

THE MIGRATION SYSTEM OF BARN SWALLOWS
HIRUNDO RUSTICA BREEDING IN SOUTHWESTERN SPAIN
 AND WINTERING ACROSS WEST AFRICA

EL SISTEMA MIGRATORIO DE LA GOLONDRINA COMÚN
HIRUNDO RUSTICA REPRODUCTORA EN ESPAÑA
 E INVERNANTE EN ÁFRICA OCCIDENTAL

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SUMMARY.—Many populations of migratory bird species are rapidly declining. As a requisite for targeting effective conservation efforts it is essential to determine the whereabouts of migrants year-round. However, our knowledge of migratory routes and spatial-temporal occurrence across periods of the annual cycle is still limited for most species. We used light-level geolocators to describe in detail the migration system of Barn Swallows *Hirundo rustica* breeding in southwestern Spain and wintering across West Africa. We were able to successfully retrieve year-round data for 38 individuals and reconstructed their migratory routes using *FLightR* R package. Many of the studied individuals remained for some time in summer wandering through southern Spain and northern Morocco, a period that we defined as pre-migration. The studied swallows started their autumn migration on average on August 18th, stopping over to refuel in northwestern Morocco and southern Mali. On average the tagged individuals arrived on September 3rd at their wintering areas, which were located across Ivory Coast and surrounding countries, in localities dominated by savannahs, grasslands and crops. After wintering, swallows started the spring migration January 26th on average, stopping over in Senegal and Mauritania. They arrived back at the Spanish breeding colonies February 18th on average (from mid-January to mid-March). Surprisingly, during the autumn migration, one of the tagged individuals travelled to England before returning south and spending a short wintering period in northwestern Spain. —López-Calderón, C., Magallanes, S., Marzal, A. & Balbontín, J. (2021). The migration system of Barn Swallows *Hirundo rustica* breeding in southwestern Spain and wintering across west Africa. *Ardeola*, 68: 335-354.

Key words: *Hirundo rustica*, light-level geolocators, migratory routes, phenology, solar geolocation, stopover areas, wintering areas.

RESUMEN.—Numerosas poblaciones de aves migratorias están disminuyendo rápidamente. Como requisito previo a implementar medidas de conservación eficaces, es esencial determinar los lugares

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utilizados por las especies migratorias durante todo el año. Sin embargo, nuestro conocimiento sobre las rutas migratorias y el uso espacio-temporal a lo largo de distintos periodos del ciclo anual es todavía limitado para la mayoría de especies. En este estudio, hemos usado geolocalizadores para describir en detalle el sistema migratorio de la golondrina común *Hirundo rustica* reproductora en el suroeste de España e invernante en África Occidental. Fuimos capaces de recuperar con éxito datos de intensidad lumínica durante toda la migración para un total de 38 individuos, y a partir de estos datos hemos reconstruido las rutas migratorias con el paquete de *R FLightR*. Muchos de los individuos de estudio permanecieron un cierto periodo de tiempo en verano vagando por el sur de España y norte de Marruecos, periodo que hemos definido como premigración. Las golondrinas de estudio comenzaron su migración de otoño en promedio el 18 de agosto, repostando en el noroeste de Marruecos y sur de Mali. En promedio, el 3 de septiembre los individuos marcados llegaron a sus zonas de invernada, distribuidas entre Costa de Marfil y países circundantes (lugares dominados por sabanas, praderas y cultivos). Después de la invernada, las golondrinas comenzaron la migración de primavera en promedio el 26 de enero, repostando a lo largo de Senegal y Mauritania. Finalmente, los individuos del estudio llegaron de vuelta a las colonias de reproducción en promedio el 18 de febrero (desde mediados de enero hasta mediados de marzo). Sorprendentemente, durante la migración de otoño, uno de los individuos marcados viajó hasta Inglaterra y volvió a España, donde realizó un corto periodo de invernada en el noroeste del país.—López-Calderón, C., Magallanes, S., Marzal, A. y Balbontín, J. (2021). El sistema migratorio de la golondrina común *Hirundo rustica* reproductora en España e invernante en África occidental. *Ardeola*, 68: 335-354.

Palabras clave: fenología, geolocalización solar, geolocalizadores, *Hirundo rustica*, rutas migratorias, zonas de invernada, zonas de repostaje.

INTRODUCTION

Migratory behaviour has evolved in a variety of taxonomic groups, such as those constituting zooplankton, insects, fish, amphibians, reptiles and mammals. However, migratory behaviour has undoubtedly developed to the greatest extent in birds, whose aerial journeys incur relatively low energy requirements (Newton, 2008). Thus, more than 50 billion birds perform regular annual movements between breeding and wintering areas, often involving thousands of kilometres (Berthold, 1993). Specifically, it is estimated that about two billion birds migrate each autumn from Europe to sub-Saharan Africa (Hahn *et al.*, 2009). This bulk of individuals constitutes a strong ecological link between different continents across the world, demanding resources along migratory routes and potentially transporting associated species (which may be parasitic or invasive), pollen, seeds, nutrients or contaminants (Kays *et al.*, 2015).

Beyond the intrinsic scientific knowledge that has always fascinated ornithologists, it is necessary to know where migratory birds stay during the non-breeding period as a prerequisite for their conservation (Faaborg *et al.*, 2010). Indeed, many migratory bird species are declining in numbers, in particular long-distance migrants (Sanderson *et al.*, 2006), aerial insectivores (Nebel *et al.*, 2010) and species with low variability in migratory performance (Gilroy *et al.*, 2016). Mortality rates are usually much higher during migration than during the stationary life-cycle stages (Newton, 2008), and conditions experienced along the journey and during overwintering may affect subsequent reproductive performance (i.e. “carry-over effects”; Norris & Marra, 2007; Harrison *et al.*, 2011). Thus, in order to inform effective management decisions, it is first necessary to determine migratory schedules as well as the distribution of habitats visited during migration and winter (Faaborg *et al.*, 2010).

Passerine species make up the majority of long-distance migratory birds (e.g. more than 73% of European breeding individuals; Hahn *et al.*, 2009). However, most detailed information on bird migration is only available for raptors and waterfowls (Kays *et al.*, 2015). This gap of knowledge is obviously led by body size, which has traditionally hampered the attachment of satellite transmitters on to small birds such as migratory passerines (Kays *et al.*, 2015). For this reason, GPS tags have been continuously miniaturised until for the first time a ~1g archival GPS tag was attached to a small migratory bird (Hallworth & Marra, 2015). However, the temporal resolution of these GPS tags is still very limited (only 28 days; Hallworth & Marra, 2015). Consequently, continued miniaturisation of this technology together with an increase in temporal resolution should be expected during the coming years (Kays *et al.*, 2015).

