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Migration Strategies of Iberian Breeding White-Rumped Swifts *Apus caffer*, Rufous-Tailed Scrub-Robins *Cercotrichas galactotes* and Bluethroats *Cyanecula svecica*

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MIGRATION STRATEGIES OF IBERIAN BREEDING
WHITE-RUMPED SWIFTS *APUS CAFFER*, RUFIOUS-TAILED
SCRUB-ROBINS *CERCOTRICHAS GALACTOTES*
AND BLUETHROATS *CYANECULA SVECICA*

ESTRATEGIAS MIGRATORIAS DE LAS AVES REPRODUCTORAS
IBÉRICAS VENCEJO CAFRE *APUS CAFFER*,
ALZACOLA ROJIZO *CERCOTRICHAS GALACTOTES*
Y RUISEÑOR PECHIAZUL *CYANECULA SVECICA*

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SUMMARY.—The migration strategies of smaller, south European, Mediterranean birds are less well known than those of northern and central European birds. We used geolocators to map individual spatio-temporal migration schedules of three species breeding in the Iberian Peninsula: the White-rumped Swift *Apus caffer*, Rufous-tailed Scrub-robin *Cercotrichas galactotes* and Bluethroat *Cyanecula svecica*. The three species crossed the Sahara desert with a westward detour, to reach West African winter grounds in the Sahel (Bluethroats and Scrub-robins) or the rainforest belt (Swifts). Despite the proximity of the breeding grounds to the desert barrier, all but one individual stopped over before the desert crossing during autumn migration. After spending six months on average in sub-Saharan Africa with variable itinerancy, spring migration was faster overall and more direct than in autumn. Autumn migration was of similar duration to that found in related northern European migrants and therefore slower in southern birds. Spring migration was completed in less time than in the northern migrants (data only for Swifts

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and Scrub-robins). The shorter migration distance and proximity to the barrier potentially allow south European trans-Saharan migrants to migrate more slowly than northern migrants but only when less time-constrained in autumn.—Lomas Vega, M., Willemoes, M., Arizaga, J., Onrubia, A., Cuenca, D., Alonso, D., Torralvo, C., Tøttrup, A.P. & Thorup, K. (2019). Migration strategies of Iberian breeding White-rumped Swifts *Apus caffer*, Rufous-tailed Scrub-robins *Cercotrichas galactotes* and Bluethroats *Cyanecula svecica*. *Ardeola*, 66: 51-64.

Key words: ecological barrier, desert crossing, geolocators, spatiotemporal schedule, stopover.

RESUMEN.—Las estrategias migratorias de aves pequeñas que se reproducen en el sur de Europa y cuenca del Mediterráneo son menos conocidas que las del norte y centro de Europa. En este estudio mapeamos con geolocalizadores el programa espacio-temporal de la migración de individuos pertenecientes a tres especies reproductoras de la península ibérica: vencejo cafre *Apus caffer*, alzacola rojizo *Cercotrichas galactotes* y ruiseñor pechiazul *Cyanecula svecica*. Los individuos marcados cruzaron el desierto del Sahara desviándose por el oeste y alcanzando áreas de invernada de África occidental, en el Sahel (pechiazules y alzacolas) o en el bosque lluvioso (vencejos). Pese a la proximidad entre las áreas de reproducción y la barrera del desierto, todos los individuos menos uno realizaron paradas de reposo antes de cruzar esta barrera durante la migración de otoño. Después de pasar una media de seis meses en África subsahariana con itinerancia variable, la migración de primavera fue en general más rápida y directa que en otoño. La duración de la migración de otoño fue similar a la de especies migratorias relacionadas que se reproducen en el norte de Europa, y por tanto, esta migración fue más lenta en las especies sureñas que estudiamos. La migración de primavera se completó en menos tiempo que en las especies norteñas (datos de vencejos y alzacolas sólo). La distancia de migración más corta y la proximidad de la barrera posiblemente permiten que especies sureñas que invernan al sur del Sahara migren más despacio que especies norteñas aunque sólo en otoño, cuando el tiempo potencialmente disponible las limita menos.—Lomas Vega, M., Willemoes, M., Arizaga, J., Onrubia, A., Cuenca, D., Alonso, D., Torralvo, C., Tøttrup, A.P. y Thorup, K. (2019). Estrategias migratorias de las aves reproductoras ibéricas vencejo cafre *Apus caffer*, alzacola rojizo *Cercotrichas galactotes* y ruiseñor pechiazul *Cyanecula svecica*. *Ardeola*, 66: 51-64.

Palabras clave: área de sedimentación, barrera ecológica, cruce del desierto, programa espacio-temporal, geolocalizadores.

INTRODUCTION

Compared to migratory birds breeding in northern Europe, less is known about the spatiotemporal schedules and non-breeding distributions of migratory birds breeding in southern Europe, particularly the smaller species (Mckinnon *et al.*, 2013). Research has mostly focused on unravelling migration strategies, migration routes and distributions of northern and central European breeding species (e.g. Åkesson *et al.*, 2012; Kristensen *et al.*, 2013; Hahn *et al.*, 2014; Lislevand *et al.*, 2015; Ouwehand *et al.*, 2016; Stach *et al.*, 2016; van Wijk *et al.*, 2016a). Thus, po-

tential effects on migration strategies of the proximity to barriers of the breeding grounds, and migration distance remain poorly known.

