



# Migration strategies and annual space-use in an Afro-Palaeartic aerial insectivore – the European nightjar *Caprimulgus europaeus*

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Obligate insectivorous birds breeding in high latitudes travel thousands of kilometres during annual movements to track the local seasonal peaks of food abundance in a continuously fluctuating resource landscape. Avian migrants use an array of strategies when conducting these movements depending on e.g. morphology, life history traits and environmental factors encountered en route. Here we used geolocators to derive data on the annual space-use, temporal pattern and migratory strategies in an Afro-Palaeartic aerial insectivorous bird species – the European nightjar *Caprimulgus europaeus*. More specifically, we aimed to test a set of hypotheses pertaining to the migration of a population of nightjars breeding in south-eastern Sweden. We found that the birds wintered across the central and western parts of the southern tropical Africa almost entirely outside the currently described wintering range of the species. The nightjars performed a narrow loop migration across Sahara, with spring Sahel stopovers significantly to the west of autumn stops indicative to an adaptive response to winds during migration. To our surprise, the migration speed was faster in the autumn ( $119 \text{ km d}^{-1}$ ) than in the spring ( $99 \text{ km d}^{-1}$ ), possibly due to the prevailing wind regimes over the Sahara. The estimated flight fraction in both autumn (14%) and spring (12%) was almost exactly as the theoretically predicted 1:7 time relationship between flights and stopovers for small birds. The temporal patterns within the annual cycle indicate that individuals follow alternative spatiotemporal schedules that converge towards the breeding season. The positive relationship between the spatially and temporally distant winter departure and breeding arrival suggests that individuals' temporal fine-tuning to breeding may be constrained, leading to potential negative fitness consequences.

The cyclical movement between spatially separated areas enables migrants to take advantage of local seasonal peaks in food abundance across a fluctuating resource landscape (Alerstam 1990, Dingle 1996). Obligate insectivorous birds breeding at high latitudes spend large parts of their annual cycle commuting to and from the tropics, which likely act selectively on these migrants and influence their ecology (Berthold 2006). The migratory journey usually consists of time spent at stopovers when the bird is refuelling for the subsequent flight with a predicted time ratio between flights and stopovers for small migrating birds of approximately 1:7 (Hedenström and Alerstam 1997). This is based on estimates from flight mechanical theory and derivations from measurements on the total energy cost of flying relative to staying (Hedenström and Alerstam 1997). The spatiotemporal scheduling of the annual cycle appears to be adjusted to complex regional and temporal resource dynamics and individual migrants probably follow an endogenous clock for timing of important events (Berthold 1996). The exact timing of each event is likely also influenced by the individuals' energetic state as well as by local environmental factors such as wind conditions and habitat quality (Alerstam 1979, Weber et al. 1998, Åkesson and Hedenström 2000, Dänhardt and Lindström 2001, Tøttrup et al. 2008, Arizaga

et al. 2011, Cohen et al. 2012). For example, many species of the Afro-Palaeartic migration system have been shown to perform lengthy stopovers in the Sahel zone immediately south of the Sahara before commencing migration to final winter destinations (Morel 1973, Hedenström et al. 1993, Tøttrup et al. 2012, Lindström et al. 2016). Empirical studies of several species have also shown that migrants may perform significant detours from the shortest route (Tøttrup et al. 2012, Åkesson et al. 2012, Willemoes et al. 2014) and that autumn and spring routes often are spatially separated to yield a loop pattern (Klaassen et al. 2010, Lemke et al. 2013, Lopez-Lopez et al. 2014, Trierweiler et al. 2014). Similarly, spring migration is often faster than in autumn (Nilsson et al. 2013), which probably is driven by fitness advantages by an early arrival to the breeding range (Kokko 1999).

The European nightjar *Caprimulgus europaeus* (henceforth nightjar) is a crepuscular and nocturnal aerial insectivore that breeds across Europe and Asia during the northern summer (Cramp 1985, Holyoak 2001). The species' nocturnal habit forces it to overlap the daily timing of fuelling and flying, which theoretically could reduce its migration efficiency relative to other Afro-Palaeartic migrants that perform nocturnal flights and allocate the daylight hours to fuelling

(Alerstam 2009). Data from ringing efforts have contributed little information about migration routes, migration strategy and stationary area of nightjars (Fransson et al. 2008). The limited information from observations on the African continent suggests a wintering range along the eastern coast of Africa from Kenya to South Africa, and in Cameroon and Senegal in western Africa (Fry et al. 1988, Cleere 1998, del Hoyo et al. 1999, Holyoak 2001). A recent study using miniature light-level geolocators however revealed that three British breeding nightjars wintered outside the currently described range (Cresswell and Edwards 2013). Two of the tracked nightjars spent the winter in the southeastern Democratic Republic of Congo (DRC), while a third bird was located in central eastern DRC.