In the meantime, archival light-level geolocators represent the most developed tracking technique available to obtain location estimates during the passerine non-breeding period (McKinnon *et al.*, 2013; Finch *et al.*, 2017; Lisovski *et al.*, 2020). These devices record light levels at fixed time intervals during the whole migration cycle. Once the marked individuals are recaptured, the stored data can be downloaded for analysis. Then, following astronomical equations (e.g. Ekstrom, 2004, 2007), latitude is calculated according to the duration of daylight or to the rate of change in light levels; whereas longitude is calculated according to the time of solar noon or midnight (Lisovski *et al.*, 2020). Light data recorded by geolocators is noisy due to different physical factors (e.g. proximity to equator, equinoxes, cloud cover) and biological factors (shading caused by dense vegetation or by the use of cavities). Consequently, efforts in this research area are currently focussed on statistical methods for quantifying uncertainty of position estimates taking into account all sources of error

(Rakhimberdiev *et al.*, 2015, 2017; Lisovski *et al.*, 2020). Although light-level geolocators present many limitations and offer relatively low precision in position estimates, their simplicity makes them able to collect data during full migration cycles at reasonable economic cost. That is why, since the first published migratory track of a passerine species (Stutchbury *et al.*, 2009), more than 7,800 small birds have been tagged across the world (Brlík *et al.*, 2020). Nonetheless, the attachment of geolocators onto small birds (body mass < 100g) slightly reduces survival rates and thus the further miniaturisation of these devices is still mandatory on ethical grounds (Brlík *et al.*, 2020). After all, geologgers have so far provided invaluable scientific information on the whereabouts of migratory passerines, such as the distribution of their non-breeding habitats, migration phenology, migratory connectivity, factors influencing migration and carry-over effects throughout different stages of the life cycle (McKinnon *et al.*, 2013; Patchett *et al.*, 2018).

The Barn Swallow *Hirundo rustica* is a small passerine (15-20g) that breeds semi-colonially and feeds on insects in flight. The available dataset on ringing recoveries for this species is one of the largest (Ambrosini *et al.*, 2009) but it is still strongly biased towards African countries with high ringing effort (e.g. South Africa). Thanks to limited ringing recoveries, we know that populations breeding in southwestern Europe overwinter from West to Central Africa, whereas northern breeding populations winter from Central to South Africa (Ambrosini *et al.*, 2009). Several breeding populations across Europe have been tracked recently with light-level geolocators, confirming these earlier results (Liechti *et al.*, 2014; Arizaga *et al.*, 2015; Klvaňa *et al.*, 2018; Briedis *et al.*, 2018). Taking into account the abundant scientific literature available for the Barn Swallow (e.g. a search in the Web of Science

for *Hirundo rustica* produces a total of 1,669 studies), filling gaps of knowledge in its migratory behaviour should benefit other research areas that use this species as a study model. For instance, different research areas such as ecological links between continents (e.g. Patchett *et al.*, 2018), avian parasites and diseases (e.g. Kays *et al.*, 2015), sexual selection (e.g. Møller, 1994) or the response of organisms to Global Change (e.g. Gilroy *et al.*, 2016), among others, would benefit from precise information on the migratory behaviour of Barn Swallows.

In this study, we used light-level geolocators to elaborate a detailed description for the migration system of Barn Swallows breeding in the southwestern Iberian Peninsula. First, we reconstructed the migratory tracks of our study individuals. Second, we determined their migration schedules. Third, we identified the stopover and wintering areas used by our study population.

MATERIALS AND METHODS

Field procedures

During 2016-2019, we monitored five breeding colonies of Barn Swallows in southwestern Spain (provinces of Badajoz and Seville): “Asesera” (38°39’ N, 7°13’ W), “La Alegría” (37°29’ N, 6°11’ W), “Las Coladas” (37°36’ N, 6°14’ W), “La Calera” (37°34’ N, 6°13’ W) and “Chaparro” (37°37’ N, 6°14’ W). In our study sites Barn Swallows breed in traditional farms surrounded by Mediterranean *Dehesa*, an extensive agrosilvopastoral management system derived from the Mediterranean forest ecosystem. The number of breeding pairs differed across the study sites and years, ranging from eight to 30 per colony.

From February to June, we captured adult Barn Swallows with mist nets and marked each individual with both metallic and colour

rings. We trapped birds each year until 90-100% of the population was captured at each breeding site. Individuals were sexed from the presence or absence of brood patch, by the length of outermost tail feathers and also by observation of breeding behaviour (Møller, 1994). From May to June 2016, 2017 and 2018, we attached respectively 64, 59 and 55 geolocator devices to adult Barn Swallows using leg-loop harness (Rappole & Tipton, 1991; Bowlin *et al.*, 2010). The tag model was ML6540 (Biotrack, Wareham, UK). In 2016, every tag incorporated a 5mm light stalk and all harnesses were made of elastic material (Street Magic cord, Pepperell Braiding Company). In this year, the weight of both tag and harness averaged 0.59g (3.34% of body weight) and the harness loop diameter was 26-31mm depending on body size. Geologger stalks place the light sensor outside the body feathers, thus reducing shading and improving the quality of light records. However, as a drawback, the stalk increases air drag with associated negative effects on survival (Bowlin *et al.*, 2010; Scandolaro *et al.*, 2014; Morganti *et al.*, 2018). In order to reduce this negative effect (Costantini & Møller, 2013), in subsequent years we only deployed stalk-less tags (so called “flat geolocators”). In 2017, 33 harnesses were made of elastic material and 26 of non-elastic material (cotton thread obtained from mist net material). In that year, the weight of both tag and harness averaged 0.56g (3.24% of body weight), loop diameter of elastic harnesses was 30-33mm and that of non-elastic harnesses was 34-40mm. Finally in 2018, all harnesses were made of elastic material (as in 2016) with a loop diameter of 30mm. In this year, the weight of both tag and harness averaged 0.57g (3.08% of body weight).

To test whether return rates of tagged birds were lower than for untagged, 48, 40 and 42 colour-ringed swallows were considered as controls in 2016, 2017 and 2018 respectively. Control individuals were: (1) individuals that

were captured under the same field procedure as the tagged birds (i.e. captured on the same day that tags were deployed within our breeding colonies) and (2) adult individuals that were captured across the breeding season (e.g. weeks before we started tagging) but that were observed staying in the breeding colonies until we finished tagging. Sample sizes were 64 and 66 individuals for control types 1 and 2 respectively.