Afro-Palaearctic long-distance migrants cross or circumvent the Sahara desert twice every year during their annual cycles (Moreau, 1952, 1972; Hahn *et al.*, 2009). Most north-western Palaearctic sub-Saharan migrants detour westwards when crossing the Sahara desert (Åkesson *et al.*, 2012; Kristensen *et al.*, 2013; Hahn *et al.*, 2014; Ouwehand *et al.*, 2016; Lerche-Jørgensen *et al.*, 2017). The desert constitutes an ecological barrier where refuelling possibilities are scarce (Moreau, 1972; Bairlein, 1988; Biebach,

1990). Before crossing an ecological barrier songbirds from northern Europe generally stop over to refuel (Alerstam & Lindström, 1990; Fransson *et al.*, 2005, 2008) and the refuelling load may depend on the extent of the barrier (Rubolini *et al.*, 2002). Studies of the desert-crossing have suggested different strategies, including regular stopovers on the desert itself (Bairlein, 1988; Schmaljohann *et al.*, 2007), crossing only at night (Biebach *et al.*, 1986) or a non-stop strategy (Moreau, 1961; 1972; Adamík *et al.*, 2016; Ouweland & Both, 2016). Non-stop flights may be prolonged into daytime to traverse the barrier (Adamík *et al.*, 2016; Ouweland & Both, 2016), although these could imply short stops of the order of hours and not days (Xenophonos & Cresswell, 2016).

Timing of migration is largely determined by breeding latitude, presumably because climatic conditions limit food resources towards the North (Holmes, 1971; Conklin *et al.*, 2010; Briedis *et al.*, 2016). In addition to food resources, other factors such as moult may also affect timing, i.e. summer moult on or near the breeding grounds can delay or slow down autumn migration (Barta *et al.*, 2008). Seasonal differences in duration and speed of migration have been studied in detail, mainly comparing spring and autumn migration (Fransson, 1995; Henningsson *et al.*, 2009; Yohannes *et al.*, 2009; Nilsson *et al.*, 2013). However, fewer studies have looked into the variation of migration duration and speed as a function of migration distance at the species or population level (but see Fransson, 1995; Briedis *et al.*, 2016). Stationary winter periods vary among species from only one period, as in Common Redstarts *Phoenicurus phoenicurus* (Kristensen *et al.*, 2013; Gersten & Hahn, 2016), to several periods or itinerant behaviour, as in Thrush Nightingales *Luscinia luscinia* (Stach *et al.*, 2012; Thorup *et al.*, 2017).

Being close to the barrier potentially allows birds to migrate directly to non-breeding

grounds, as recently found in Cyprus Wheatears *Oenanthe cypriaca* (Xenophonos & Cresswell, 2016), thus avoiding unnecessary stopovers that could incur higher mortality. Southern species wintering in West Africa are likely to use similar detoured routes as more northerly breeding species (Åkesson *et al.*, 2012; Kristensen *et al.*, 2013; Hahn *et al.*, 2014; Ouweland *et al.*, 2016; Lerche-Jørgensen *et al.*, 2017). The timing of migration may be more flexible in southern migrants because good foraging conditions at southerly breeding latitudes last longer than in more northerly latitudes (Holmes, 1971; Conklin *et al.*, 2010; Briedis *et al.*, 2016) and thus, autumn migration would potentially be later, and spring migration earlier, in southern migrants, yet timing can be more spread out. Furthermore, while many northern migrants moult in winter, many southern migrants moult before autumn migration (Barta *et al.*, 2008) presumably because good foraging conditions last longer, which in itself delays migration. For time-constrained migrants, the migration speeds of ecologically similar species are likely to be similar and, consequently, migration duration in southern migrants can be shorter.

Here, we used geolocators to map the spatiotemporal schedule of three southern European, long-distance migrants: White-rumped Swift *Apus caffer*, Rufous-tailed Scrub-robin *Cercotrichas galactotes* and Bluethroat *Cyanecula svecica* (ssp. *azuricollis*), from breeding sites in the Iberian Peninsula. We investigated and discuss the migration strategies of migrants with breeding grounds close to the desert barrier and winter grounds, and compare these with those from more northerly breeding grounds. Specifically, we describe overall migration routes and spatiotemporal migration and wintering strategies. Because migration often occurs close to the equinox, when latitude estimation using geolocators is impossible, we restricted our identification of spatiotemporal

migration-strategy measures to (1) timing of arrival and departure on breeding and winter grounds, (2) stopovers before barrier crossing, (3) detours when crossing the barrier, (4) duration, distance and speed of spring and autumn migration, and (5) itinerancy during winter. For comparison with the schedule of the southern species, we used a range of published accounts of northern breeding migrants that belong to the same genera or families and migrate via central-western Africa, assuming that similar species would experience similar pressures (Jacobsen *et al.*, 2017).

MATERIALS AND METHODS

Field work

Adult males and first-year birds of the southern species were fitted with archival light-level loggers (geolocators) on breeding grounds in central and southern Spain. Mk20 (British Antarctic Survey, BAS, UK; 0.60g), Mk6 (Biotrack Ltd., UK; 0.60g), and Intigeo W55 (Migrate Technology Ltd, UK; 0.55g) geolocators were fitted on 19 White-rumped Swifts at Barbate (36°22'N 5°39'W) in 2012 (3 birds), 2013 (6) and 2015 (10). Mk10 (BAS, UK; 1.1g) geolocators were fitted on 38 Rufous-tailed Scrub-robins breeding at Tarifa (36°7'N 5°43'W) in 2011 (10), 2012 (8), 2013 (6) and 2015 (15), of which 13 were first-year birds. Forty Intigeo W55 geolocators were fitted on Bluethroats breeding at a high-elevation site in the Sierra de Béjar (40°21'N 05°41'W; Arizaga & Alonso, 2015), in 2014 (20) and 2015 (20). All geolocators had no light stalk except for 21 of the loggers fitted on Scrub-robins. Leg-loops (Bluethroats and Scrub-robins) and body harnesses (Swifts) made of 1 mm-wide nylon string were used to fit the tags. For Swifts and Scrub-robins, three geolocators were recovered for each species (in 2014 and 2016),

