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Short communication

Migratory pathways, stopover zones and wintering destinations of Western European Nightjars *Caprimulgus europaeus*

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Little is known about the wintering distribution of the European Nightjar *Caprimulgus europaeus*. We combined geolocator and GPS-logger data from different sites in Western Europe to analyse migration routes and migration timing of this trans-equatorial migrant. Nightjars followed a loop migration route during which they cross two ecological barriers, and converged near common stopover zones in Northern, Central and Western Africa, where they stayed for 2–3 weeks. Nightjars used the same stopover sites as several other European migrants, relying on small and discrete wintering areas within the Democratic Republic of Congo. This confirms the importance of these specific zones and highlights the vulnerability of Western European populations to habitat loss in their non-breeding areas.

Keywords: geolocator, GPS-logger, loop migration, wintering areas.

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The European Nightjar *Caprimulgus europaeus* is a long-distance, trans-equatorial migrant, protected under the Conservation of Migratory Species of Wild Animals (UNEP 2014). It breeds on dry soils in Eurasia, mainly in open semi-natural habitats such as pine forests and glades in deciduous forests (Cramp *et al.* 1985, Alexander & Cresswell 1990, Sierro *et al.* 2001). While numerous studies have focused on their behaviour during the 4-month breeding season (e.g. Alexander & Cresswell 1990, Sierro *et al.* 2001, R.E., N.B, N.W. and T.A. unpubl. data), little is known about the Nightjar's migratory behaviour (Cresswell & Edwards 2013). Recovery rates of ringed Nightjars in their non-breeding areas are extremely low, with only two found in Africa of a total of 131 ring recoveries globally up until 2009 (du Feu *et al.* 2009).

Apart from the recent discovery of new wintering sites in the Democratic Republic of Congo (DRC) and the identification of a possible loop migration pattern (Cresswell & Edwards 2013), detailed information about general migration routes, migration timing, stopover zones and wintering range is lacking. In the present study, we add significant detail to the understanding of some fundamental aspects of Nightjar migration. We used a combination of eight geolocators and three GPS-loggers to reconstruct the entire migratory cycle of 11 Nightjars from five sites in three Western European countries (Fig. 1).

METHODS

Geolocator deployment

We attached 50 archival geolocators to Nightjars breeding in several locations (Fig. 1, Table S1): one site in Belgium (one male, one female, one juvenile in 2012 at Bosland, 51.17°N, 5.34°E), two sites in England (five males in 2008, and five males and one female in 2010 at Wareham Forest, 50.73°N, 2.17°W; and nine males and 10 females in 2011, and one male in 2012 at Thetford Forest, 52.45°N, 0.65°E) and one site in France (15 males and one female in 2013 at Forêt de Fontainebleau, 48.42°N, 2.50°E). We also attached seven GPS-loggers to Nightjars at two sites in Belgium in 2014 (four males at Bosland and three males at Meeuwen-Gruitrode; 51.04°N, 5.30°E). We caught all birds using song playback and mist-nets.

We used Mk12s geolocators (Belgium; 1.1 g; Biotrack Ltd, Wareham), lightbugs (UK; 1.8–2 g; Biotrack Ltd, Wareham), GDL1 geolocators (France; 1 g, Sempach) and PinPoint GPS-loggers (Belgium; Pinpoint-40 = 2.2 g and Pinpoint-10 = 1.1 g; Biotrack Ltd, Wareham). We glued an Ag376 connectivity tag (CTx-tag, 0.9 g; Biotrack Ltd, Wareham) to each of the Pinpoint-10 GPS-loggers. The tags were programmed to send a unique VHF (very

Figure 1. Five study sites in the UK, France and Belgium: T, Thetford Forest; W, Wareham Forest; F, Forêt de Fontainebleau; M, Meeuwen-Gruitrode; and B, Bosland.

high frequency) signal from 15 May to 15 July 2015 to facilitate relocation of the GPS-loggers. Starting from October 2014, GPS-loggers were programmed to take a GPS fix every 6 days (PinPoint-40) or every 30 and 152 days (Pinpoint-10) at 00:00 h GMT, when birds were expected to be in active flight. We attached all devices dorsally between the wings with a full body harness made of Teflon ribbon (Bally Ribbon; Åkesson *et al.* 2012). The total weight of the devices and harness represented ≤ 3.5% of the body mass at the time of logger attachment (body weight 63.0–86.2 g).