Light data analysis

The geolocators measured light levels each minute and recorded the maximum light value every two minutes. Raw light data were corrected for clock drift with *Decompressor* (British Antarctic Survey). Twilight transitions were individually inspected with package *BAStag* (Wotherspoon *et al.*, 2016) of *R* (R Core Team, 2017). Transitions with light peaks or non-linear transitions that substantially disrupted twilight time were manually excluded from further analysis. On average \pm SD, this process resulted in the rejection of $17.82 \pm 11.67\%$ of twilight events in each tag record (range: 3.30-51.37%; $N = 38$). We never edited non-natural twilights; we deleted them but did not fill these gaps with an expected twilight time. This latter restriction should lead to higher uncertainty in position estimates during periods of low quality light data but we were confident that this is the most conservative approach. A minimum dark period of five hours was considered, and the arbitrary threshold value defining twilight was set at 16 (the geolocators measured light levels from 0 to 64). Additional information regarding the quality of our raw light records is available in the Supplementary Material, Appendix 1.

We followed the general guidelines for solar geolocation analyses (Lisovski *et al.*, 2020) and we reconstructed migratory routes from light data with package *FLightR*

(Rakhimberdiev *et al.*, 2017) of *R* (R Core Team, 2017). This method provides refined accuracy and precision of calculated positions by using a hidden Markov chain model and a template fit observation model (Rakhimberdiev *et al.*, 2015). Because geolocator units measure light levels with varying precision, *FLightR* finds the linear relationship between the observed light values (measured by the tag) and the theoretical light values (calculated from current sun angle). This calibration (i.e. “template fit”) can be estimated by recording light measurements at a known position. Thus, we adjusted the selection of calibration periods for each migratory track in order to maximise the number of days with high quality light records at a known position. We used one, two or three different calibration periods whose duration (e.g. two, three weeks) varied among tags depending on data quality. For migratory tracks with more than one calibration period, we accounted for the loss of transparency in the surface of the light sensor (implemented in *FLightR*). The use of buildings for nesting had a strong impact on the light profiles (Liechti *et al.*, 2014; Hobson *et al.*, 2015), and thus the main calibration period was taken usually after nesting but before departure from the breeding colony. Depending on the light data available at a known position, the calibration of a given tag included periods when it was already attached to the bird and, additionally, when it was exposed to the sun on a rooftop. In case we included any rooftop calibration period, we checked that the variability of slopes between observed and expected light values was not constrained so much for subsequent simulations to perform adequately. If that was the case, we did not include the rooftop calibration period but instead used a calibration period at the wintering areas for an estimated stationary position. We used a spatial-mask, constraining our model to consider states of residence only over land, with a buffer distance of 30km out to sea. Following

Rakhimberdiev *et al.* (2015), we incorporated as priors (Bayesian marginal probabilities) 0.1 for probability of migratory behaviour and 300 ± 150 km for distance covered between consecutive twilights.

We defined the start date of a given migratory track as the first day of the first on-bird calibration period, or alternatively as the first day of clean light records after breeding. The end date of a given migratory track was defined as the first day in which twilight times dramatically changed after the wintering period. This could be done by visual inspection of light profiles with function `preprocessLight` of the *BAStag* package (the same function as in the *TwGeos* package). In this way, the start of breeding behaviour after migration could be identified as the appearance of frequent shading events (i.e. use of buildings for nesting). Because twilight times were dramatically disrupted after the start of breeding behaviour (see “BOX 1” in Lisovski *et al.*, 2020), we excluded this period from the analysis and we assumed that the tagged bird had arrived at its breeding colony on the end date of the track (Liechti *et al.*, 2014; Hobson *et al.*, 2015).

After having calibrated light measurements for each tag, and having once defined the spatial mask as well as the Bayesian priors, *FLightR* discretizes the space and uses the particle filter to approximate the posterior distribution (Rakhimberdiev *et al.*, 2015). At the start date of each track (“twilight *i*”), the particle filter generates a sample of 10^6 particles (i.e. points with positions). For each particle, a new position is calculated at “twilight *i* + 1”, according to the observation model as well as the movement model that discerns periods of residence and true migration. All new particles are then resampled according to their weight and continue to the next stage (“twilight *i* + 2”). The process repeats for each twilight until generating 10^6 possible migratory pathways that start and

finish at the breeding colony. From these 10^6 Bayesian simulations, the median position at a given twilight synthesises the most probable location where the tagged individual could be found at that particular twilight. This position estimate matches locations given by high-precision GPS tags adequately (Rakhimberdiev *et al.*, 2016). In addition, the credible intervals (in latitude and longitude) including 95% of particle positions at the given twilight represent the uncertainty associated with the position estimate of that particular twilight.

We ran a total number of 218 trial simulations in which different settings of the analysis were changed to find the best performance for each migratory route (biologically and technically). Such settings include minor differences in prior data filtering, calibration periods and start/end dates. Some trial simulations were even repeated keeping the same settings, and median position estimates did not change substantially. Thus, on average, we repeated the *FLightR* simulation six times for each track. In general, those tracks with lower light data quality required more trials to be run. Once a given simulation performed adequately, we accepted that result as the migratory route for that individual.

After we reconstructed the migratory route for each individual, we defined five key dates across the migration cycle. We defined (1) “departure date from breeding colony” as the first day on which the tagged bird moved from the breeding colony to a different position and did not return. We defined (2) “onset of autumn migration” as the first day on which the tagged bird started to move southwards steadily. We defined (3) “arrival date at wintering area” as the first day on which the tagged bird stopped moving southwards steadily. Some birds arrived at their wintering areas by moving eastwards with constant latitude; in those cases we defined arrival at the wintering area as when the tagged bird stopped moving in that direction. We de-

defined (4) “onset of spring migration” as the first day on which the tagged bird started to move northwards steadily (i.e. departure date from wintering area). Some birds left their wintering areas by moving westwards with constant latitude; in those cases we defined the onset of spring migration as when the bird started to move in that direction. The arrival date at the wintering area and the onset of spring migration that we estimated based on our definitions were virtually the same as these dates inferred with the function `find.times.distribution` of *FLightR*. Finally, we defined (5) “arrival date at breeding colony” as the first day on which the tagged bird arrived at its breeding colony (based on the Markov chain simulation). The function `plot_slopes_by_location` of the *FLightR* package provides a complementary way to determine arrival date at the breeding colony by retrieving the day in which calibration slopes show little variation in time after the wintering period. We also used this function to further confirm arrival date, which was especially useful when the particular swallow started to use buildings some days after its actual arrival at the breeding area. In these cases, we could select these periods for an additional on-bird calibration period at a known location. For the purposes of other ongoing studies, we monitored exhaustively the reproductive performance of our swallows; for example, we inspected each nest weekly from February to July. We therefore knew the breeding date of each tagged individual. This information was very useful to check that the arrival date at the breeding colony estimated by solar geolocation must be earlier than the breeding date estimated by our field monitoring.