and for Bluethroats four were recovered (in 2015 and 2016). One Scrub-robin and one Bluethroat returned with the geolocator in 2016 and 2015, respectively but retrapping was not possible, and another recaptured Scrub-robin had lost the geolocator. The return rates of birds fitted with geolocators were 0.16 for Swifts, 0.20 for adult and 0 for first-year Scrub-robins, and 0.12 for Bluethroats. The return rate of the ringed-only Swifts was 0.3 (ringed-only individuals: 10 recaptured in subsequent years of 35 ringed). The return rate of ringed Scrub-robins was 0.17 for adults (8/47) with no first-year birds recaptured (0/27). No control sample was available for the Bluethroats. For another Spanish population, the return rate ranged from 0.05-0.3, depending on year, site and sampling effort (Arizaga & García, 2013).

We obtained tracking data on complete annual cycles for two Swifts and three Scrub-robins, and until stationarity in the winter grounds for three Bluethroats and one Swift. One set of the Bluethroat light data was only used for timing of migration analysis since the migration periods were well defined but the location estimates were highly imprecise, possibly due to a high degree of shading. Another Bluethroat logger did not record data. Due to high variability in the light data, especially at the end of the battery life, it was not possible to determine the number of stationary winter periods and wintering duration for Bluethroats and one Swift (Supplementary material, Figures S1–S3).

Data analysis

Geolocator data was analysed using the *Geolight* R-package. The threshold method (*twilightCalc* function, Ekstrom, 2004) was used to define sunrises and sunsets, with a light intensity threshold of three lux for Intigeo tags and two (arbitrary units) for BAS

tags, and all the light events were visually revised. Sunrise and sunset data were filtered using a smoother function (*LoessFilter*) to eliminate outliers, with five interquartile ranges before excluding values as outliers (K parameter), since a lower value eliminated relevant data. To estimate latitudes, the Hill-Ekstrom calibration (Lisovski *et al.*, 2012) was first applied to the main stationary winter periods (defined by stable longitude patterns) obtaining the sun elevation angles.

The resulting sun elevation angles varied individually for Swifts between -6.1° and -5.3° , for Scrub-robins between -6.5° and -4.6° and for Bluethroats between 0° and 0.5° . Longitude estimates were used to define stopovers (Thorup *et al.*, 2017), i.e. interruption of migration, of four days or more (Figure 1; Supplementary material, Figures S1–S3). Stopover positions were calculated as the mean of longitude and latitude estimates during each stationary period. Stop-

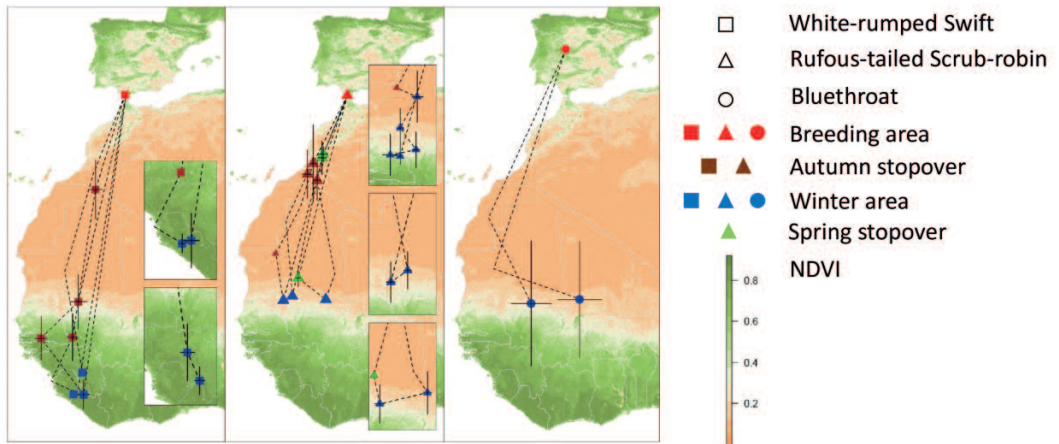


FIG. 1.—Migration routes of White-rumped Swifts ($N = 3$, left, squares), Rufous-tailed Scrub-robins ($N = 3$, center, triangles) and Bluethroats ($N = 2$, right, circles) tracked with geolocators. Breeding areas, autumn stopovers, winter areas and spring stopovers are indicated in red, brown, blue and green colours, respectively. Stopovers affected by the equinox are represented with a smaller icon or with a line bend. Inset maps represent the stationary winter periods of five individuals and for Scrub-robins are extended into spring. Standard deviation of longitude and latitude of the position estimates are shown for stopovers not affected by the equinox and for winter periods. Background layer represent MODIS MOD13C1 Normalized Difference Vegetation Index (NDVI) 16-days values at 0.05° resolution, and values are means for September–October, 2013–2015.