Data analysis

Between 2009 and 2015, we recovered eight geolocators and three GPS-loggers (Table S1b). Because data from MK12-loggers are not suitable for analysis with template-fit methods (Fox 2010), we analysed data from this logger using the threshold-method, whereby the position of a bird is derived from a specified irradiance-value during every twilight period (Fox 2010). Data from the other geolocators were analysed using the template-fit method, whereby frequent high-resolution light data are used to calculate sunrise and sunset from the twilight curves in order to derive a bird's location more accurately (Cresswell & Edwards 2013, Lisovski & Hahn 2012, for details see Appendix S1). We also reanalysed the original data from Cresswell and Edwards (2013) using the same template-fit methods.

We distinguished between migration and stationary periods (migratory stopover, breeding, wintering) by visually inspecting subsequent positions (Fudickar *et al.* 2012). We identified stopover sites as locations when individuals interrupted migration for 3 days or more, or when PinPoint-40 birds were stationary for at least two GPS-fixes (i.e. 12 days). We defined stopover zones as regions that included the stopover sites of several Nightjars. Migration routes were determined by plotting the cumulative tracks of 3-day mean positions. Total migration distance was the sum of cumulative tracks between stopover sites (Åkesson *et al.* 2012). Travel speed was calculated as migration distance divided by duration of the migration period. Because we used direct routes between stationary periods to calculate migration distance for both geolocator data and GPS-loggers, we were likely to have underestimated the distance travelled by each bird and its migration speed. For details concerning the accuracy of location estimates and information on equinox periods, see Appendix S1. We did not include results from Pinpoint-10 GPS-loggers in estimating migration timing and duration due to their large sampling interval (for group sizes and results see Table S3).

RESULTS

From 57 individuals fitted with remote tracking devices, 13 devices were retrieved from adult males (Table S1b), constituting a 23% recapture rate from tracked birds. The recapture rate for GPS-loggers was high (57%: PinPoint-40 = 50%; two of four and PinPoint-10 = 66%; two of three). Eleven devices (eight geolocators and three GPS-loggers) contained usable data, covering 12 annual migration tracks, indicating a mean total annual distance of 16 854 ± 927 km between breeding periods, travelling to wintering sites in sub-equatorial Africa (Fig. 2).

Migration timing and duration

Autumn migration started in August (range: 24 August to 11 September) and wintering areas were reached from late October onwards (22 October to 6 November). Spring migration started in late February (range: 17 February to 15 March) and Nightjars reached their breeding areas again in early May (range: 28 April to 8 June). The fastest travel speeds were found when