With these five key dates, we could divide the migration cycle into four different time periods: i) “pre-migration period”, characterised by erratic short-distance movements around the breeding colonies (i.e. the period between key dates 1 and 2); ii) “autumn mi-

gration period”, characterised by long movements southwards (i.e. between key dates 2 and 3); iii) “wintering period”, characterised by relatively short-distance movements within Africa (i.e. between key dates 3 and 4); and iv) “spring migration period”, characterised by long movements northwards (i.e. between key dates 4 and 5). Limiñana *et al.* (2008) developed a standardised methodology to define the pre-migration period. Nonetheless, because their approach was designed for GPS tracks that allow a precision of < 1km in position estimates, we established our own criteria to define this stage.

We determined the wintering area for each tracked swallow as polygons generated by the function `plot_util_distr` from the *FLightR* package (Rakhimberdiev *et al.*, 2017). This function calculates the accumulated probabilities of occurrence during a specified period, i.e. between the arrival and departure dates at wintering areas. For example, the polygons obtained with this function setting the parameter `percentiles` equal to 0.5, indicate the grid points that accumulated more than 50% of probability of occurrence during winter. These polygons were circles of ~85km diameter because *FLightR* discretizes the space to reduce computation time (Rakhimberdiev *et al.*, 2015).

In order to identify the stopover areas used during pre-migration and migration, we generated our own function in *R* (R Core Team, 2017). We first found the median position estimates in which the tagged bird stayed for at least three consecutive twilights. If the median position estimate of twilight “i” matched that of twilight “i + n” but there were missing twilights among them due to poor quality light data, we filtered this location only if the bird remained there for at least three consecutive twilights (we obtained the stopover duration from the first and last twilight at this location). Then, because any median position estimate may change across repeated Markov chain simu-

lations, we defined the stopover area as the error square generated by 95% credible intervals in latitude and longitude for that median position estimate. A given stopover site is indicated by several twilights with the same median position but with specific associated uncertainty estimates that can be different. Therefore, for a given stopover site, we defined the credible interval in latitude and longitude as the shortest among the twilights involved.

To depict the wintering and stopover areas used by our whole population under study we rasterized, respectively, polygons with accumulated probabilities of occurrence during winter, and error squares of stopover locations. Pixels within these polygons were coded as one, and pixels outside these polygons as zero, resulting in one binary map per individual. Finally, for each stage of the migration cycle, we summed over each individual raster layer. All GIS operations were conducted in *R* version 3.3.1 (R Core Team, 2017) with packages *raster* (Hijmans, 2016) and *sp* (Pebesma & Bivand, 2005).

RESULTS

In 2017, we recaptured 21 out of 64 tagged birds (32.8%) and 27 out of 48 control birds (56.2%). In 2018, we recaptured eight out of 59 tagged birds (13.5%) and eight out of 40 control birds (20%). Finally, in 2019, we recaptured 16 out of 55 tagged birds (29.0%) and 20 out of 42 control birds (47.6%). Thus, survival rates were lower for tagged birds than controls across all our study years, this difference being statistically significant for 2017 ($\chi^2 = 6.15$; $df = 1$; $p = 0.01$) and 2019 ($\chi^2 = 4.01$; $df = 1$; $p = 0.045$), but not for 2018 ($\chi^2 = 1.15$; $df = 1$; $p = 0.28$).

Five of the recovered tags did not provide any useful light data and two tagged individuals (excluded from the Chi-squared tests above) had lost their geolocator upon recap-

ture. Thus, this study was based on a total sample size of 38 year-round migratory tracks. Eleven individuals were tagged in more than one year but only two of them survived the second migration episode. Therefore, we only obtained longitudinal data on migratory routes for two individuals.

Supplementary Material, Appendix 2 presents an interactive map with the 38 migratory pathways. Figure 1 shows a subsample of three migratory tracks: two of them indicating the usual pathways for this migration system (Figure 1A-1C), and the other depicting a single individual that migrated north instead of south (Figure 1B). Similar routes for both autumn and spring migrations were followed by 14 individuals, whereas 24 individuals used different routes across migrations. Among birds that changed migratory pathways between seasons, ten followed an anti-clockwise loop, five a clockwise loop and nine of them a double loop (i.e. a figure-of-eight).

The pre-migration period

Barn Swallows tagged with geolocators left their breeding colonies on average \pm SD on July 28th \pm 17.23 days (range: June 23rd-August 25th; $N = 38$) (Figure 2). Up to 32 study individuals then spent some time wandering across southern Spain and northern Morocco (Figure 3A), whereas only six individuals started their migration directly from the breeding colonies. The pre-migration period averaged 21.61 \pm 17.09 days (range: 0-55 days; $N = 38$). Before starting migration, the studied individuals stopped over on average 2.84 \pm 2.40 times (range: 0-8 stopovers; $N = 38$). Mean stopover duration per individual averaged 8.98 \pm 10.68 days (range: 1-47 days; $N = 30$), whereas maximum stopover duration per individual was on average 14.65 \pm 12.30 days (range: 1-47 days; $N = 30$).

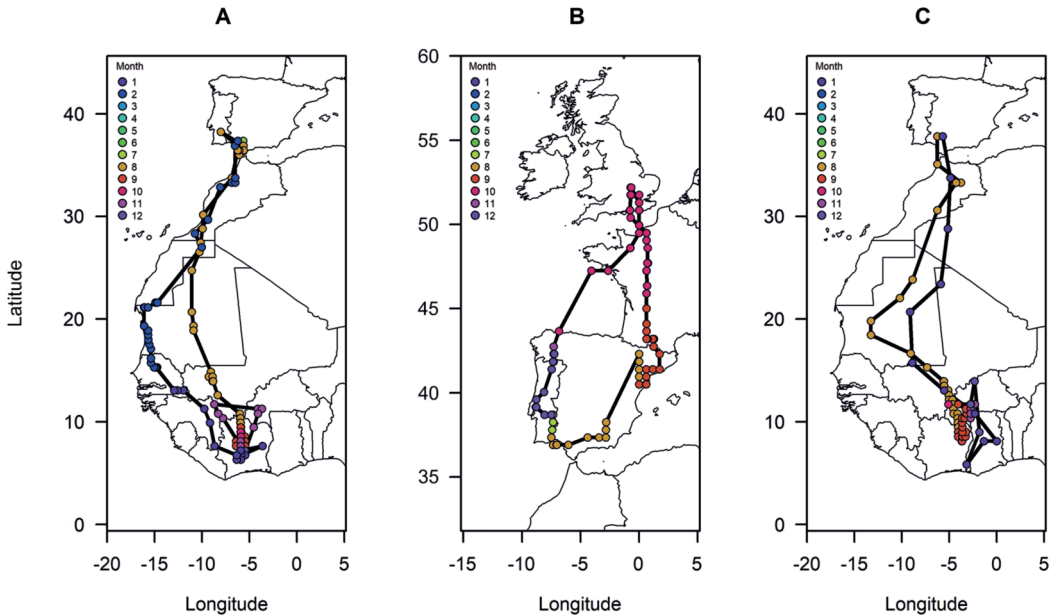


FIG. 1.—Migratory tracks of three different Barn Swallows tagged in 2016, 2017 and 2018, respectively. Subfigures A, B and C, represent birds ringed 2L12365, 2L12590 and 1Y83581, respectively. Dots indicate median position estimates given by the Markov chain simulation run with *FLightR* (Rakhimberdiev *et al.*, 2017). Dot colours indicate the month of the year (see legend). Credible intervals of median positions are shown in Supplementary Material, Appendix 2.

