and adults) to determine how frequently the post-breeding primary moult occurs north of the Sahara. The taxonomic status of all studied individuals was confirmed by morphometrics, including detailed wing formula (Jiguet *et al.* 2010, Olsson *et al.* 2016).

## METHODS

### Light loggers

To fit birds with light loggers (also called GLS for global location sensors), we captured breeding reed warblers at two different sites in Spain in 2017 and 2018, at Arroyo Ardachón, Sanlúcar la Mayor, Sevilla, in Andalucía (37.40°N 6.26°W), and at Delta del Ebro in Catalunya (40.74°N 0.79°E). Tag deployments occurred on 9 July 2017 for BD505 and BD508, 27 May 2018 for BL945, 10 June 2018 for BL947 and 1 June 2018 for BL955. Both sites are located within the Iberian breeding range of *ambiguus* (Olsson *et al.* 2016). These warblers were being considered as local breeders because they displayed either an obvious brood patch or cloacal protuberance, and were therefore tagged, and recaptured the next year at the same site, again with a confirmed breeding status. GLS loggers record light intensity which, if retrieved after a migration cycle, enables the calculation of the approximate position of the logger given the duration of daylight and the time of solar noon. Light loggers do not transmit data, so birds have to be recaptured and the tag retrieved to download recorded data. We used data collected by Intigeologgers (P30Z11-7-DIP, 0.36g, Migrate Technology). We attached loggers with UV-proof string leg-loop harness to the bird's back. The device and associated attachment material (0.03-

0.04g) represented 3.0 to 4.0% of a warbler's body mass (10-13 g). Overall, we retrieved five loggers from 40 equipped birds (recapture rate 12.5%).

We analysed the light intensity data recorded by the GLS devices with a threshold approach following the guidelines described in Lisovski *et al.* (2020). First, we used the TwGeos package (Lisovski *et al.* 2015) to define twilights with the preprocessLight function, using a threshold of 2.5 lux. Since all loggers stopped recording data from the March-April period (before arrival at the breeding site), we visually inspected the raw recordings to remove obviously erroneous twilight periods. We then applied an additional automated screening using the twilightEdit function (settings were window = 4, outlier.mins = 45 and stationary.mins = 25), removing a few location outliers per track (0-1%). Second, using the GeoLight package (Lisovski & Hahn 2012), we calibrated the recorded twilight events against the actual sunrise and sunset times at the respective breeding locations of the birds (in-habitat calibration; Lisovski & Hahn 2012). We estimated sun elevation angles varying between -5.11 and -5.70°. Since we assume that reed warblers use similar habitats across their annual cycle, we used the same elevation angles for sub-Saharan non-breeding and migratory stationary locations. Finally, using the changelight and MergeSites2 functions (Lisovski & Hahn 2012), we separated stationary and movement periods with a threshold at the 0.9-quantile of change point probability, a minimum stationary time of 3 days and by merging consecutive stationary periods that did not differ by more than 200 km. We then used the schedule function to extract approximate departure and arrival dates on each stationary locations and estimate the phenology of each individual.

### Stable isotopes

In Spain, we sampled an outer tail feather on most breeding adults that we captured for tagging (n = 39). In Morocco, we captured reed warblers in the lower Loukkos valley near Larache (35.16°N, 6.06°W) in September 2009 (n=36 *ambiguus* and 28 *scirpaceus*) and June 2011 (n=6 *ambiguus*). In autumn, we separated first-year and adult individuals based on plumage wear and iris colour (Svensson 1992), while we used biometrics and bare part coloration to identify the Moroccan warblers to subspecies (*ambiguus* vs. *scirpaceus*; Jiguet *et al.* 2010, Olsson *et al.* 2016). We sampled one innermost primary (P10) on all birds, except on those adults actively moulting the innermost primary. The total feather sample included 31 first-calendar and 11 adults of *ambiguus*, and 16 first-calendar and 12 adults of *scirpaceus*.