[*Rutas migratorias de vencejo cafre* ($N = 3$, izquierda, cuadrados), *alzacola rojizo* ($N = 3$, centro, triángulos) y *ruiseñor pechiazul* ($N = 2$, derecha, círculos) monitoreadas con geolocalizadores. Áreas de reproducción, paradas de reposo de otoño, áreas de invernada y paradas de reposo de primavera se indican con color rojo, marrón, azul y verde respectivamente. Paradas de reposo afectadas por el equinoccio se representan con iconos más pequeños o con una curvatura de línea. Los mapas insertados representan los periodos de estacionamiento de invernada de cinco individuos y para los alzacolas estos periodos se extienden durante la primavera. Desviaciones estándar de las longitudes y latitudes de las posiciones estimadas se muestran para las paradas de reposo no afectadas por el equinoccio y para los periodos de invernada. La capa del fondo representa el Índice de Vegetación de Diferencia Normalizada (NDVI, MODIS MOD13C1), con resolución espacial de $0,05^\circ$ y resolución temporal de 16 días, y los valores representados son medias de septiembre-octubre, 2013-2015.]

over latitude during equinox periods (spanning one to three weeks before and after the equinox, depending on the individual bird) were estimated using theoretical individual speed between two stopovers that included an equinox stopover. These stopovers were only used for illustrative purposes and to tentatively describe the desert crossing. We think that the large variability obtained in the sun elevation angle between species and the variable period affected by equinox may be related to the ecological preferences of the species resulting in different shading effects in the light data (Lisovski *et al.*, 2012). It was not possible to investigate whether individual birds crossed the Sahara desert by prolonging flights by day, overall, because the crossing largely overlapped with the period affected by the equinoxes and, specifically, because the Swifts stay airborne, and the light profiles of Scrub-robins and Bluethroats were too shaded to study this aspect.

We also investigated whether the locations of non-breeding sites could potentially be affected by unusual environmental conditions. We visually inspected vegetation-condition anomaly maps for the non-breeding areas used (Supplementary material, Figure S4) based on the Normalized Difference Vegetation Index (NDVI). We used the January NDVI anomalies as an overall measure of the conditions in each year with tracking data (2013-2016).

Comparison of southern and northern migrants

Migration schedules of southern migrants were compared to those of migrants breeding at more northern European latitudes. These two groups were called southern and northern migrants, respectively. Geolocator-based documentation on Common Swifts *Apus apus* (N = 6; Åkesson *et al.*, 2012), Common Nightingales *Luscinia megarhynchos*

(N = 11 in autumn; N = 7 in spring; Hahn *et al.*, 2014) and Common Redstarts (N = 7; Kristensen *et al.*, 2013) breeding in northern and central Europe was used for comparison with the southern group. Timing, duration, distance and speed of migration were compared using Mann-Whitney U-tests (Supplementary material, Table S3). Values are shown as means with standard deviation (SD), and the distances were calculated as great circle distances connecting stopover estimates with the *geosphere* package in R 3.3.2 (R Development Core Team 2011).

RESULTS

Migration and wintering in southern migrants

During autumn migration, the White-rumped Swifts, Rufous-tailed Scrub-robins and Bluethroats breeding in the Iberian Peninsula crossed the Sahara on a western detour (longitudinal range: 9°–15°W). All individuals except one stopped over before the Sahara crossing. Departure from breeding grounds by Bluethroats was less variable and approximately a month earlier (early August) than in Scrub-robins and Swifts. Timing of arrival at the winter grounds was most variable in the Bluethroats. The Bluethroats and Swifts arrived on average at the beginning of November while the Scrub-robins did so one month earlier (Supplementary material, Table S1, S2). The interval between departure from breeding grounds to reaching the wintering grounds was three months overall for the Bluethroats, one month for the Scrub-robins and one month and a half for the Swifts, so the Bluethroats apparently migrated more slowly than the Scrub-robins and the Swifts (Table 1; Supplementary material, Figures S1, S2).

Individuals of the three species spent most of the winter in West Africa, the Bluethroats

and Scrub-robins in the Sahel (Mauritania and Mali) and the Swifts over the rainforest (Guinea and Liberia). They showed variable intraspecific itinerancy, from one main winter period to five stationary periods extending into spring (Figures 1, 2, Table 1). The total wintering duration for the Bluethroats was uncertain because of tag failure but lasted

at least three months, while the Swifts and Scrub-robins showed long total wintering durations (six to nine months; Supplementary material, Table S1).

Longitude estimates indicated an overall straighter migration route (Figure 1) and shorter time stopping over in spring (average stopover time: Scrub-robins 8 ± 2 days

TABLE 1

Migration parameters of individual southern migrants. Number of stopovers, total duration (days), distance (km), and speed (km/day; including stopovers) of autumn and spring migration, and wintering period (with number of periods and duration in days). WS = White-rumped Swift; SR = Rufous-tailed Scrub-robin; BT = Bluethroat. *Stopover number of Bluethroats is the minimum observed due to noise in the light data.

[Parámetros de migración de las aves sureñas. Número de paradas de reposo, duración total (días), distancia (km) y velocidad (km/h; incluyendo paradas de reposo) durante la migración de otoño y primavera, y periodo de invernada (con número de periodos y duración en días). WS = vencejo café; SR = alzacola rojizo; BT = ruiseñor pechiazul. *El número de paradas de reposo de pechiazul es el mínimo observado debido al ruido en los datos de luz de los geolocalizadores.]

PARAMETER	Southern migrants								
	WS 1	WS U012	WS U014	SR 007	SR 012	SR 2016	BT 1	BT T020	BT T008
Autumn migration									
Stopover number	3	2	2	3	3	2	2*	1*	—
Migration duration	54	51	35	21	58	19	74	85	109
Migration distance	2893	3567	3466	1852	2159	2195	2632	2691	—
Migration speed	54	70	99	88	37	116	36	32	—
Wintering period									
Wintering areas	2	1	2	5	2	2	1	1	—
Winter duration	≥ 92	190	181	270	197	199	≥ 108	≥ 115	≥ 117
Spring migration									
Stopover number	—	0	0	1	1	1	—	—	—
Migration duration	—	20	4	12	20	32	—	—	—
Migration distance	3090	3185	3198	2464	2463	2789	—	—	—
Migration speed	—	159	800	205	123	87	—	—	—