Here we used geolocators to address six hypotheses pertaining to the migration of nightjars breeding in south-eastern Sweden. The hypotheses are as follows: 1) the tracked nightjars will winter outside the 'wintering range' currently described in the literature; 2) the birds will make stopovers immediately south of the Sahara; 3) autumn and spring routes will differ spatially, illustrating a loop pattern; 4) the relationship between time spent airborne versus that at stopovers on migration should be 1:7, or near to it; 5) spring migration should be faster than autumn migration; and 6) the timing of events in the annual cycle (breeding, migration, wintering) should be positively correlated within individuals.

## Material and methods

### Trapping and deployment

Fieldwork was conducted in north east Småland (16°E, 57°N), Sweden during the breeding seasons of 2011–2015 and on southern Öland (16°E, 56°N), an island in the Baltic Sea off the Swedish east coast, in 2013–2015. Mist-netted individuals were ringed, weighed on an electronic balance to the nearest 0.1 g and the length between the carpal joint and tip of longest primary was measured to nearest mm (Svensson 1992). Nightjars conduct a complete feather moult, including primaries and rectrices, with the onset during their first winter, and can thereafter be sexed based on plumage characters (Cramp 1985, Jackson 2008). Males usually show prominent white markings on the tips of outer tail-feathers and on the longest primaries, while females may at most show smaller buff-coloured markings. Geolocators were mounted on the back of the birds with a nylon string using a full body harness as described in Åkesson et al. (2012). Different geocator models from different manufacturers (Biotrak and Migrate Technology) were used in different years, with a mass of less than 2 g for all models used, corresponding to < 3% of the nightjar body mass. In 2011–2014 a total of 78 geolocators were distributed among 70 males and three females (five males were tagged twice). In total 19 geolocators were retrieved up to 2015, and 12 of these contained light-data that could be used to reconstruct complete tracks from 12 different individuals (11 males and one female; Supplementary material Appendix 1, Table A1). The retrieval of geolocators is dependent on site fidelity (and breeding dispersal) of surviving birds and the efficiency of

relocating and trapping them. The overall return rate of logged birds was 24% (19 out of 78 birds), which did not differ significantly from the return rate of ringed only birds during the study period (16%; 7/42;  $\chi^2 = 0.32$ ,  $p = 0.57$ ). This was also similar to return rates reported elsewhere (14%; Cresswell and Edwards 2013). We did not detect any noticeable negative effects of the geolocators on the birds in the study.

### Data analysis

We linearly corrected the retrieved light-level data for clock drift by using the software BASTrak (Fox 2010) and translated the data into two daily geographic positions using the software IntiProc ver. 1.03 (Migrate Technology 2015) which uses the threshold method in the R package GeoLight ver. 2.0 for the transformation into positions (Hill 1994, Hill and Braun 2001, Lisovski and Hahn 2012). This approach enabled us to perform the same methods for geolocators using an arbitrary light scale as well as those having a 'full-range' light scale. We used a threshold level of 2 for the arbitrary scale data (Biotrak), and a level 10 for full-range lux scale data (Migrate Technology). We visually inspected the data and removed obvious erroneous transitions, caused by repeated shading events throughout the day. We used the 'calibration' function in the IntiProc software on light data from at least two weeks from both breeding seasons to derive a preliminary sun angle corresponding to the threshold level for each individual geocator. We were not able to ground-truth the birds' actual position during the calibration period, but instead used the distinct event when the birds crossed the Baltic Sea as a measure of arrival to, and departure from, the breeding grounds.

We distinguished stationary periods by visually inspecting the time series of latitudes and longitudes and identified periods down to four consecutive days. The latitude component of geocator-derived positions is particularly prone to uncertainty which vary relative to time of year and location of the animal (Ekstrom 2004, Fox 2010). We therefore used a kernel density estimation (KDE) based approach, rather than a fixed distance when distinguishing subsequent stationary periods, and by that procedure taking into account some of the temporal and spatial variability and directionality in the uncertainty of the positions (Silverman 1986). We merged stationary periods and derived a new KDE if the areas within the arbitrarily chosen isocline of 60% KDE overlapped. The 60% KDE corresponded to a longitudinal uncertainty on the breeding ground of on average 155 km (SD = 51 km,  $n = 24$ ), which is within the typical range for geolocation accuracy estimates (Phillips et al. 2004). We interpret this estimate as a baseline measure of position accuracy, from which the geolocators' position accuracy will vary depending on time of year and location of the carrier. The smoothing parameter for each KDE, representing each stationary period, was calculated separately for latitude and longitude, respectively, with the function 'kde2' in MatLab (release 2010b, The MathWorks, Natick, MA, USA). This function uses a non-parametric approach to calculate the KDE's smoothing factor that minimizes the risk of under- or over-smoothing when applied to non-normal distributed

data, such as geolocator-derived positions (Silverman 1986, Hemson et al. 2005, Botev et al. 2010).