Feathers were stored dry in plastic bags until analysis. Upon analysis, they were first rinsed in a 2:1 chloroform:methanol solution and air-dried in a fume hood. For  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses, we weighed feather vane subsamples of approximately 1mg into small tin cups and then combusted with a RoboPrep elemental analyser interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (CFIRMS) interfaced.

We report measurements in conventional  $\delta$ -notation relative to the VPDB (carbon) and atmospheric AIR standards in parts per thousand (‰). Replicate assays of internal laboratory standards (albumen) included in each run indicated measurement errors (SD) of  $\pm 0.1$  and  $\pm 0.3\%$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, respectively. We ran all samples at the Department of Soil Science, University of Saskatchewan in Saskatoon, Saskatchewan, Canada. We further compared  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values according to the taxonomy (*ambiguus* vs. *scirpaceus*) and age (first calendar year vs. adult) and the interaction of both predictors in a general linear model.

The  $\delta^2\text{H}$  of the non-exchangeable hydrogen of feathers was determined using a method based on two calibrated keratin hydrogen-isotope reference materials (CBS, KHS). We performed hydrogen isotopic measurements on  $\text{H}_2$  gas derived from high-temperature (1350 °C) flash pyrolysis on glassy carbon (Eurovector 3000; Milan, Italy) of  $350 \pm 10 \mu\text{g}$  feather subsamples and keratin standards loaded into silver capsules. We analyzed resultant separated  $\text{H}_2$  on an interfaced Isoprime (Crewe, UK) continuous-flow isotope-ratio mass spectrometer. Measurement of the two keratin laboratory reference materials corrected for linear instrumental drift were both accurate and precise with typical within-run mean  $\delta^2\text{H} \pm \text{SD}$  values of  $-197 \pm 0.79\text{‰}$  ( $n=5$ ) for CBS and  $-54.1 \pm 0.33\text{‰}$  ( $n=5$ ) for KHS. We report all results for non-exchangeable H expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale.

For  $\delta^2\text{H}$  values, we used a spatially-explicit likelihood assignment method to delineate probable origins by converting an amount-weighted growing season precipitation surface (Bowen *et al.* 2005) to a feather isoscape using a calibration equation previously developed for Eurasian Reed Warblers ( $\delta^2\text{H}_f = -10.29 + 1.28 * \delta^2\text{H}_p$ ) (Procházka *et al.* 2013). The residual standard deviation ( $\text{SD} = 10.36\text{‰}$ ) from the linear regression model used to calibrate the precipitation surface for Eurasian Reed Warbler feathers was included in the assignments as an estimate of error. We produced assignments to origin using two different geographical ranges where the species could be wintering or moulting: (a) the known sub-Saharan winter range of the species; (b) a longitudinal window (20°W to 20°E) covering South-West Europe and West Africa which includes the range of the species in the area, and including the breeding range of the sampled *ambiguus* individuals. We obtained the digital distribution map of reed warblers from BirdLife International and HBW (2021). We used an odds ratio of 2:1 to assign each feather sample to potential origin where cells in the isoscape in the upper 67% of probabilities were considered as likely (1) origins and all others were considered unlikely (0). Assignments resulted in a spatially explicit binary surface for individual birds, which we subsequently summed across assignments for all individuals within a group to represent potential origins for that group. For each pixel in the assignment raster, the presented value is the proportion of all sampled individuals which could potentially have grown the analyzed feathers within the pixel, rescaled to range from 0 to 1.

## RESULTS

### Light loggers

The analysis of data collected by geolocators allowed to estimate stopovers and wintering locations of six Iberian *ambiguus* reed warblers originating from three different breeding populations (Fig. 1). All birds left their breeding areas in August, migrated rapidly, without making any long stopovers in North-West Africa to reach their non-breeding areas in September. Between September and March, the five individuals hence occupied 2-3 non-breeding sites located in the sub-Saharan area (Fig. 1). Taking into account the uncertainties related to latitude estimation, we may assume that the four breeding birds from Andalusia (BD508 and BD505 from 2017-2018; BL945 and BL947 from 2018-2019) occupied wintering sites located between Mauretania, Senegal, the Gambia and Guinea-Bissau. Unlike the other four individuals, the bird from Catalunya (BL955) occupied two wintering sites located further south-east, probably in southern Mali and Ivory Coast.