[Rutas migratorias de tres golondrinas marcadas en 2016, 2017 y 2018, respectivamente. Subfiguras A, B y C representan los individuos anillados 2L12365, 2L12590 y 1Y83581, respectivamente. Los puntos indican las posiciones medianas estimadas en la simulación desarrollada por *FLightR* (Rakhimberdiev *et al.*, 2017). El color de los puntos indica el mes del año (leyenda). Los intervalos de confianza de las posiciones medianas se muestran en el Material Suplementario, Anexo 2.]

The post-nuptial or autumn migration period

The tracked Barn Swallows started autumn migration on average \pm SD on August 18th \pm 4.34 days (range: August 10th-26th; N = 38), and the autumn migration period lasted on average 15.57 \pm 5.11 days (range: 8-35 days; N = 37) (Figure 2). The key dates were very different for the single individual that migrated to the north and is consequently excluded from the summary results hereafter. During the autumn migration, individuals usually stayed to refuel in northwestern Morocco and southern Mali (Figure 3B). The

studied individuals stopped over on average 1.38 \pm 1.36 times (range: 0-5 stopovers; N = 37). Mean stopover duration per individual averaged 1.80 \pm 0.89 days (range: 1-5 days; N = 25) and the maximum stopover duration per individual averaged 2.18 \pm 1.24 days (range: 1-5 days; N = 25).

The wintering period

Barn Swallows arrived at their wintering areas on average \pm SD on September 3rd \pm 5.90 days (range: August 21st-September 18th; N = 37), and the wintering period averaged

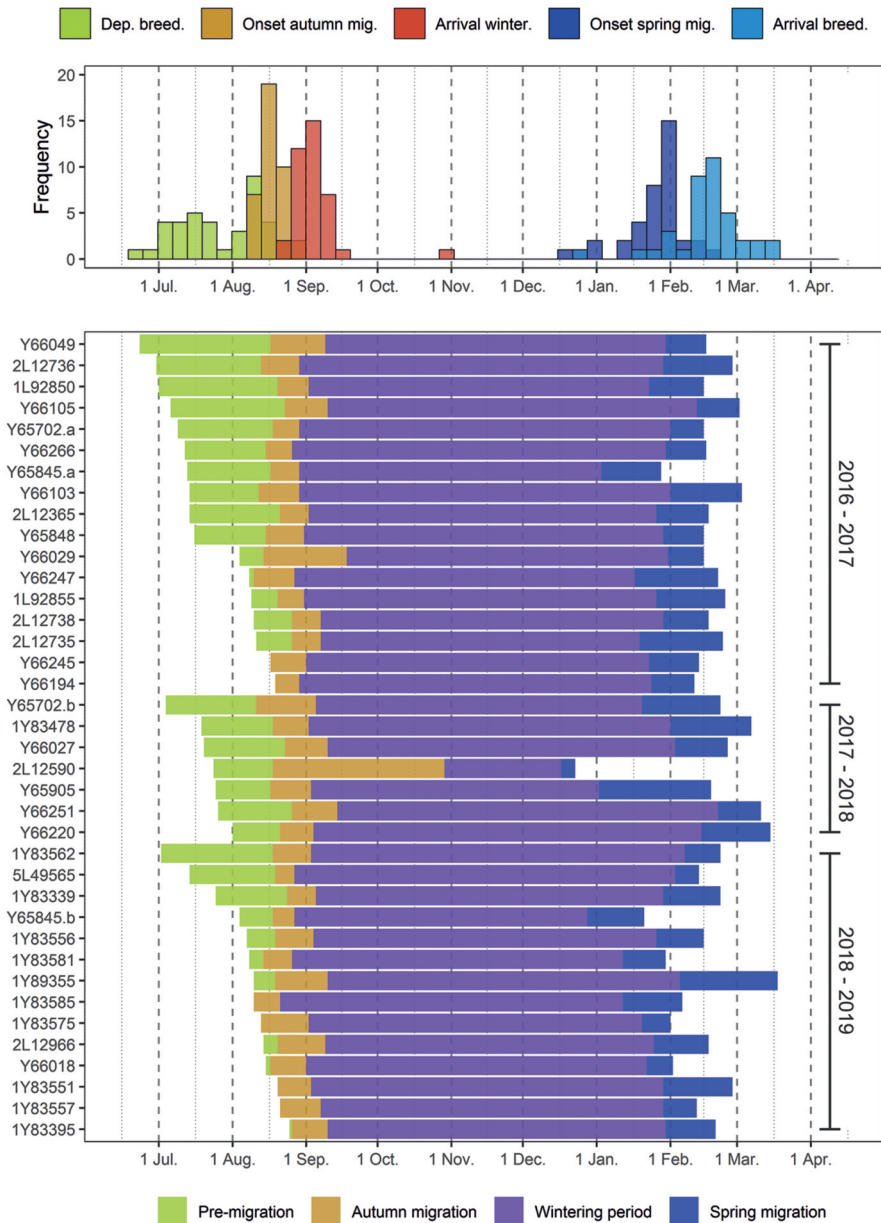


FIG. 2.—Distribution of migration schedules for our study population (histogram with key dates), and timelines with individual migration schedules of 38 Barn Swallows (horizontal bar plot with different stages along the life cycle). Individual 2L12590 conducted reverse migration northwards, the shortest track recorded.

[Distribución de los tiempos de migración para nuestra población de estudio (histograma con las fechas clave), y líneas temporales con los periodos de migración para cada una de las 38 golondrinas de estudio (gráfica de barras horizontal con las diferentes etapas del ciclo vital). El individuo anillado 2L12590 realizó la migración inversa, por tanto es la migración más corta de todas.]