Geolocator-derived positions may potentially be subject to directional error if the carrier alters behaviour and/or habitat use between different parts of the annual cycle (Fudickar et al. 2012, Lisovski et al. 2012). We therefore applied two alternative approaches using the stationary periods distinguished above to evaluate the preliminary sun angle. Both are based on the theoretical expectations that latitudinal errors decrease when the proposed sun angle approaches the sun angle corresponding to the chosen threshold value (Ekstrom 2004). First, we tested this by applying the Hill–Ekstrom function in GeoLight on the light data corresponding to the longest stationary period during the winter (Lisovski and Hahn 2012). Secondly, following Lindström et al. (2016), we plotted the latitude for a series of sun angles (including the preliminary one) to evaluate the shape of the curves close to the equinoxes. For all individuals, except one, the sun-angles derived from the three approaches differed less than 0.3 degrees. This indicates that the geolocators have been exposed to similar light conditions throughout the annual cycle and that the primary calibration was sufficient (Lisovski et al. 2012). The exception was an individual trapped on Öland (bird F) that was breeding in an open habitat relative to the other birds, which we suspect influenced the primary calibration. For this bird we choose the sun angle suggested from the Hill–Ekstrom function, which was similar to the sun-angles derived for the other devices in the same cohort of geolocators (Supplementary material Appendix 1, Table A1).

We defined the location of the stationary periods by the centroid (i.e. the coordinates with the highest estimated density) of each period's KDE, the migration route as the track between subsequent locations and added the corresponding great circle distances to estimate the route length. We calculated the autumn route from the breeding site to the first wintering area and measured the spring route from the last wintering area to the breeding site. We divided the estimated migration distances by the direct route between the breeding site and the wintering areas to estimate the migration detour. We calculated the duration of migrations as the time taken from departure from breeding area to arrival to wintering area, and vice versa for spring migration. We defined the travel time as the number of days spent on migratory movement only, excluding time at distinguished

stopovers, and calculated migration/travel rate by dividing the total migration distance with time spent on migration or travel, respectively.

We adopted the approach described in Lindström et al. (2016) to evaluate the relationship in timing of events in the annual cycle of the tracked nightjars. Here, we selected the following important annual events: departure from breeding area, departure from the temperate zone (i.e. the onset of the Mediterranean and trans-Saharan flight), arrival in the wintering area, departure from the wintering area, spring arrival to the temperate zone (after the trans-Saharan flight), and arrival to the breeding area. We also tested the temporal relationships between these events and the duration of the subsequent major stationary periods. Finally, we tested the effect of departure timing from breeding area on the arrival time on wintering ground, and vice versa, to evaluate the presence of temporal inter-relationships between temporally and spatially more distant events in the annual cycle. We tested the above-mentioned relationships by using a linear mixed model with the timing of the preceding event (or the duration of the preceding stationary period) as a fixed factor and year as a random factor. We performed the tests by using the 'lmer' function in the R package lme4 ver. 1.1 (Bates et al. 2015).

We produced maps and figures with the R-package ggplot2 ver. 1.0.1. (Wickham 2009) and used R ver. 3.0.2 (<www.r-project.org>) for the statistical analyses. Sample sizes in the statistics may vary depending on to what extent individual data were masked by the influence of the equinoxes. All 12 birds were included in analyses unless stated otherwise.

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.m5g71>> (Norevik et al. 2016).

## Results

### Autumn migration

Average departure date from southern Sweden was 20 August (SD = 11.9 d, range = 6 August–11 September; Table 1). The birds spent on average 25 d (SD = 5.2 d, range = 17–32 d,

Table 1. Comparison of characteristics of the autumn- and spring migration in the tracked birds.