### Stable isotopes

Figure 2 presents  $\delta^{13}\text{C}_f$  and  $\delta^{15}\text{N}_f$  values obtained for reed warblers captured and sampled at Larache, Morocco, in September 2009 and June 2011, with boxplots. We found a significant difference in  $\delta^{13}\text{C}_f$  values between first-calendar year and older warblers ( $t = 3.33$ ,  $df = 66$ ,  $P = 0.001$ ), differentially structured between subspecies (interaction age\*subspecies,  $t = 4.27$ ,  $P < 0.001$ ) (but no global effect of subspecies,  $t = -0.42$ ,  $P = 0.67$ ) (59% of variance explained by the predictors). The low values of  $\delta^{13}\text{C}_f$  in all first-calendar-year warblers captured at Larache, regardless of their taxonomic status (*ambiguus* and *scirpaceus*), indicate that they grew their inner primary north of the Sahara. Indeed, in juveniles this feather was grown in the nest north of the Sahara. Most adult *scirpaceus* had moulted the inner primary feather south of the Sahara, with two individuals which either moulted north of the Sahara or may have been wrongly aged as adults. For  $\delta^{15}\text{N}_f$  values, we found significant differences between subspecies ( $t = -2.59$ ,  $df = 66$ ,  $P = 0.012$ ), between ages ( $t = -2.12$ ,  $P = 0.038$ ), and an age structure difference between subspecies (interaction age\*subspecies,  $t = -3.12$ ,  $P = 0.003$ ) (57% of variance explained by the predictors). Adults considered to be of the local breeding Moroccan population all had similar  $\delta^{15}\text{N}_f$  values, but two had high (> \*\*‰)  $\delta^{13}\text{C}$  values, similar to those of feathers moulted south of the Sahara in adult migrant *scirpaceus*.

Outputs of the probabilistic assignments to origin of the feathers sampled on Spanish breeding adult *ambiguus* are presented in Figure 3. When restricting the assignment area to the sub-Saharan winter range of *scirpaceus* (panel a), then most likely locations where feathers might have grown in West Africa extend from Senegal to Liberia, southern Mali and northern Ivory Coast. If the assignment areas includes North Africa and the breeding range of *ambiguus* within the assignment area, (panel b),

then the likely growth area of feathers includes Iberia, northern Morocco and Algeria, with restricted probability in the West African winter range, mainly in Guinea.

## DISCUSSION

### Moroccan reed warblers

Comparing feather  $\delta^{13}\text{C}_f$  and  $\delta^{15}\text{N}_f$  values, we report that juvenile, locally-fledged reed warblers at Larache had similar isotopic values to first-calendar-year *scirpaceus* captured *en route* at the same site (Fig. 2; lower values of  $\delta^{13}\text{C}_f$  and higher values of  $\delta^{15}\text{N}_f$ ), but different from the isotopic values of feathers collected in adult *scirpaceus* (higher values of  $\delta^{13}\text{C}$  and lower values of  $\delta^{15}\text{N}$ ). As expected, our results confirm that juveniles of both taxa grew their feathers north of the Sahara, but more interestingly, that the  $\delta^{13}\text{C}_f$  and  $\delta^{15}\text{N}_f$  values of feathers grown in Morocco were similar to those of feathers grown in Europe, but different from those of feathers grown in sub-Saharan Africa. Of the adults captured in September at Larache, all individuals identified as belonging to the local breeding population had isotopic values similar to the locally hatched juveniles. These results confirm that adult *ambiguus* present in Morocco in early September moulted north of the Sahara the year before, while we do not know whether they stay for winter north of the Sahara or whether they later migrate south of the Sahara to winter (e.g. in Mauretania or Senegal). Two of the adults breeding at Larache and sampled there in June had  $\delta^{13}\text{C}_f$  similar to those of adult *scirpaceus*, so values typical of feathers grown south of the Sahara. That means that at least part of the population breeding in North Africa cross the Sahara before the complete post-breeding moult, and most probably winter there. But globally, our results confirm that most adult *ambiguus* breeding in Morocco do undergo their post-breeding complete moult on the breeding grounds, while their subsequent wintering grounds remain to be discovered. Amezian *et al.* (2010) reported that 9% of first-calendar-year and nearly 50% of adults captured in autumn at Smir, Morocco, had moulted or were in active moult of the primaries. These reports, together with our isotopic results based on non-moulting adults at similar dates, confirm that the vast majority of Moroccan *ambiguus* moult primaries north of the Sahara, probably on or near their breeding grounds, though the few samples collected at Larache in spring also suggest that nearly 20% of breeding birds moult their primaries in sub-Saharan Africa. Whether these birds are second-calendar-year birds is not known but it remains a possibility. Amezian *et al.* (2010) suspected Moroccan birds to winter north of the Sahara. The alternative scenario is that they moult north of the Sahara but an unknown proportion of birds move south of the Sahara after moulting, as the species is present in Moroccan reedbeds in winter, but not in high numbers matching those of the breeding season (Taillandier *et al.* 2006).