[mean \pm SD], no stopovers in Swifts) than in autumn (Scrub-robins: 24 ± 19 days; Swifts, $32 \text{ days} \pm 12$; Figure 2; Supplementary material, Table S1, S2). The Scrub-robins initiated spring migration on average 12 days earlier than Swifts (close to mid-May) and timing was less spread out than in autumn for the Swifts (SD of departures, 2 days in spring and 19 days in autumn; Supplemen-

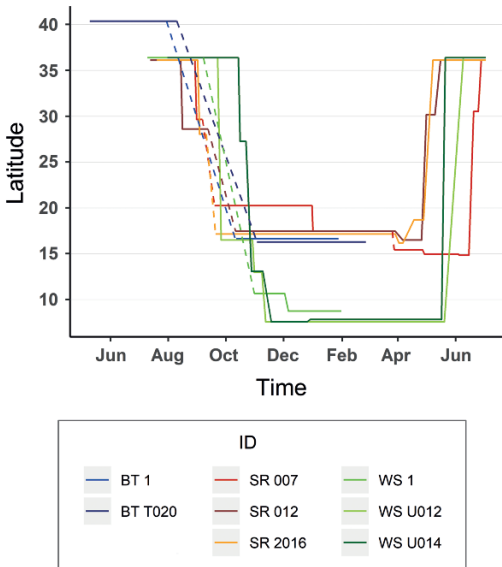


FIG. 2.—Latitude crossings ($^{\circ}$ N) from breeding to winter grounds and back of White-rumped Swifts ($N = 3$, green colours), Rufous-tailed Scrub-robins ($N = 3$, red, brown and orange colours) and Bluethroats ($N = 2$, blue colours) with time (days). Data logging of one White-rumped Swift and the two Bluethroats stopped during winter. WS = White-rumped Swift, SR = Rufous-tailed Scrub-robin; BT = Bluethroat.

[Cruce latitudinal ($^{\circ}$ N) desde las zonas de reproducción hasta las de invernada y vuelta, de vencejo cafre ($N = 3$, colores verdes), alzacola rojizo ($N = 3$, colores rojo, marrón y naranja) y ruiseñor pechiazul ($N = 3$, colores azules) con el tiempo en días. El registro de datos de un vencejo y de dos pechiazules paró durante el invierno. WS = vencejo cafre; SR = alzacola rojizo; BT = ruiseñor pechiazul.]

ary material, Table S2). Both the Scrub-robins and Swifts arrived at the breeding grounds at approximately the same time (end of May; Figure 2; Supplementary material, Table S1, S2). Migration duration was shorter in spring than in autumn for both species (spring versus autumn in Scrub-robins: 21 ± 10 days and $33 \text{ days} \pm 22$; in Swifts: 12 ± 11 and 47 ± 10 days) and longer for the Scrub-robins than the Swifts in spring. The Scrub-robins spent less time stopping over, making migration speed faster than in autumn, while the Swifts did not stopover and were much faster (Table 1; Supplementary material, Tables S1, S2).

In West Africa, the NDVI anomalies were slightly above the long-term average during all tracking years, with little interannual variation (Supplementary material, Figure S4).

Comparison with northern migrants

Both southern and northern birds stopped over after leaving their breeding grounds and before the barrier crossing. Unlike southern birds, most northern birds (but not Common Redstarts) also stopped over after crossing the Sahara. Breeding grounds departure and winter arrival times tended to be later and more variable in southern than in northern species (average breeding departure: 3 August–24 September in southern, 2–29 August in northern; winter arrival: 27 September–10 November in southern, 5–10 October in northern; Supplementary material, Table S2). Autumn migration duration was on average similar in southern and northern species despite the different migration distance, resulting in slower migration speeds in southern migrants (southern mean range $34\text{--}80 \text{ km day}^{-1}$; northern: $54\text{--}170 \text{ km day}^{-1}$; Supplementary material, Table S2, S3).

Both groups wintered in sub-Saharan Africa and showed variable wintering strategies involving only one stationary winter period

(one White-rumped Swift and Common Redstarts), to several stationary periods (Scrubrobins, two White-rumped Swifts and Common Nightingales). Total wintering duration was not markedly different between southern and northern species (southern mean at least 113–222 days; northern mean approximately 150–198 days; Supplementary material, Table S1, S2).

In southern species, less time was spent stopping over in spring compared to northern species (southern: means 0–8 days; northern: means 8–16 days; Supplementary material, Table S1, S2). The spring timing of migration in southern species was later than in northern species (average winter departure: 7–19 May in southern, 21 March–26 April in northern; breeding arrival: 27–31 May in southern, 19 April–25 May in northern; Supplementary material, Table S2, S3). Spring migration duration was shorter in southern compared to northern species (average duration: 12–21 days in southern, 27–30 days in northern; Supplementary material, Table S2, S3).

DISCUSSION

All individuals of the three southern species crossed the Sahara to winter in West Africa. Prolonged stopovers normally occurred after leaving the breeding grounds and before a fast desert crossing. Timing of the different stages of migration in southern migrants was generally late and spread out. Itinerancy during winter varied among individuals. Spring migration was more direct and faster than in autumn. Autumn migration duration did not differ between northern and southern migrants, despite the different migration distances, resulting in slower migration speed in southern migrants. In spring, migration duration was shorter in southern migrants and speeds similar between northern and southern migrants. The locations used were unlikely to be biased because of unusual vegetation

conditions but obviously, given our limited sample, these results cannot be generalised and further data collection is needed to assess the generality of the similarities and differences between southern and northern migrants.