	Autumn				Spring			
	mean	SD	range	n	mean	SD	range	n
Start	20-Aug	11.9 d	6-Aug–11-Sep	12	23-Feb	14.3 d	7-Feb–15-Mar	12
Stop	28-Oct	12.0 d	6-Oct–11-Nov	12	16-May	7.7 d	5-May–27-May	12
Distance (km)	7931	463	7390–8785	12	8039	564	7398–9008	12
Detour (%)	2	2.4	0–8	12 <sup>a</sup>	3	2.4	0–7	12 <sup>a</sup>
Days travel	23	4.7	18–30	5	29	6.6	20–39	10
Days migration	69	13.1	51–97	12	82	8.7	68–93	12
Travel rate (km d <sup>-1</sup> )	363	83.7	261–487	5	293	75.3	194–435	10
Migr. rate (km <sup>-1</sup> )	119	20.4	78–158	12	99	14.3	86–129	12
Flight in travel (%)	43	10.0	31–58	5	35	9.0	23–52	10
Flight in migr. (%)	14	2.4	9–19	12	12	1.7	10–15	12

a: Including birds where stops may have been missed due to the influence of the equinox.

n = 9) stationary at stopovers within the temperate region, divided into 1–3 periods per individual (Fig. 1). The spatial distribution of stops in central and southeast Europe suggests an overall south to southeastern direction of the first part of the migration. After spending on average 9 d (SD = 2.9 d, range = 7–13 days, n = 5) crossing the eastern Mediterranean Sea and the Sahara desert the nightjars stopped for on average 16 days (SD = 7.0 d, range = 7–26 d, n = 8) immediately south of the Sahara desert. These stops were distributed between 15.8°E–30.0°E longitudes with a concentration in southern Chad, southwestern Sudan and the Central African Republic (Fig. 1). Four individuals

(C, D, G and L) moved between the stops in Europe to their wintering areas during the time near the equinox, and therefore any potential stops en route were masked by the influence of the equinox. The number of days the four birds spent between Europe and southern tropical Africa (range = 32–44 d) suggests that they also spent time stationary at stopovers after crossing the Sahara desert. During the final leg on the autumn migration three birds (D, F and I) stopped an additional 5–13 d south of the equator before arriving to the final wintering destinations. The mean date of arrival to the wintering sites was 28 October (SD = 12.0 d, range = 6 October–11 November; Table 1).

### Wintering area

The birds spent on average 118 d (SD = 10.2 d, range = 100–136 d) in the wintering area, where ten birds used one single winter site. The female (E) divided its tropical wintering between three different areas and moved approximately 600 km further to the southeast in late November and about 50 d later it moved 800 km northwest. One bird (K) spent 23 d in central Angola before moving 700 km further to the southwest, where it stayed for the rest of its winter residency. The southernmost KDE centroids encompass a large portion of southern tropical Africa (1900 km N–S by 1600 km E–W, n = 12; Fig. 1) including the DRC (4 individuals), Namibia (3), Angola (2), Zambia (1), Zimbabwe (1) and Mozambique (1).

### Spring migration

The northward migration started on average 23 February (SD = 14.3 d, range 7 February–15 March; Table 1). Two birds (K and L) each made a shorter stop (13 and 5 d) prior the crossing of the Central African rain forest belt (Fig. 1; Supplementary material Appendix 1, Fig. A1). Most birds spent on average 34 d (SD = 9.8 days, range = 22–50 d, n = 10) stationary immediately south of the Sahara desert. These stops were distributed between 9.9°E–27.1°E longitudes with a concentration in the Central African Republic (seven individuals; Fig. 1). For two birds (A and D) any potential stops were masked by the influence of the equinox, but the time they spent moving between the tropical and temperate zones (49 and 45 d) suggests a similar stop as observed in the other individuals. After crossing the Sahara desert and the Mediterranean Sea in on average 9 d (SD = 2.1 d, range = 6–12 d, n = 10), the birds spent on average 28 d (SD = 6.3 d, range = 17–39 d, n = 11) stationary within the temperate zone, divided into 1–3 periods per individual prior to arrival at the breeding area. Four individuals (E, G, I and L) stopped in Greece, suggesting a similar route across the Mediterranean Sea as in the autumn, while four birds (A, B, C and K) made stops in Algeria, Tunisia and Italy and appear to have crossed the central Mediterranean Sea (Fig. 1; Supplementary material Appendix 1, Fig. A1). The other birds (D, F, H and J) made their first stop in central and eastern Europe, while the longitudinal positions of their sea crossing were uncertain. The mean arrival date to the breeding area was 16 May (SD = 7.7 d, range 5 May–27 May).