### Iberian reed warblers

Accepted Article

Procházka *et al.* (2008) reported four winter (December-February) recoveries in sub-Saharan Africa of ringed birds with known breeding origin in central Spain and Portugal that could be reasonably considered *ambiguus* given current knowledge. Three of them were recorded in the Djoudj National Park in Senegal and one in Guinea-Bissau. However, ring recoveries are highly dependent on ringing effort and recovery probability. The tracks obtained from the geolocators indicate a more extended winter range in West Africa, from Mauretania to Ivory Coast. Furthermore, two MNHN specimens collected in Senegal (CG1966-2270 and CG1962-780) and showing short wing lengths (60 and 63mm, respectively) display overall morphometric characters typical of *ambiguus* (see Olsson *et al.* 2016) with a high probability of belonging to this taxon. All these tracks confirm that Barbary Reed Warblers breeding in Iberia winter in West Africa. This is helpful when interpreting the isotopic results, as geographical probabilistic assignments can provide different explanations of the moulting strategy of the same birds depending on the geographical area of assignment. If we consider that these birds moulted south of the Sahara as do all West European Eurasian Reed Warblers (Svensson 1992) and all other African Reed Warblers, then the highest probabilities cover a continuous area ranging from southern Senegal and Mali to north-western Ivory Coast. This area includes autumn or winter stationary areas identified from geolocators for most of the tracked birds, and is consistent with an autumn or winter moult of Iberian *ambiguus* after crossing the Sahara. If we broaden the potential moulting area up to North Africa and the European breeding range of *ambiguus*, we find a quite similar pattern in West Africa, but we cannot exclude that Spanish *ambiguus* moult on their breeding grounds or in North Africa before crossing the Sahara. However, the scarcity of records of actively moulting reed warblers in reedbeds of Spain in autumn does not favour the hypothesis of a generalized post-breeding primary moult on the breeding grounds, and the short duration of stopovers in North Africa – if any – identified from geolocators does not in favour the hypothesis of a moult in North Africa. Indeed, as an example, more than 3260 reed warblers have been ringed during 2011-2020 at a Constant Effort Site in La Janda (Strait region, southern Spain), with only 15 captures in winter (15 November to 15 January), 5 of them being in active primary moult in November (Alejandro Onrubia pers. comm.). This represents less than 0.5% of the total number, so a tiny fraction of Iberian birds overwinters there, with some moulting there. We therefore suggest that primary moult generally occurs south of the Sahara for Iberian Barbary Reed Warblers, while it generally occurs north of the Sahara for Moroccan Barbary Reed Warblers.