Overall, migration strategies tend to vary only little among individuals in trans-Saharan migratory species (Thorup *et al.*, 2017). Thus, although our sample sizes were small, these data allow a discussion of the migration strategies of trans-Saharan migratory species from the western Mediterranean area in the light of the direct migration reported in Cyprus Wheatears from the eastern Mediterranean (Xenophontos & Cresswell, 2016). That the southern migrants stopped over before the desert crossing differs from the strategy used by Cyprus Wheatears. The crossing of inhospitable terrain is potentially shorter using the western route because the Atlas region, extending from Morocco to Tunisia, offers good fuelling possibilities for migrants (Biebach, 1995). The western route over the most arid part of the desert may be feasible only when selecting days and altitudes with favourable winds and with stopping over at the scarce fuelling sites (Erni *et al.*, 2005, Hahn *et al.*, 2014). Despite the potentially longer desert-crossing, the eastern flyway provides other advantages such as more favourable winds (Erni *et al.*, 2005; Kranstauber *et al.*, 2015) possibly allowing some species to perform rapid, non-stop, barrier-crossing as in Cyprus Wheatears (Xenophontos & Cresswell, 2016). A time-saving strategy to reduce the cost of barrier crossing might explain absence of stopovers (Adamík *et al.*, 2016; Ouwehand & Both, 2016; Xenophontos & Cresswell, 2016).

The overall later and more spread out timing of migration in southern migrants may be because birds breeding in southern latitudes, where favourable climate conditions and food resources last longer (Holmes, 1971; Conklin *et al.*, 2010; Briedis *et al.*, 2016),

have a wider time window for different stages of the annual cycle i.e. breeding and moult. In fact, complete moult in Rufous-tailed Scrub-robins and Bluethroats usually occurs in summer before autumn migration (Cramp *et al.*, 1993; Arizaga & Alonso, 2015), which potentially contributes to the later and slower observed autumn migration. Unfortunately, we were not able to obtain accurate data to determine when Bluethroats started migration from potential moulting areas. Also, *azuricollis* Bluethroats may have a migration strategy of short nocturnal flights interrupted by daytime stops (Arizaga *et al.*, 2010, 2011) which could slow down migration. However, White-rumped Swifts moult mainly on their winter grounds (Chantler & Driessens, 1999). Consequently, the timing of migration in southern migrants may be more flexible than in northern migrants. The fact that migration distance was much shorter in southern birds may also contribute to a less time-constrained migration strategy but only in autumn when breeding is finished.

Bluethroats and Swifts had lower apparent return rates than Scrub-robins, despite the slightly-higher geolocator weight and the presence of a stalk on many of the Scrub-robin geolocators. The potential negative effects of geolocators have been extensively discussed. A few studies suggest no effects during the breeding season of geolocator deployment (Raybuck *et al.*, 2017) and negative effects on apparent survival in subsequent years (Arlt *et al.*, 2013; Raybuck *et al.*, 2017; Morganti *et al.*, 2018), and there are signs that the effect depends on the tagging technique and device drag, specifically from the use of a light stalk (Blackburn *et al.*, 2016; Streby & Kramer, 2017; Morganti *et al.*, 2018). However, these results should be carefully interpreted, e.g. sample size and period can also influence the apparent geolocator effect, possibly in relation to environmental stochasticity and chance events (van Wijk *et al.*, 2016b). Compared to other studies, our

apparent return rates of individuals fitted with geolocators are similar (0.16, Raybuck *et al.*, 2017) or slightly lower (0.30, Arlt *et al.*, 2013), especially for the swifts.

Migration in small insectivores relates to seasonal changes of vegetation surplus and is generally consistent in space and time among years (Thorup *et al.*, 2017), although there can be timing changes shaped by inter-annual variation in environmental conditions (Tøttrup *et al.*, 2013). Vegetation conditions were not highly different among tracking years and the stopovers observed are likely representative of typical individuals.

In summary, we found only small differences in migration strategies between these southern and northern trans-Saharan migrants despite their ecological differences. The differences in timing may well be caused by differences in how time-constrained migrants are at each stage of the annual cycle. It should be noted that the White-rumped Swifts and Scrub-robins are among the latest migrants to return to Europe and at the same time have breeding populations south of the Sahara unlike most other sub-Saharan migrants (Chantler & Driessens, 1999; Cramp *et al.*, 1993). Our data suggest that southern migrants shorten the time spent on spring migration compared to autumn migration and that migrants may be selected for minimal duration of spring migration to be able to access food resources, mates and breeding territories as soon as possible when they reach breeding grounds (Fransson, 1995). The difference between southern and northern migrants was most apparent during autumn migration. Northern migrants potentially compensate for the longer migration distance with higher speed and earlier arrival at the winter grounds to compete for resources there (Price, 1981). Collecting more data in the future will shed more light on the variation in migration strategies across latitudes and the ecological mechanisms behind. We recommend the continued use of miniaturised

tracking-devices and comparative approaches with appropriate control groups as a suitable method for understanding migration strategies in small birds.