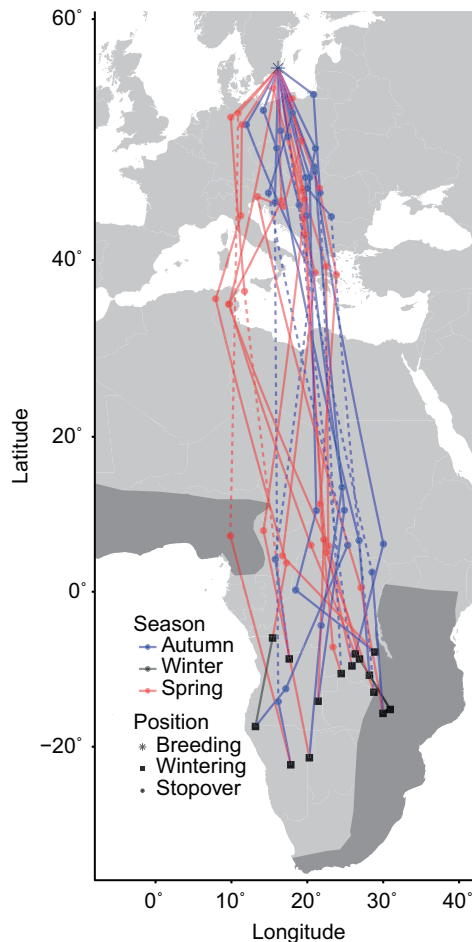


Figure 1. Positions of the stationary periods as represented by the centres of KDEs during the northern winter (dark squares), autumn (blue dots) and spring (red dots) respectively. Lines connect the succession of stationary periods and are coloured based on season; blue = autumn, dark = winter and red = spring. Dashed lines indicate periods of movements when a stop may have been missed due to the influence of the equinoxes. Dark grey areas represent the currently described wintering range downloaded from The IUCN red list of threatened species (2014). The tracked individuals were distributed in the southern parts of the tropical zone with several birds located far outside the currently described wintering range. All birds except two individuals were resident in one single wintering site as recognized by the geolocators. The spring stops in the Sahel were to the west of the autumn stop resulting in a narrow loop migration in the tracked birds. The map is in a Mercator projection.



## Migration strategy

The total distance along the autumn route described by the geolocators was on average 7931 km (SD = 463 km, range = 7390–8785 km; Table 1). The routes (including all birds) resulted in an average detour of 2% (SD = 2%, range 0–8%) relative to the direct great-circle distance between breeding and wintering sites. The average total distance along the spring route was 8039 km (SD = 564 km, range = 7398–9008 km; Table 1), with a mean detour of 3% (SD = 2%, range 0–7%). The longitudinal range of stops of the tracked birds overlapped at large between autumn and spring (Fig. 1). On an individual level, however, the birds conducted a narrow clockwise loop with spring stops in the Sahel significantly to the west of the autumn stops (matched paired *t*-test:  $t = -4.40$ ,  $DF = 6$ ,  $p = 0.004$ ; Supplementary material Appendix 1, Fig. A1–A2).

The average migration speed in autumn was 119 km  $d^{-1}$  (SD = 20.4 km  $d^{-1}$ , range = 78–158 km  $d^{-1}$ ; Table 1), while the mean spring migration speed was 99 km  $d^{-1}$  (SD = 14.3 km  $d^{-1}$ , range = 86–129 km  $d^{-1}$ ). Individual migration speed was significantly faster in autumn than in spring (matched paired *t*-test:  $t = 2.79$ ,  $DF = 11$ ,  $p = 0.02$ ; Supplementary material Appendix 1, Fig. A3). The average autumn travel speed (363 km  $d^{-1}$ , SD = 83.7 km  $d^{-1}$ , range = 261–487 km  $d^{-1}$ ,  $n = 5$ ) and spring travel speed (293 km  $d^{-1}$ , SD = 75.3 km  $d^{-1}$ , range = 194–435 km  $d^{-1}$ ,  $n = 10$ ) did not differ significantly (matched pair *t*-test:  $t = 2.33$ ,  $DF = 4$ ,  $p = 0.07$ ). With the assumption that nightjars fly at an airspeed of about 10 m  $s^{-1}$  (approximately 34 km  $h^{-1}$ ), which is a radar based measurement on the morphologically similar red-necked nightjar *Caprimulgus ruficollis* (Bruderer and Boldt 2001), the birds would only need to be flying on average 43% and 35% of the measured travel time in autumn and spring, respectively. The corresponding numbers for the whole journey including stopovers en route were 14% and 12% for autumn and spring migrations, respectively.

## Annual cycle

The annual cycle of the tracked birds was allocated into the four main parts as follows: breeding (26%), autumn migration (19%), wintering (32%) and spring migration (23%; Fig. 2). Timing of major events throughout the annual cycle was positively associated with the individual's timing of the preceding event (Fig. 2, 3). A significant positive effect could also be seen between more distant events in spring (arrival time in breeding area ~ departure time from wintering grounds:  $r = +0.35$ ,  $p = 0.016$ ), but in autumn this was not significant (arrival time in wintering grounds ~ departure time from breeding area:  $r = +0.36$ ,  $p = 0.25$ ). A near significant positive correlation was found across the entire non-breeding season (arrival time in breeding area ~ departure time from breeding area:  $r = +0.21$ ,  $p = 0.07$ ). Earlier arriving birds spent longer time stationary within the wintering areas as well as in the spring stops in the Sahel and temperate zones. The negative association between the spring stopover duration in the temperate zone and subsequent arrival to the breeding grounds was the only stationary period where duration was significantly correlated to a subsequent event (Fig. 2, 3). No significant relationship was found between the durations of consecutive stationary periods in any part of the annual cycle.