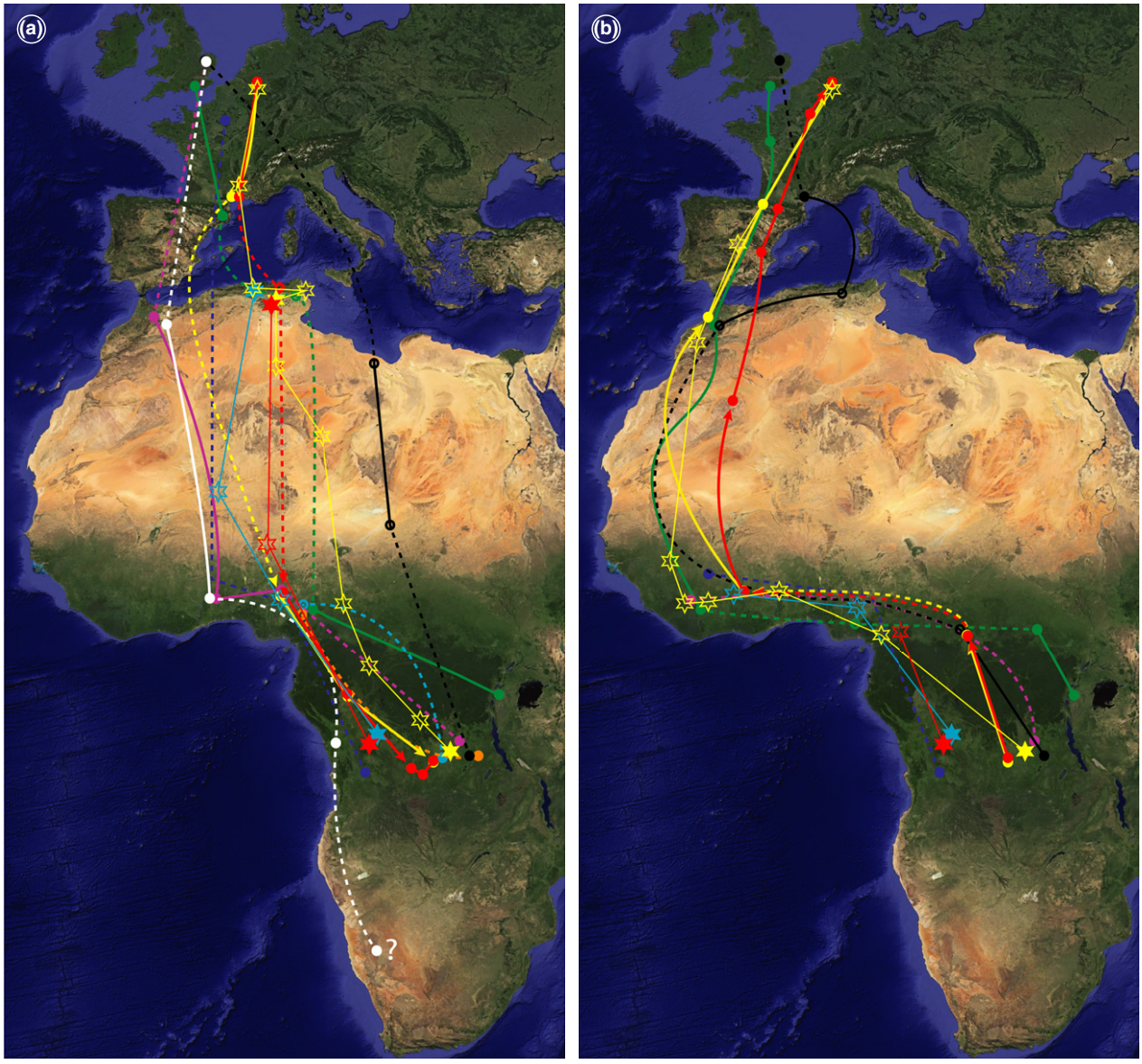

Figure 2. Migration routes and staging areas from 12 tracks of 11 tagged Nightjars: (a) autumn (n = 12), (b) spring (n = 9). Each colour represents one individual. Star symbols represent GPS-loggers, circles represent geolocator data. Migration routes were constructed by simplifying 3-day cumulative tracks. Solid lines are actual routes, whereas dashed lines are assumed routes based on longitudinal data during equinox periods. Solid symbols represent the calculated average location of an individual's staging area and open symbols represent calculated average location of an individual's assumed staging area based on longitudinal data during equinox periods. Visualized staging areas of geolocators are calculated average coordinates of geolocator data without standard deviation and consequently represent a simplification of the original data clouds.

crossing the Mediterranean Sea, the Sahara and the Central African Tropical Rainforest (CATR; Table 1).

Migration routes

Autumn migration started with a rapid southward migration towards Southern Europe (Fig. 2a). Crossing of the Mediterranean Sea happened during the autumn equinox and occurred at different locations along the French and Italian coastlines. It is not clear whether all birds made a brief stopover before crossing the Mediterranean. After crossing the Mediterranean, most birds made a prolonged stopover in Northern Africa. Autumn crossing of the Sahara occurred on a broad front

Table 1. Average migration speed across ecological barriers (km per night).