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REFERENCES

- Adamík, P., Emmenegger, T., Briedis, M., Gustafsson, L., Salewski, V. & Hahn, S. (2016). Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Scientific Reports*, 6: 21560.
- Åkesson, S., Klaassen, R., Holmgren, J., Fox, J.W. & Hedenström, A. (2012). Migration routes and strategies in a highly aerial migrant, the common swift *Apus apus*, revealed by light-level geolocators. *PloS one*, 7: e41195.
- Alerstam, T. & Lindström, Å. (1990). Optimal bird migration: the relative importance of time, energy, and safety. In, E. Gwinner (Ed.): *Bird migration: the physiology and ecophysiology*, pp. 331-350. Springer-Verlag. Berlin.
- Arizaga, J., Barba, E., Alonso, D. & Vilches, A. (2010). Stopover of bluethroats *Luscinia svecica cyanecula* in northern Iberia during the autumn migration period. *Ardeola*, 57: 69-85.
- Arizaga, J., Mendiburu, A., Alonso, D., Cuadrado, J.F., Jauregi, J.I. & Sánchez, J.M. (2011). A comparison of stopover behaviour of two subspecies of Bluethroat (*Luscinia svecica*) in Northern Iberia during the autumn migration period. *Ardeola*, 58: 251-265.
- Arizaga, J. & García, J. (2013). Apparent survival rate in a bluethroat *Luscinia svecica azuricollis* population in Spain. *Ardeola*, 60: 371-376.
- Arizaga, J. & Alonso, D. (2015). Phenological parameters of a bluethroat *Luscinia svecica azuricollis* population breeding at high altitude in Spain. *Ardeola*, 62: 173-178.
- Arlt, D., Low, M. & Pärt, T. (2013). Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. *PloS one*, 8: e82316.
- Bairlein, F. 1988. How do migratory song birds cross the Sahara? *Trends in Ecology and Evolution*, 3: 191-194.
- Barta, Z., McNamara, J., Houston, A., Weber, T., Hedenstrom, A. & Fero, O. (2008). Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363: 211-229.
- Biebach, H. (1990). Strategies of trans-Saharan migrants. In, E. Gwinner (Ed.): *Bird migration: the physiology and ecophysiology*, pp: 352-367. Springer Heidelberg. Berlin.
- Biebach, H. (1995). Stopover of migrants flying across the Mediterranean Sea and the Sahara. *Israel Journal of Zoology*, 41: 387-392.
- Biebach, H., Friedrich, W. & Heine, G. (1986). Interaction of bodymass, fat, foraging and stopover period in trans-Saharan migrating passerine birds. *Oecologia*, 69: 370-379.
- Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C. & Cresswell, W. (2016). An experimental evaluation of the effects of geolocator design and attachment method on between-year survival on whinchats *Saxicola rubetra*. *Journal of Avian Biology*, 47: 530-539.

- Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M. & Adamík, P. (2016). Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *Journal of Avian Biology*, 47: 743-748.
- Chantler, P. & Driessens, G. (1999). *Swifts: A Guide to the Swifts and Tree swifts of the World*, pp. 39. Pica Press. Sussex.
- Conklin, J.R., Battley, P.F., Potter, M. & Fox, J.W. (2010). Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nature Communications*, 1: 67.
- Cramp, S., Perrins, C. & Brooks, D. (1993). *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 5. Tyrant Flycatchers to Thrushes*. Oxford University Press. Oxford.
- Ekstrom, P.P. (2004). An advance in geolocation by light. *Memoirs of National Institute of Polar Research*, Special Issue: 210-226.
- Erni, B., Liechti, F. & Bruderer, B. (2005). The role of wind in passerine autumn migration between Europe and Africa. *Behavioural Ecology*, 16: 732-740.
- Fransson, T. (1995). Timing and Speed of Migration in North and West European Populations of *Sylvia* Warblers. *Journal of Avian Biology*, 26: 39-48.
- Fransson, T., Jakobsson, S. & Kullberg, C. (2005). Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas. *Journal of Avian Biology*, 36: 6-11.
- Fransson, T., Barboutis, C., Mellroth, R. & Akriotis, T. (2008). When and where to fuel before crossing the Sahara desert – Extended Stopover and Migratory Fueling in First-Year Garden Warblers *Sylvia borin*. *Journal of Avian Biology*, 39: 133-138.
- Gersten, A. & Hahn, S. (2016). Timing of migration in Common Redstarts (*Phoenicurus phoenicurus*) in relation to the vegetation phenology at residence sites. *Journal of Ornithology*, 157: 1029-1036.
- Hahn, S., Bauer, S. & Liechti, F. (2009). The natural link between Europe and Africa – 2.1 billion birds on migration. *Oikos*, 118: 624-626.
- Hahn, S., Emmenegger, T., Lisovski, S., Amrhein, V., Zehntindjiev, P. & Liechti, F. (2014). Variable detours in long-distance migration across ecological barriers and their relation to habitat availability at ground. *Ecology and Evolution*, 4: 4150-4160.
- Henningsson, P., Karlsson, H., Bäckman, J., Alerstam, T. & Hedenström, A. (2009). Flight speeds of swifts (*Apus apus*): seasonal differences smaller than expected. *Proceedings of the Royal Society B: Biological Sciences*, 276: 2395-2401.
- Holmes, R.T. (1971). Latitudinal Differences in the Breeding and Molt Schedules of Alaskan Red-Backed Sandpipers (*Calidris alpina*). *Condor*, 73: 93-99.
- Jacobsen, L.B., Jensen, N.O., Willemoes, M., Hansen, L., Desholm, M., Fox, A.D., Tøttrup, A.P. & Thorup, K. (2017). Annual spatiotemporal migration schedules in three larger insectivorous birds: European nightjar, common swift and common cuckoo. *Animal Biotelemetry*, 5: 4.
- Kranstauber, B., Weinzierl, R., Wikelski, M. & Safi, K. (2015). Global aerial flyways allow efficient travelling. *Ecology Letters*, 18: 1338-1345.
- Kristensen, M.W., Tøttrup, A.P. & Thorup, K. (2013). Migration of the Common Redstart (*Phoenicurus phoenicurus*): a Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. *The Auk*, 130: 258-264.
- Lerche-Jørgensen, M., Willemoes, M., Tøttrup, A.P., Snell, K.R.S. & Thorup, K. (2017). No apparent gain from continuing migration for more than 3000 kilometres: willow warblers breeding in Denmark winter across the entire northern Savannah as revealed by geolocators. *Movement Ecology*, 5: 17.
- Lislevand, T., Chutný, B., Byrkjedal, I., Pavel, V., Briedis, M., Adamík, P. & Hahn, S. (2015). Red-spotted Bluethroats *Luscinia s. svecica* migrate along the Indo-European flyway: a geolocator study. *Bird Study*, 62: 508-515.
- Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W. & Hahn, S. (2012). Geolocation by light: Accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, 3: 603-612.