## Discussion

### Winter distribution

Our results provide further evidence that the extent of the nightjars' wintering range has been underestimated (Fry et al. 1988, Cleere 1998, del Hoyo et al. 1999, Holyoak 2001), which is in accordance to our hypothesis 1 (Introduction). The tracked birds wintered throughout the tropical grassland, savannah and shrubland (Olson et al. 2001) of southern tropical Africa. This supports the suggestion by Cresswell

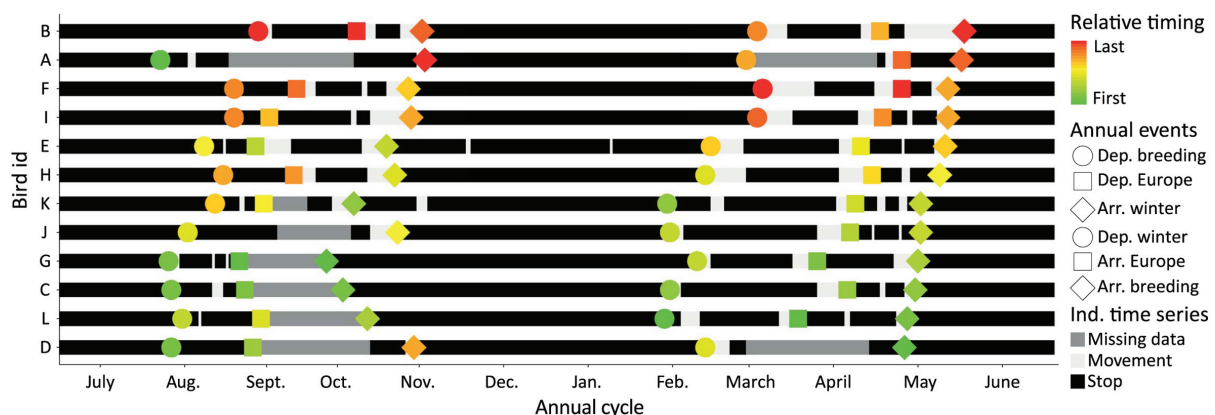


Figure 2. A graphical presentation of the individuals' distributions of stops and movements in the annual cycle, starting on 1 July. Black bars represent periods when the birds were stationary as recognized by the geolocators and the pale gaps show time of movement. Grey sections are periods where the occurrence of stops could not be resolved. The dots show the individual's timing of the six distinct annual events presented in Fig. 3 and the colour gradient show the order of the birds in each event. Green show the first bird and red represent the last bird. The birds are sorted by the arrival time to the breeding area. The colour pattern in the graph with warmer colour tones (orange–red) consistently in the upper part illustrates the significant positive relationships between the annual events presented in Fig. 3. Notably individual A was the first to depart from the breeding range but the last to arrive to the wintering area, and then kept being among the latest birds. This is also the reason for its relatively slow autumn migration rate (Supplementary material Appendix 1, Fig. A3).

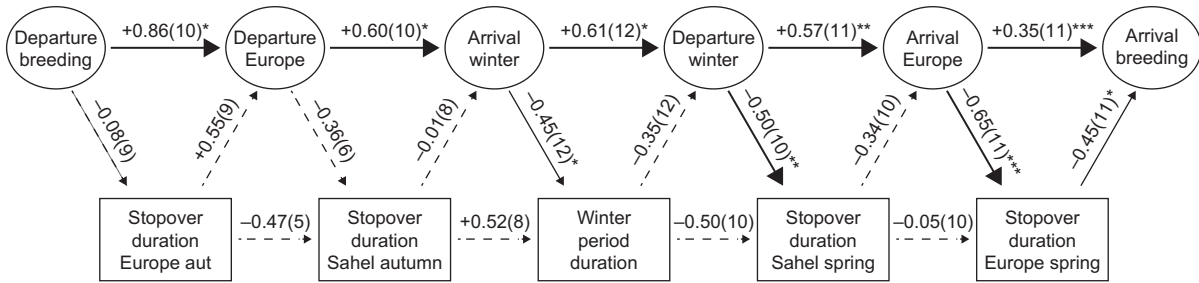


Figure 3. A schematic presentation of the time relationships between different relevant events (top row) and durations of major stationary periods (bottom row) in the annual cycle. Arrows with solid lines represent significant relationships between subsequent events/durations with following significance levels: \* $< 0.05$ , \*\* $< 0.01$  and \*\*\* $< 0.001$ . Strong relationships ( $> 0.5$ ) or high significance level (\*\* or \*\*\*) are presented with thick arrows. Arrows with dashed lines show non-significant relationships. The n-value varies throughout the annual cycle and is presented within brackets. A strong positive relationship can be seen between subsequent events throughout the annual cycle. The arrival date to the wintering area as well as the arrivals to the two spring stops are negative related to the duration of the stop.