## Conclusions

Stable isotopes and tracks allowed us to identify the main wintering range of the Barbary Reed Warbler in West Africa, which is not confined to a restricted area but extends across different countries. The tracked individual from Catalunya was the one wintering most to the east, most likely in Ivory Coast,

so the winter range is not restricted to coastal western Africa. This is indeed expected as the breeding range of *ambiguus* extends across Iberia and North Africa, eastwards at least to Libya. Olsson *et al.* (2016) indeed reported three individuals belonging to the *ambiguus* genetic clade at Lake Chad in winter. It is therefore highly probable that at least part of the *ambiguus* populations breeding in Tunisia and Libya do winter in the central Sahel, and the winter presence of Barbary Reed Warblers in Niger, Chad or Nigeria would not be surprising. All these elements suggest a potential longitudinally structured connectivity, as found from ring recovery data in the Eurasian Reed Warbler (Procházka *et al.* 2008, Andueza *et al.* 2013).

To conclude, by combining data obtained from ring recoveries, stable isotopes and light loggers, the winter range of the Barbary Reed Warbler can be considered to extend from western to central Sahel, with a post-breeding moult occurring north of the Sahara for North African populations, and south of the Sahara for Iberian populations. Further studies should investigate  $\delta^{13}\text{C}_f$  of feathers collected from Iberian birds, and  $\delta^2\text{H}_f$  of feathers collected from Moroccan birds, as well as geolocator tracking data for the latter, to confirm or refine our proposals.

#### Data availability

All data used in this study are available upon request to the corresponding author. Tracking data are archived on Movebank.org under the ID reference 1077717864.