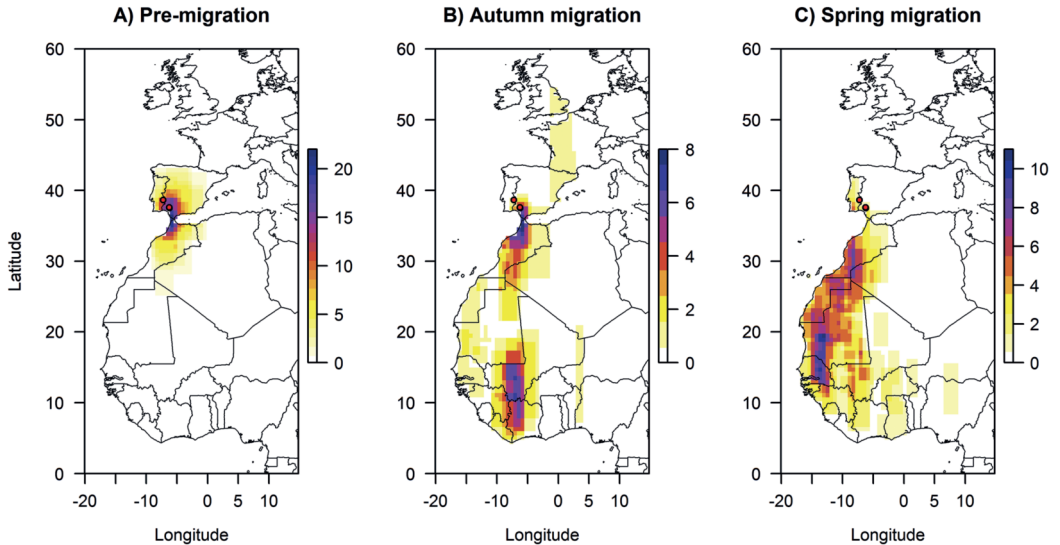


FIG. 3.—Stopover areas used by our study population during pre-migration (A), autumn migration (B) and spring migration (C). Colours indicate the number of birds that were located at the specific pixel. Stopover areas for each individual were defined as error squares of stopover locations (see Methods for details). Breeding colonies are denoted by red dots.

[Zonas de repostaje utilizadas por nuestra población de estudio durante la premigración (A), la migración de otoño (B) y la migración de primavera (C). Los colores indican el número de individuos que fueron localizados en un píxel determinado. Las zonas de repostaje para cada individuo fueron definidas como los polígonos de error de las posiciones medianas repetidas (véase Métodos). Las colonias de reproducción se muestran por los puntos rojos.]

145.35 ± 9.71 days (range: 121-163 days; N = 37) (Figure 2). The wintering areas were widely spread across West Africa (Figure 4), roughly from 5° to 17° in latitude and from -15° to 0° in longitude. The core winter quarters (i.e., grid points that accumulated over 50% of probability of occurrence) were concentrated within Ivory Coast, Mali, southern Mauritania, Guinea, Sierra Leone, Liberia, Burkina Faso and Ghana. These areas were mainly dominated by savannahs, grasslands and croplands (Allen, 2016). Considering also the areas used occasionally during winter (i.e., grid points that accumulated more than 95% of probability of occurrence), our studied populations spread out through other African biomes such as desert and broadleaf forest.

One of the geolocator-tagged Barn Swallows was found dead at a farm of Gbarnga (Liberia). That individual is excluded from our analysis but it constitutes independent validation of the wintering areas that we identified with solar geolocation.

The pre-nuptial or spring migration period

The studied individuals started spring migration on average ± SD on January 26th ± 11.19 days (range: January 2nd-February 21st; N = 37), and spring migration period lasted on average 23.08 ± 8.46 days (range: 10-47 days; N = 37) (Figure 2). During the spring migration journey, swallows usually refuelled in Senegal and Mauritania (Figure 3C). The

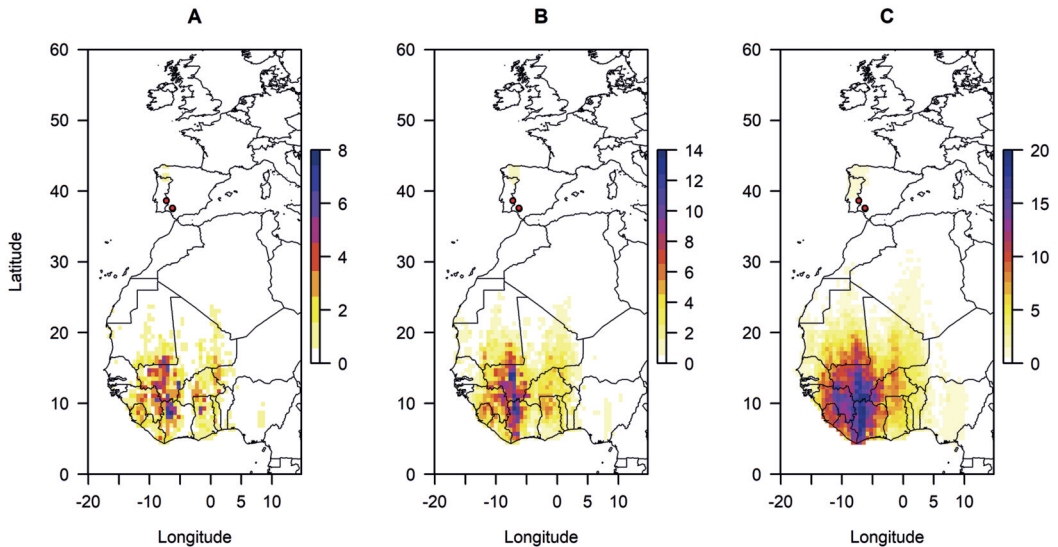


FIG. 4.—Wintering areas used by our study population. Subfigures show different spatial scales used to define individual winter areas: grid points that accumulated more than 50% (A), 75% (B) and 95% (C) of probability of occurrence during winter. Colours indicate the number of birds that were located at the specific pixel. Breeding colonies are denoted by red dots.

[Zonas de invernada utilizadas por nuestra población de estudio. Cada subfigura muestra una escala espacial diferente a la hora de definir los lugares de invernada individuales: puntos de cuadrícula que acumularon más del 50% (A), 75% (B) y 95% (C) de la probabilidad de presencia durante el invierno. Los colores indican el número de individuos que fueron localizados en un píxel determinado. Las colonias de reproducción se muestran por los puntos rojos.]

tagged individuals stopped over on average 3.30 ± 1.78 times (range: 0-7 stopovers; $N = 37$). The mean stopover duration per individual averaged 2.53 ± 1.51 days (range: 1-8 days; $N = 35$), and maximum stopover duration per individual averaged 4.37 ± 3.15 days (range: 1-15 days; $N = 35$). Finally, the tagged individuals arrived back at their breeding colonies on average on February $18^{\text{th}} \pm 12.07$ days (range: January 21^{st} -March 18^{th} ; $N = 37$) (Figure 2).