and Edwards (2013) that wintering nightjars potentially can be found in much of the semi-open and open landscape from the rainforest in the north to the Kalahari Desert in the south. One should however note that this area is included in the rather generous (but sketchy) winter distribution map of the European nightjar by Moreau (1972).

Most nightjars used a single stationary area throughout the winter and thus demonstrated a sedentary lifestyle similar to red-backed shrikes *Lanius collurio* and European rollers *Coracias garrulus* that also winters in southern tropical Africa (Tøttrup et al. 2012, Finch et al. 2015). The long period of residency enables the birds to conduct the complete moult of flight feathers (Jackson 2008), an event that probably negatively affects their flight performance (Hedenström and Sunada 1999). Additionally, nightjars rely on their cryptic plumage during the light hours and have shown to use the same roost sites repeatedly (Holyoak 2001). Hence, it is likely important for individuals to have knowledge of the local area, not only to maximise feeding efficiency, but also to minimise daytime predation risk. Being sedentary however means that seasonal food resources will vary over time (Sinclair 1978). Analyses on wintering nightjars' stomach contents however suggest that these birds may opportunistically feed on insect prey that is temporarily abundant (Jackson 2000a, b, 2003, Cramp 1985). Two of the birds conducted long migratory-like movements within the winter range, which suggests some flexibility with respect to wintering strategies. The temporally and spatially relatively coarse sampling by geolocators leaves much room for speculation about what triggers the onsets (and stops) of movements. Repeated tracking of the same individuals may be one approach to enable the exploration of the drivers for these 'mid-winter' movements.

Given the relatively small sample of birds from a restricted breeding area in Sweden (where the two sites are within a less than 100 square km range) the vastness of their winter distribution indicates a moderate connectivity between the Swedish breeding area and the general wintering range, broadly overlapping with the British breeding birds (Webster et al. 2002, Cresswell and Edwards 2013). In the literature the nightjar is described as common in east and southeast Africa, in particular as a passage migrant in Kenya (Pearson and Backhurst 1976, Fry et al. 1988, Pearson and Lack 1992). Interestingly, the Swedish birds tracked here show

limited overlap with the eastern winter range, prompting us to assume that birds with a more eastern origin populate this area. This is supported by two recoveries/controls of nightjars ringed at Ngulia, Kenya, from Iran and Kazakhstan, respectively (Pearson et al. 2014).

### The importance of a stopover in the Sahel zone

Major parts of both autumn- and spring migrations were spent just south of the Saharan desert similar to other trans-equatorial migrants (Tøttrup et al. 2012, Willemoes et al. 2014, Finch et al. 2015) and thus supports hypothesis 2 (Introduction). This zone has earlier been described as an important fuelling area for insectivorous birds on passage (Morel 1973, Zwarts et al. 2009). The precision of the estimated locations of sub-Saharan stopovers was affected by the low resolution of the latitude component due to the period around the equinox. The birds were however most likely located in the Sahel or Sudan open savannah zones, reminiscent of the open and semi-open landscape that the species is associated with in the wintering range in southern Africa (Fry et al. 1988, Cleere 1998, del Hoyo et al. 1999, Holyoak 2001). The relatively short duration of the sub-Saharan stopover suggests that nightjars mainly allocate time to fuelling for the next migratory leg, without initiating moult as other species (Pearson and Backhurst 1976, Pearson 1990, Hedenström et al. 1993). The onset of the final autumn migration leg, which includes the passage of the rain-forest belt in central Africa, is probably related to the southward movement of the Intertropical Convergent Zone (ITCZ). This is where the tradewinds from the northeast and southeast converge and form an equatorial belt of convective clouds governing the seasonal rains within the tropics (Waliser and Gautier 1993). Except for an apparent shift in local food abundance, the southward movement of the ITCZ brings the steady north-easterlies further into the tropics, potentially providing migrants with reliable tailwinds. The spring movement starts in late February and the birds arrive to the stopovers north of the central African rainforest with the first spring rains, and thus when the insect abundance is rising (Moreau 1972, Morel 1973). How trans-equatorial migrants have incorporated the timing of the movement of the ITCZ into their annual cycles and what proximate factors they use are still to be resolved.