	Autumn			Spring		
	Mean	se	*n*	Mean	se	*n*
Mediterranean Sea	500	287	2	250	50	2
Sahara	532	78	3	497	50	4
CATR	494	145	3	544	153	4
Central-Western Africa	n/a	n/a	n/a	385	47	4

CATR, Central African Tropical Rainforest

($sd_{longitude}$ = 4.91°) compared with spring crossing ($sd_{longitude}$ = 2.54°). All individuals made stopovers in Nigeria or Cameroon before crossing the CATR (Fig. 2a), except the French birds, which made a stopover in Togo.

Spring migration started with a rapid crossing of the CATR in a NW to NNW direction (Fig. 2b), followed by a brief stopover in Cameroon or Nigeria. From there, migration continued rapidly towards Western Africa with prolonged stopovers in the Ivory Coast and Guinea before continuing in a N to NNE direction across the Sahara. All birds made a brief stopover in Morocco before entering Europe via Gibraltar, with the exception of one bird, which entered Europe through Corsica and France after a detour across Northern Africa (Fig. 2b). The autumn migration route was on average 12.05% (n = 12) longer than a direct route between the breeding area and the wintering site (Belgium = 6800 ± 160 km; UK = 7350 ± 670 km; France = 7250 km), whereas the spring migration route was on average 34.5% (n = 4) longer (Belgium = 9160 ± 140 km; UK = 9100 km).

Stopover and wintering locations

We identified three stopover zones that were visited by at least seven individuals: Northern Africa (10 ± 6 days, range 3–20; we had sufficient data to perform calculations for six birds) during autumn migration, Cameroon and Nigeria during both autumn migration (16 ± 6 days, range 9–23, sufficient data for four birds) and spring migration (10 ± 4 days, range 6–16, sufficient data for four birds) and Western Africa (19 ± 10 days, range 9–36, sufficient data for six birds) during spring migration. Additional stopover zones were visited by a maximum of three individuals (range: 3–19 days): in Southern France and Congo during autumn migration, and in Congo, Morocco, Northeastern Spain and Central France during spring migration.

Wintering areas were all situated in southern regions of the DRC, ranging from the Angolan border towards the borders with Rwanda and Burundi, south of the CATR (mean: 113 days, se = 23.6, range = 115–143, based on data from eight birds). One individual overwintered east of the CATR. All Nightjars were sedentary on the non-breeding grounds, with GPS-logged birds (n = 3) staying within a 750-m radius of the centroid of their logged locations from November to February (Fig. 3). One Nightjar initially overwintered in the southwestern parts of the DRC, but migrated to Namibia in late December (Fig. 2a).

DISCUSSION

Recapture probability of GPS-tagged male birds was higher (57%) than previous estimates (35 ± 0.07%) but lower than the estimated survival rates (70 ± 0.05%) of Nightjars (Silvano & Boano 2012). The higher recapture rate may have been due to the increased probability of relocating CTx-tags, which allowed accurate recapture attempts. Our tracking results confirm that there is a well-defined loop migration pattern, as previously suggested by Cresswell and Edwards (2013). This pattern, which was consistent among individuals from the five Western European sites, indicates that Nightjars follow different trajectories during autumn and spring migration, making an elaborate detour through Western Africa in spring. Loop migration appears to be a common trait among European migratory birds (Weimerskirch *et al.* 2000, Gschweng *et al.* 2008, Klaassen *et al.* 2010, López-López *et al.* 2010), possibly originating from adaptations to changing habitat quality and foraging abilities between seasons (Pearson *et al.* 1992, Tøttrup *et al.* 2008, Yohannes *et al.* 2009) and/or favourable wind conditions, especially during migration across the Sahara (Kemp *et al.* 2010).

We observed a strong convergence near common stopover zones in Northern, Central and Western Africa at which our birds stayed for 2–3 weeks. These zones are situated in areas with a high normalized difference vegetation index (NDVI; www.vito-eodata.be). It seems plausible that, as with other sub-Saharan migrants (Pearson *et al.* 1992, Yohannes *et al.* 2009), Nightjars track seasonal rains in these regions in order to profit from the emergence of aerial insects (Pearson *et al.* 1992, Vickery *et al.* 2014) to regain maximal fuel loads. These fuel loads may be required to ensure successful crossing of ecological barriers, such as the Mediterranean Sea and the Sahara, at high speed (Bairlein 1988, Åkesson & Hedenström 2007, Schmaljohann *et al.* 2007, Strandberg *et al.* 2009, Lemke *et al.* 2013, McLaren *et al.* 2013). Based on this information, our observation of high migration speeds across the CATR, and the potential lack of foraging and sleeping possibilities (Catry *et al.* 2014), we suggest that the CATR is also an ecological barrier for Nightjars.