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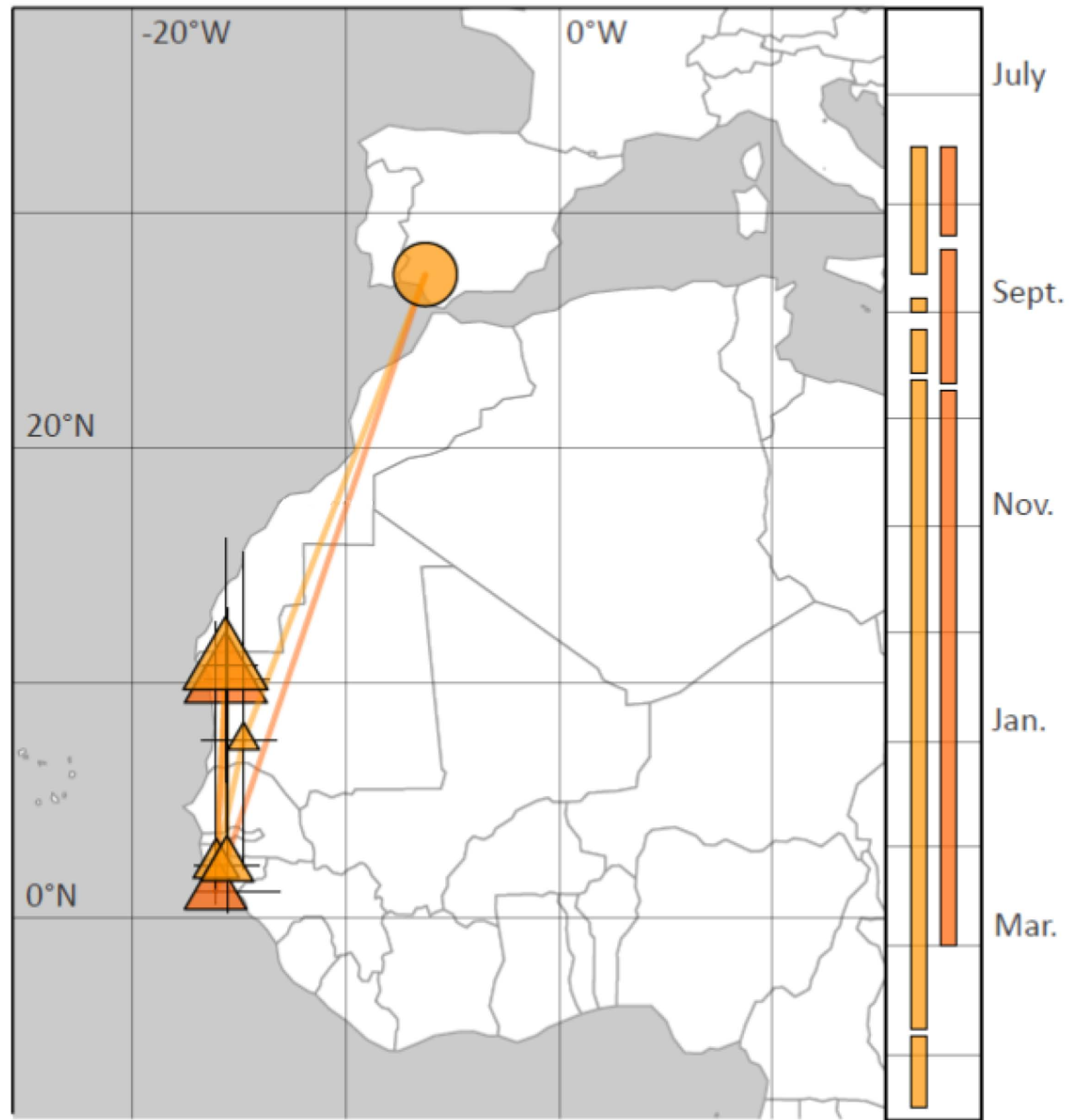
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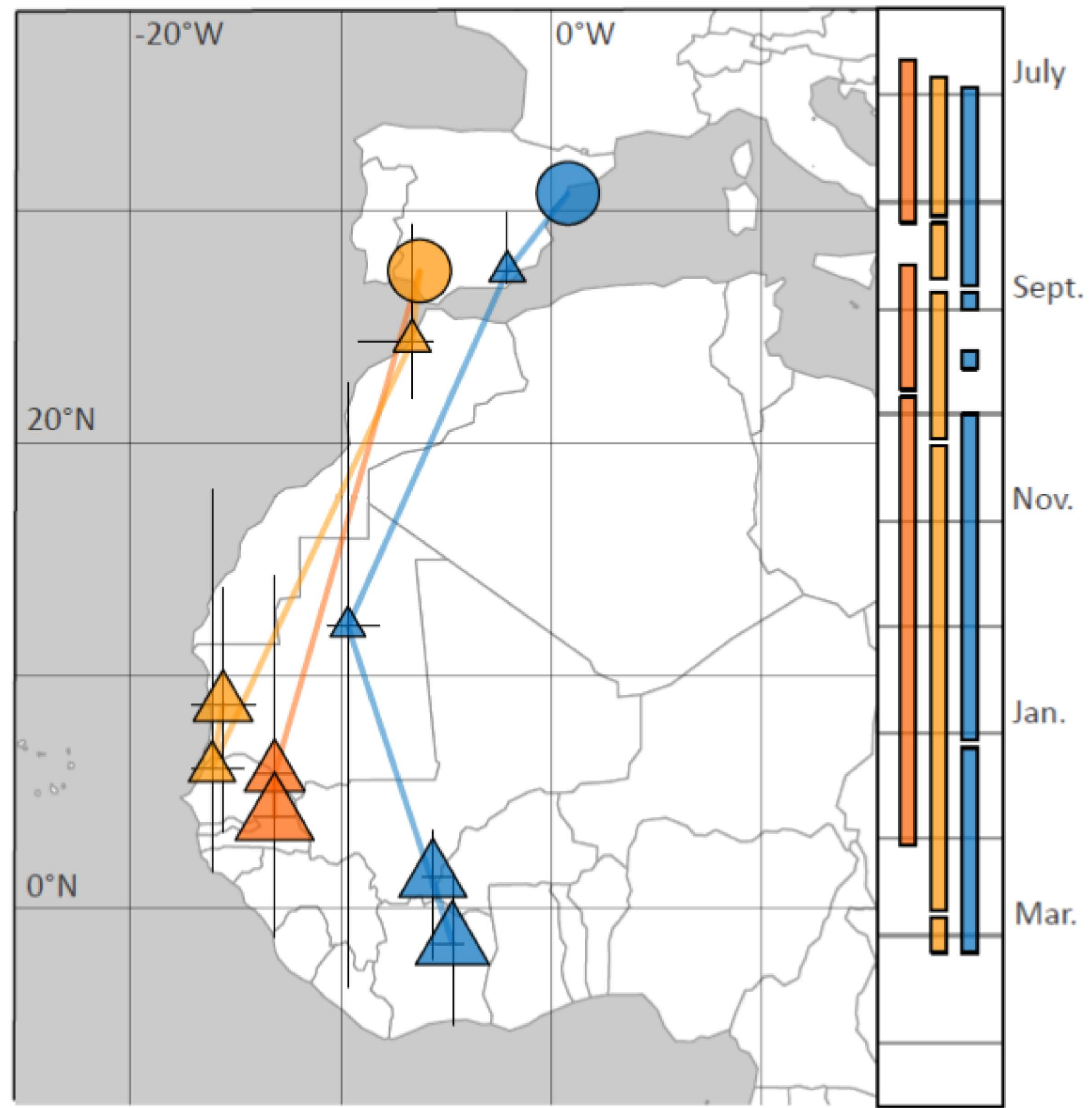
**Figure 1.** Wintering locations of five GLS-tracked Barbary Reed Warblers *Acrocephalus baeticatus ambiguus* tagged in Spain. The two panels represent the deployment year in (a) 2017-2018 and (b) 2018-2019. Colours indicate breeding locations and individuals: Doñana NP, Andalucía, Spain (orange: BD505, BD508, BL945, BL947), and Ebro Delta, Catalunya, Spain (blue: BL955). The dots represent breeding locations and triangle represents stationary locations of more than three days during the non-breeding periods. The size of the triangles represents stationary period duration and error bars represent uncertainty in the estimation of latitudes and longitudes. Coloured lines represent the schematic migratory route between successive stationary locations. For each individual, an estimation of the migration phenology is indicated alongside the map where coloured bars indicate stationary periods and white spaces between them represent movement periods.