An exception to the rule: an individual with reverse migration

Surprisingly, one of the 38 tagged individuals did not migrate south to Africa as

expected. Instead, it travelled northwards to England during its autumn migration (Figure 1B). This individual started migration on August 18^{th} . It stopped over to refuel up to 13 times and it took almost two months to reach England (UK). There it remained for two weeks, moving from Southampton to the Midlands (52.2°N , 0.7°W), from where it started to return southwards. It travelled through Brighton, Normandy and the Bay of Biscay to reach Spain in eight days. Based on median position estimates, this bird conducted a non-stop flight over 500km of open sea in just one day. However, the 95% credible intervals were wide enough to include a corridor along the coasts of France and northern Spain. We cannot therefore be completely sure about this long flight over the sea. On

October 29th this individual settled to winter in Galicia (northwestern Spain), remaining there for only 50 days. Thereafter it began its spring migration southwards on December 18th, arriving at its breeding colony just six days later (on December 24th). This individual was the first to return at the breeding colony and, indeed, it was the first individual captured in 2018.

DISCUSSION

This study elucidates the migration system of Barn Swallows breeding in southwestern Spain. We have identified that most individuals remain for some time wandering through southern Spain and northern Morocco before starting to move steadily southwards. We have also determined that: (1) autumn migration generally starts in mid-August; (2) arrival at the wintering areas occurs around the beginning of September; (3) spring migration usually starts in late January; and (4) arrival at breeding colonies mostly occurs during February. The main stopover areas used during autumn migration are located in northwestern Morocco and southern Mali. Wintering areas were found mainly in Ivory Coast and surrounding countries, places dominated by savannahs, grasslands and crops. During spring migration, the majority of individuals stopped over to refuel across Senegal and Mauritania. An exceptional individual migrated in autumn to England, returning to spend the winter in northwestern Spain before arriving back at its breeding colony still very early in winter.

We found a lower survival rate in tagged than in control birds, which resembles previous findings with aerial insectivores (Scandolaro *et al.*, 2014; Szép *et al.*, 2017; Morganti *et al.*, 2018). In order to reduce this negative effect, we attached geolocators without light stalks in 2017 and 2018 (Bowlin *et al.*, 2010; Scandolaro *et al.*, 2014; Costantini & Møller,

2013; Morganti *et al.*, 2018). However, flat geolocators still reduced survival rates and we believe that the low sample size prevented finding a significant difference in survival during the second year of our study.

The pre-migration period

Most tagged Barn Swallows departed from their breeding colonies during the first half of the summer. We could infer from our light data that most individuals did not start autumn migration directly after leaving their colonies. Instead, they spent 22 days on average moving and refuelling across southern Spain and northern Morocco. This well-defined period, which could be named the pre-migration period, has not been defined for all bird species studied so far. Instead the pre-migration period has usually been disregarded in studies tracking migratory passerines (e.g. McKinnon *et al.*, 2013). This could be due to the large uncertainty in position estimates provided by light-level geolocators, which usually include the breeding colony together with potential areas used before migration. However, this stage of the life cycle could be very important for migratory birds since it allows them to gain enough fat reserves to cross large ecological barriers during the ensuing migration (e.g. Rubolini *et al.*, 2002). In addition, the pre-migration period may be used to explore the available resources, to establish social bonds and also, in the case of yearlings, to select suitable sites for breeding during the following spring. Further studies may seek for the reasons behind the high variability among individuals that we found here for the pre-migration period.

The post-nuptial or autumn migration period

Barn Swallows breeding in southwestern Spain began their autumn migration in mid-

August, some 20-30 days earlier than previously reported for other European Barn Swallow populations (Liechti *et al.*, 2014; Arizaga *et al.*, 2015; Briedis *et al.*, 2018). These differences could be explained by latitude, which is lower in our study area when compared to other studied European populations. An earlier study analysing Barn Swallow migration across a wide geographical range in North America similarly showed that the earliest departure date was in the southernmost breeding population (Hobson *et al.*, 2015). Our findings show that autumn migration lasted 16 days on average, which matches previous findings for another Spanish breeding population (Arizaga *et al.*, 2015). In contrast, results for other European populations show that the duration of autumn migration depends on migratory distance; averaging 31, 38 and 41 days for Switzerland-Italy, Czech Republic and Lithuania, respectively (Liechti *et al.*, 2014; Klvaňa *et al.*, 2018; Briedis *et al.*, 2018).

We also found that 25 out of 37 individuals stopped over up to five times and for a maximum period of five days during their autumn migration. A study of Common Swifts *Apus apus* revealed that five out of six individuals stopped over up to five times and for between 10 and 56 days during autumn migration (Åkesson *et al.*, 2012). Thus, the frequency of individuals stopping-over in autumn, as well as the number of stopovers, was similar for Barn Swallows and Common Swifts. However, the latter species remained much longer at a given stopover site than the former, which might be explained by differences in migratory distance or body size. The first main stopover site used in autumn migration by the swallows in our study was in north-western Morocco: eight of 38 individuals stayed to refuel here for at least three twilights. It would be expected that many migratory birds use habitats across northern Morocco to gain fat reserves (Schaub & Jenni, 2000; Rubolini *et al.*, 2002; Hama *et al.*,

2013), given that these habitats constitute some of the last patches of Mediterranean influence before the harsher conditions in the desert beyond. The last main stopover site used, by up to seven birds, was in southern Mali (an area used mainly for wintering).

The wintering period

Barn Swallows breeding in southwestern Spain arrived at their wintering areas in Africa at the beginning of September, some 1-2 months earlier than reported for other European populations (Liechti *et al.*, 2014; Arizaga *et al.*, 2015; Klvaňa *et al.*, 2018; Briedis *et al.*, 2018). The overwintering period lasted about five months, which matches previous results found for hirundines (Liechti *et al.*, 2014; Arizaga *et al.*, 2015; Szép *et al.*, 2017; Klvaňa *et al.*, 2018; Briedis *et al.*, 2018). We also found that some of the tagged individuals remained at a single wintering location whereas others performed significant within-winter movements in West Africa (see Supplementary Material, Appendix 2). Many of these within-winter movements were just latitudinal shifts, which may have arisen from certain periods of lower quality light records or alternatively by the much larger 95% credible interval in latitude compared to longitude (especially close to the autumn equinox). Consequently, these latitudinal shifts may just be an artefact of the Markov chain simulation or raw light data filtering. Future studies might aim to analyse these within-winter movements and to investigate if they are related to ecological factors (e.g. seasonal greening of vegetation), individual intrinsic traits (e.g. age and sex classes) or maybe just due to technical limitations of the light-level analysis.

The wintering areas identified in this study were spread across most of West Africa, with the core situated between Ivory Coast, Mali, southern Mauritania, Guinea, Sierra Leone,

Liberia, Burkina Faso and Ghana. These wintering areas fall within those expected for Barn Swallows breeding in Spain (de Lope, 1980; Ambrosini *et al.*, 2009; Arizaga *et al.*, 2015) and are also similar to wintering areas identified for some other trans-Saharan migrant species (e.g. Walther & Pirsig, 2017; Finch *et al.*, 2017). Clearly the importance of these wintering sites requires consideration when proposing measures for the conservation of Palearctic migrants. At a landscape-level, overwintering Barn Swallows used savannahs, grasslands or croplands as well as occasionally open dry areas and broadleaf forests. These are the main biomes that we can infer by matching the information obtained in this study with available maps of land cover (e.g. Allen, 2016). Nevertheless, the study individuals may forage and roost specifically in wetlands and reedbeds. It is interesting that the main core of wintering areas was located at a very similar longitude to the breeding colonies (approximately 6-7°W).