Ringing activities in Bosland indicated that Nightjars accumulate extra fuel loads at the end of the breeding

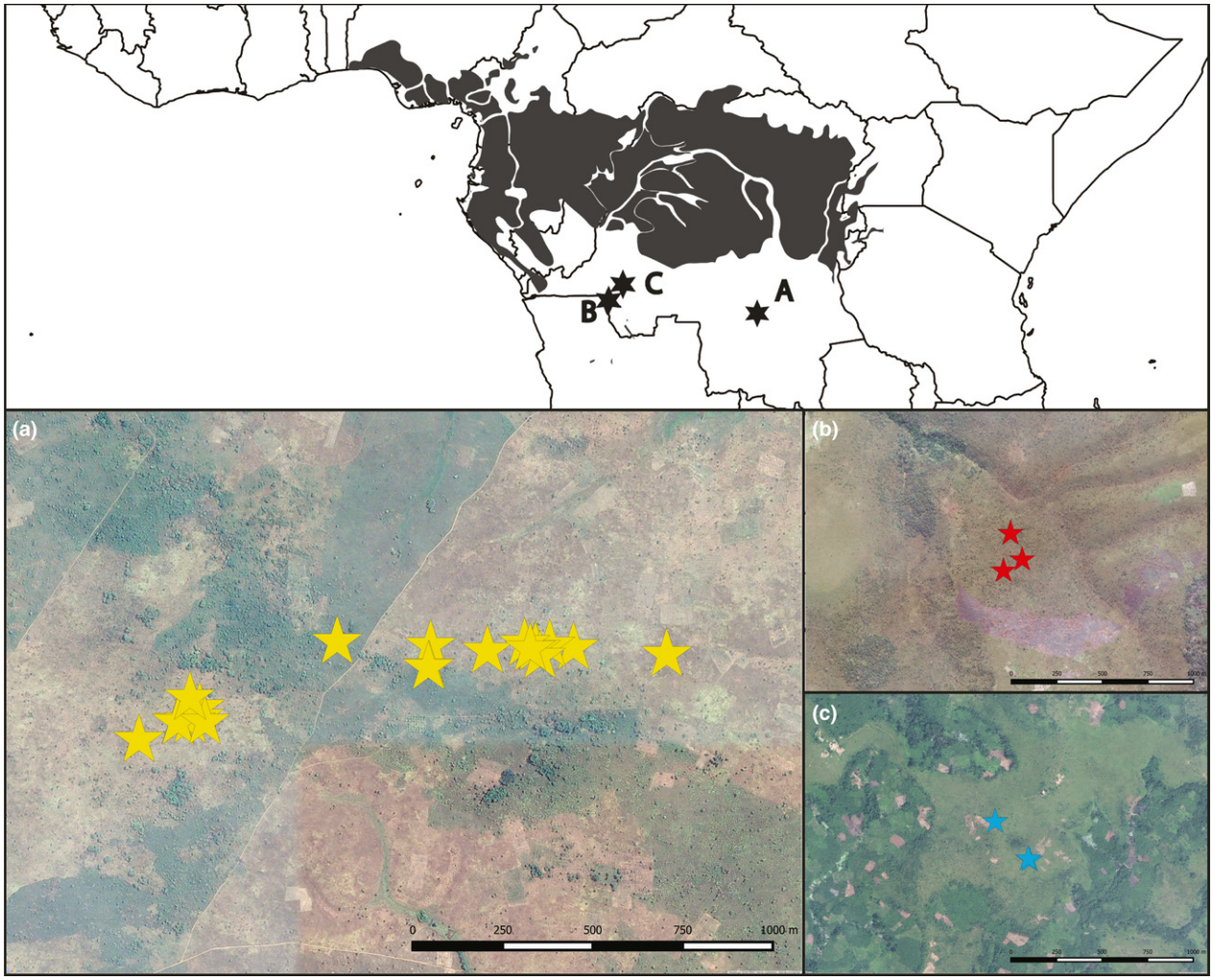

Figure 3. Wintering range occupied by three Nightjars with GPS-loggers (PinPoint-40 and two PinPoint-10s). Top: Central Africa with Central African Tropical Rainforest (dark grey) and distribution of wintering areas. Bottom: Wintering range per individual from early November until late February. (a) E15 (n = 21, yellow), (b) E44 (n = 4, red) and (c) E47 (n = 3, blue). Wintering habitat comprises steppe vegetation with scattered trees and dense tree stands.

season (20–30 g, n = 18, mean = 88.6 ± 7.7 g: 28–42% greater than mean weight during breeding season, n = 157, mean = 68.8 ± 6.5 g). This would enable Nightjars to make 25–39 h non-stop flights without foraging (Delingat *et al.* 2008). Based on the interpretation of geolocator data (Adamík *et al.* 2016), we found that Nightjars in our study flew solely at night. Assuming that they fly at air speeds in the range of 35–50 km/h (Kemp *et al.* 2010), that they use flapping flight and that they fly at a normal energy deposition rate (Hedenström & Alerstam 1998), Nightjars should be able to cover 200 km per night. Flying at maximum deposition rate would yield migration speeds of up to 300–400 km per night. This corresponds to 7–10.5 h of flight per night during normal migration and 11–15.7 h when crossing ecological barriers. In fact, we observed that during autumn migration in Europe, some Nightjars chose to cover fewer kilometres per night compared with nightly distances covered across ecological barriers (Table 1). Lower migration speeds and high fuel reserves in autumn can therefore serve as an insurance to avoid making prolonged stopovers in Southern France before crossing the Mediterranean Sea. Following the crossing of the Mediterranean Sea, Nightjars need to restore fuel reserves. These reserves are necessary to ensure the crossing of the Sahara (Bairlein 1988, Schmaljohann *et al.* 2007, Strandberg *et al.* 2009, Lemke *et al.* 2013, McLaren *et al.* 2013) at high speed in four to six nights. Due to the lack of detailed data, we cannot provide a clear explanation for the observed variation in