(a) 2017-2018



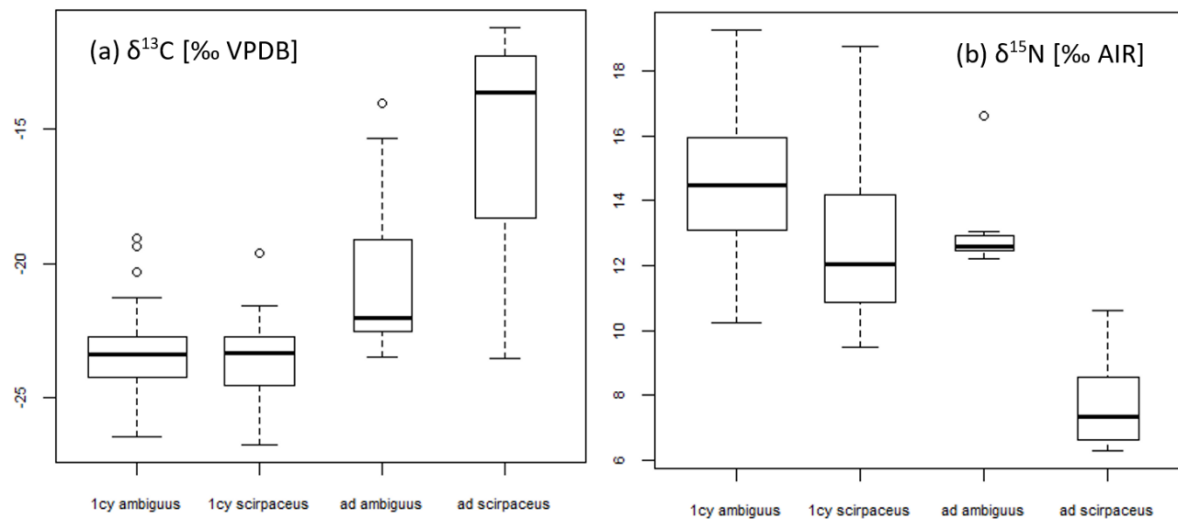
BD508 BD505

(b) 2018-2019

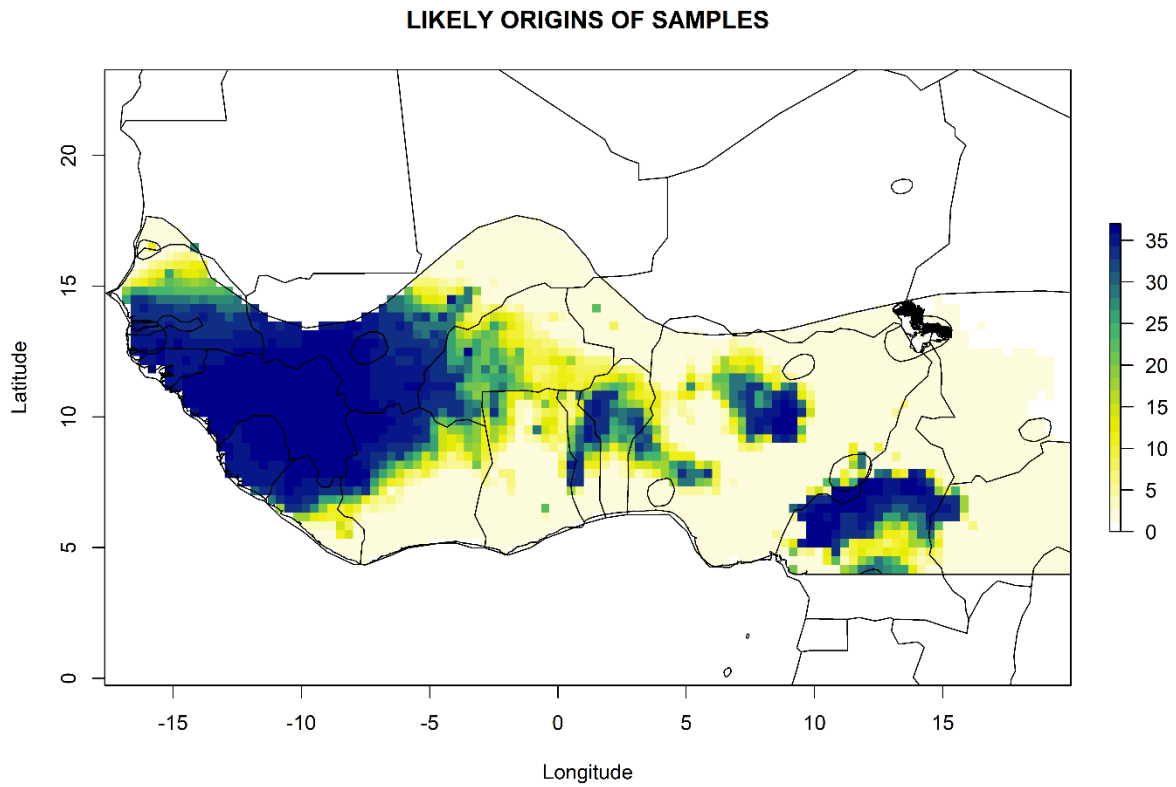


BL945 BL947 BL955

**Figure 2.** Boxplots of feather (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  values from reed warblers captured and sampled at Larache, Morocco, by age (first-calendar-year vs adult) and taxonomy (*Acrocephalus baeticatus ambiguus* vs *A. scirpaceus*). Beyond the median, the boxes extend between the first and third quartiles, bars for the minimum and maximum values, dots are outliers.



**Figure 3.** Assignment to origin of Barbary Reed Warblers *Acrocephalus baeticatus ambiguus* using  $\delta^2\text{H}$  measurements in feathers collected in two breeding populations in Spain (n=39 individuals) (a) within the sub-Saharan winter range of *A. scirpaceus* and (b) within a window covering western North Africa and the European breeding range of *A. b. ambiguus*, both between 20°W and 20°E. The colour gradient represents the number of individuals assigned to a pixel in the feather isoscape using a 2:1 odds ratio.



# LIKELY ORIGINS OF SAMPLES