The pre-nuptial or spring migration period

Barn Swallows breeding in southwestern Spain departed their wintering areas in late January, about two months earlier than the departure dates reported for other European populations (Liechti *et al.*, 2014; Arizaga *et al.*, 2015; Klvaňa *et al.*, 2018; Briedis *et al.*, 2018). This was to be expected since the breeding season for Barn Swallows in southern Spain starts much earlier than in the rest of Europe. Thus, individuals from this study adjusted migratory schedules to take advantage of the longer breeding season that is possible in southern areas. Hence, the tagged Barn Swallows arrived at their breeding colonies mainly in mid-February, again some two months earlier than reported for other European populations (Liechti *et al.*, 2014; Arizaga *et al.*, 2015; Briedis *et al.*,

2018). Previous studies on hirundines have shown that the onset of autumn migration is more synchronised among individuals than both the onset of spring migration and the arrival time at the breeding areas (Liechti *et al.*, 2014; Arizaga *et al.*, 2015; Szép *et al.*, 2017). Here we found a similar pattern, which may help to explain carry-over effects from the winter to the breeding stage (Norris & Marra, 2007; Harrison *et al.*, 2011). Thus, it could be expected that, because of larger variability in departure times from wintering areas and arrival times at breeding areas, some individuals start nesting much earlier than others and hence they would experience benefits in subsequent fitness (Møller, 1994; Newton, 2008).

The duration of the spring migration for Barn Swallows averaged 23 days, a week longer than found for another tracked Spanish population (Arizaga *et al.*, 2015). In contrast, spring migration lasted about one month for other, more northerly, European Barn Swallow populations (Liechti *et al.*, 2014; Klvaňa *et al.*, 2018; Briedis *et al.*, 2018). Previous studies have found that either the duration of both migrations is similar or that the autumn migration takes longer than spring migration (Stutchbury *et al.*, 2009; Åkesson *et al.*, 2012; McKinon *et al.*, 2013; Liechti *et al.*, 2014; Szép *et al.*, 2017; Klvaňa *et al.*, 2018; Briedis *et al.*, 2018). A more rapid spring migration could be expected taking into account the strong incentive for individuals to arrive early at the breeding grounds, given the benefits associated with earlier arrival (Møller, 1994; Newton, 2008). In contrast, we found a longer duration for spring than for autumn migration, which clearly arises from the inclusion of pre-migration period within the life cycle. We advocate distinguishing pre-migration from autumn migration since individuals indeed behave differently during each of these stages and are thus subject to different environmental risks (e.g. lower survival rate on route).

We found that during the spring migration all but two of the 38 tracked individuals stopped over to refuel, and they did so up to seven times and for a maximum period of 15 days. They stopped-over to refuel 3.3 times on average during spring migration and stayed for 2.5 days at these stopover sites. In comparison, Sand Martins *Riparia riparia* stopped over 5-6 times for 1.5 days on average and House Martins *Delichon urbicum* stopped over 3-7 times for one day on average (Szép *et al.*, 2017). The longer migration distances of these martins may require more frequent and briefer stop-overs than those of Barn Swallows from southern Spain, perhaps because longer flights demand more energy resources and permit less delay. The main stopover site, used by 11 of the 38 tagged birds during their spring migration, ranged from Senegal to southwestern Mauritania. Senegal offers a range of African biomes from savannah to the Sahel, and hence Barn Swallows can stopover here to gain sufficient fat reserves for crossing the Sahara desert (Rubolini *et al.*, 2002; Briedis *et al.*, 2018). The identified stopover areas in Mauritania correspond to the Sahel but also to certain oases such as Lake Gabbou, Lake Aleg and riparian corridors. Barn Swallows may use these Mauritanian oases as temporary refuges to recover from fatigue while crossing the desert as well as for foraging areas to increase fat loads for the rest of the journey (Maggini & Bairlein, 2011; Arizaga *et al.*, 2013).

An exception to the rule: an individual with reverse migration

A single individual did not migrate south to Africa (Figure 1B). Instead, it travelled north in autumn until it reached England. To the best of our knowledge, this reverse migration has not been reported previously for any other Palearctic Barn Swallow. Although

this was unexpected, it is possible that a small fraction of a given population could perform reverse migration route and still survive the winter in northern latitudes. For instance, two Barn Swallows were sighted along the coast of Dorset (UK) during December 2017 (<http://dorsetbirds.blogspot.com/2017/12/>; accessed 21 January 2018), which indicates that migrating individuals can use this region in winter. The wintering quarters used by this individual in northwestern Spain were very close to a known winter roost of Barn Swallows in Aveiro, northern Portugal (van Nus & Neto, 2017), where environmental conditions are clearly good enough for Barn Swallows to overwinter. One out of 38 constitutes 2.6% of the tagged population, which might explain the observations of Barn Swallows in England and northern Portugal during winter. It is nonetheless possible that climate change could be favouring the persistence of enough insects during winter (Bale & Hayward, 2010) to allow the survival of individuals with rare migration phenotypes. Such extraordinary migrations may be driven by mutations in specific genes or by epigenetic mechanisms (reviewed in Merlin & Liedvogel, 2019). Thus, future studies should try to identify such genes or epigenetic mechanisms that could explain the variability in migratory phenotypes of Barn Swallows.

CONCLUSIONS

In summary, we have extensively deployed light-level geolocators to investigate the migration system of Barn Swallows breeding in southwestern Spain. Such information relates to the phenology of migration and the geographical distribution of the non-breeding habitats. Solar geolocation is starting to elucidate what have been long-standing gaps in ornithological knowledge.

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AUTHOR CONTRIBUTIONS.—Study conception: CLC and JBA; Methodology: CLC and JBA; Computation: CLC; Formal analysis: CLC; Data collection: CLC, SMA, AMR and JBA; Resources: AMR and JBA; Data curation: CLC; Writing the initial draft: CLC; Critical review, commentary or revision: CLC, SMA, AMR and JBA; Data presentation: CLC; Supervision: AMR and JBA; Project administration: JBA; Funding acquisition: AMR and JBA.

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Appendix 2. Interactive map with 38 migratory routes (it must be opened with Google Chrome). [*Mapa interactivo con 38 rutas migratorias (debe ser abierto con Google Chrome).*]

SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the online version of this article. See the volume 68(2) on www.ardeola.org

Appendix 1. Additional information on light data quality.

[*Información adicional sobre la calidad de los registros de luz.*]

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