migration speed. Therefore, this question remains unanswered and open for further research.

All Nightjars overwintered south of the CATR, outside their formerly presumed wintering range. Before Cresswell and Edwards' (2013) study, it was generally assumed that the Nightjar wintering range covered two main regions: the first extending along the eastern coast of Africa from Kenya to South Africa, and the second in the western sub-Saharan region from Senegal to Cameroon (Cleere & Nurney 1998, Holyoak 2001). However, all birds in our study appeared to be sedentary during the entire winter in small and discrete habitat patches within two sub-tropical ecoregions: the Southern Congolian Forest-savanna Mosaic and the Central Zambezian Miombo Woodlands (White 1983). This suggests that these ecoregions are very important for wintering Western European Nightjars.

Nightjars in our study followed a loop migration route that converged at common stopover zones. Wintering areas were situated in sub-tropical Africa where Nightjars are confined to aggregated wintering sites. Nightjars use the same stopover sites as several other European migrants such as Common Swift *Apus apus*, Great Reed Warbler *Acrocephalus arundinaceus* and European Roller *Coracias garullus* (Åkesson *et al.* 2012, Lemke *et al.* 2013, Catry *et al.* 2014). This indicates the importance of these zones and highlights the vulnerability of Western European bird populations to habitat destruction, and/or to a mismatch between arrival times and food availability caused by climate change (Both *et al.* 2006, Tøttrup *et al.* 2008, Saino *et al.* 2011). In terms of Nightjar migration, we anticipate that technological improvements and further studies of migration routes will provide supplementary information on their migratory decisions and facilitate the development of conservation measures in non-breeding areas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. More details on geolocator data analysis: accuracy of content.

Table S1. Summary of tracking device deployment and capture/recapture data.

Table S2. Dates between which no migration data could be extracted.

Table S3. Comparisons between the timing and duration of migration in autumn and spring.