- Mckinnon, E.A., Fraser, K.C. & Stutchbury, B.J.M. (2013). New discoveries in landbird migration using geolocators, and a flight plan for the future. *The Auk*, 130: 211-222.
- Moreau, R.E. (1952). The place of Africa in the Palearctic migration System. *Journal of Animal Ecology*, 21: 250-271.
- Moreau, R.E. (1961). Problems of Mediterranean-Saharan migration. *Ibis*, 103: 373-427.
- Moreau, R.E. (1972). *Palaeartic-African bird migration systems*. Academic Press. New York.
- Morganti, M., Rubolini, D., Åkesson, S., Bermejo, A., de la Puente, J., Lardelli, R., Liechti, F., Boano, G., Tomassetto, E., Ferri, M. & Caffi, M. (2018). Effect of light-level geolocators on apparent survival of two highly aerial swift species. *Journal of Avian Biology*, 49: 1-10.
- Nilsson, C., Klaassen, R.H.G. & Alerstam, T. (2013). Differences in speed and duration of bird migration between spring and autumn. *The American Naturalist*, 181: 837-45.
- Ouwehand, J., Ahola, M.P., Ausems, A.N.M.A., Bridge, E.S., Burgess, M., Hahn, S., Hewson, C.M., Klaassen, R.H.G., Laaksonen, T., Lampe, H.M., Velmala, W. & Both, C. (2016). Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology*, 47: 69-83.
- Ouwehand, J. & Both, C. (2016). Alternate non-stop migration strategies of pied flycatchers to cross the Sahara desert. *Biology Letters*, 12: 10-13.
- Price, T.D. (1981). The ecology of the Greenish Warbler *Phylloscopus trochiloides* in its winter quarters. *Ibis*, 123: 131-44.
- R Development Core Team. (2011). R: A Language and Environment for Statistical Computing. (The R Foundation for Statistical Computing, ISBN: 3-900051-07-0). <http://www.r-project.org>.
- Raybuck, D.W., Larkin, J.L., Stoleson, S.H. & Boves, T.J. (2017). Mixed effects of geolocators on reproduction and survival of Cerulean Warblers, a canopy-dwelling, long-distance migrant. *Condor*, 119: 289-297.



- Rubolini, D., Pastor, A., Pilastro, A. & Spina, F. (2002). Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. *Journal of Avian Biology*, 33: 15-22.
- Schmaljohann, H., Liechti, F. & Bruderer, B. (2007). Songbird migration across the Sahara: the non-stop hypothesis rejected! *Proceedings of the Royal Society B: Biological Sciences*, 274: 735-739.
- Stach, R., Jakobsson, S., Kullberg, C. & Fransson, T. (2012). Geolocators reveal three consecutive wintering areas in the thrush nightingale. *Animal Migration*, 1: 1-7.
- Stach, R., Kullberg, C., Jakobsson, S., Ström, K. & Fransson, T. (2016). Migration routes and timing in a bird wintering in South Asia, the Common Rosefinch *Carpodacus erythrinus*. *Journal of Ornithology*, 157: 671-679.
- Streby, H.M. & Kramer, G.R. (2017). Comment on "Mixed effects of geolocators on reproduction and survival of Cerulean Warblers, a canopy-dwelling, long-distance migrant". *Condor*, 119: 848-851.
- Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega, M.L., Dasari H.P. & Araújo, M.B. (2017). Resource tracking within and across continents in long-distance bird migrants. *Scientific Advances*, 3: e1601360.
- Tøttrup, A.P., Klaassen, R.H.G., Kristensen, M.W., Strandberg, R., Vardanis, Y., Lindström, Å., Rahbek, C., Alerstam, T. & Thorup, K. (2012). Drought in Africa caused delayed arrival of European songbirds. *Science*, 338: 1307-1307.
- van Wijk, R.E., Bauer, S. & Schaub, M. (2016a). Repeatability of individual migration routes, wintering sites, and timing in a long-distance migrant bird. *Ecology and Evolution*, 6: 8679-8685.
- van Wijk, R.E., Souchay, G., Jenni-Eiermann, S., Bauer, S. & Schaub, M. (2016b). No detectable effects of lightweight geolocators on a Palaearctic-African long-distance migrant. *Journal of Ornithology*, 157: 255-264.
- Xenophontos, M. & Cresswell, W. (2016). Survival and dispersal of the Cyprus wheatear *Oenanthe cypriaca*, an endemic migrant. *Journal of Ornithology*, 157: 707-719.
- Yohannes, E., Biebach, H., Nikolaus, G. & Pearson, D.J. (2009). Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. *Journal of Avian Biology*, 40: 126-134.

SUPPLEMENTARY ELECTRONIC MATERIAL

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Table S1. Individual and mean migration parameters of southern and northern species, respectively.

Table S2. Mean and standard deviation (SD) of migration parameters in southern and northern species.

Table S3. Wilcoxon-Mann-Whitney test results comparing different migration parameters of individual southern and northern migrants.

Figure S1. Estimates of longitude and latitude from geolocator data from Iberian White-rumped Swifts.

Figure S2. Estimates of longitude and latitude from geolocator data from Iberian Rufous-tailed Scrub-robins.

Figure S3. Estimates of longitude and latitude from geolocator data from Iberian Bluethroats.

Figure S4. Anomalies of the Normalized Difference Vegetation Index (NDVI) in January for the years with tracking data, 2013-2016.

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