## Spatial structure of the annual movement

The individual stationary areas in the Sahel zone in autumn and spring were separated and the tracks illustrated narrow clockwise loops. This supports our hypothesis 3 (Introduction) about the shape of the annual migration route. The cost of transport of flapping flight is relatively high (Schmidt-Nielsen 1972) and a deviation from the shortest route can be explained by a selective force (such as the distribution and availability of food and/or wind conditions along the route) that equilibrates the higher cost of the detour (Alerstam 1979, 2001, Erni et al. 2005, Klaassen et al. 2010, Kranstauber et al. 2015). The fact that the nightjars' routes in the two seasons largely overlapped between individuals is perhaps speaking against a resource driven loop-pattern. Nor does it appear to exist an apparent east–west gradient in general habitat quality in the central African Sahel zone (Olson et al. 2001). The weather pattern over tropical Africa with a steady eastern wind component is perhaps a more plausible explanation for the clock-wise migration routes consistently seen among the tracked birds. The detours seen among the nightjars were minimal in both autumn and spring (on average 2 and 3% of the direct track) relative to detours seen in other tropical migrants breeding in Scandinavia (Åkesson et al. 2012, 2016, Tøttrup et al. 2012, Willemoes et al. 2014). In common swifts *Apus apus* a combination of favourable wind conditions and local abundances of food resources are likely explanations for the 50% detour via west Africa during spring (Åkesson et al. 2012). Similar suggestions have been made for red-backed shrikes that conduct a 40% detour via the Arabian Peninsula in spring and thereby circumnavigate the Saharan desert – Mediterranean Sea (Tøttrup et al. 2012). However, one cannot exclude that some observed migration routes (at least partly) are results of an evolutionary constraint in route choice, which for example have been proposed for the Iberian breeding red-back shrikes migrating via eastern Europe (Korner-Nievergelt et al. 2012).

## Time ratio between migratory flights and stops

The derived flight fractions of about 14% and 12% on autumn and spring migration, respectively, are in agreement with the predictions from migration theory about a division of time between flight and stopover as 1:7 (Hedenström and Ålerstam 1997), and supports our hypothesis 4 (Introduction). Applying the same calculation only to the travel days shows that the birds need to spend on average 43% and 35% of autumn and spring travel time on actual movement in the migratory direction. This suggests that the nightjars very well may keep their crepuscular and nocturnal lifestyle also during the migration period. The few observations of diurnally migrating nightjars we are aware of are related to crossings of extensive water bodies, such as the Mediterranean Sea (Cramp 1985) and the Baltic Sea (Norevik et al. unpubl.).

## Speed comparison between seasons

The nightjars join a minority of species, where spring migration is slower than autumn migration (Nilsson et al.

2013). Hence, the data reject our expectation formulated as hypothesis 5 (Introduction). The reasons for that may be one or a combination of the following factors: 1) the speed derived from the geolocators are estimates of ground speed, which in most wind conditions en route will differ from the birds' airspeeds. This means that the ground speed and its comparison between the two seasons will be affected by the routes taken. The prevailing wind directions over northern Africa are from northeast providing tailwinds in autumn and headwinds in spring, which would affect time and energy spent on migration (Alerstam 1979, Erni et al. 2005, Kranstauber et al. 2015, Åkesson et al. 2016). Also the observed travel speed show a tendency of being faster in autumn than in spring which indicates that more time and energy is spent on migration in spring than autumn. 2) Tracking devices recognize when the carrier initiate the first movement in the migration but not the preparation of the same (i.e. initial fuelling event). These preparations will account for different amount of time depending on the amount of fuel spent on the first flight leg, which may affect the estimated migration rate differently between spring and autumn (Alerstam and Lindström 1990, Hedenström and Ålerstam 1997). However, provided that the migration of nightjars is relatively long, exclusion of the initial fuelling episodes is likely negligible. 3) The birds may be selected for maximizing the probability of matching their movement with local peaks in food resources and/or profitable wind conditions rather than maximizing the migration speed (cf. Ålerstam and Lindström 1990). The spring migration can for example be fine-tuned to regional events such as the northward movement of the ITCZ rather than to be programmed for the fastest movement between the wintering range and the breeding area.

## Temporal relationships within the annual cycle

The positive relationships in timing between subsequent annual events show that relative timing of individuals is maintained throughout the annual cycle, supporting our hypothesis 6 (Introduction). This indicates that there is an element of individuality in the scheduling of the annual cycle (Vardanis et al. 2011, Conklin et al. 2013). Alternatively, the quality of the habitats the birds encounter in the annual cycle may affect fuelling rates and thus influence the start and stop of migratory movements (Marra et al. 1998, Norris et al. 2004). In the case of the nightjars a later arrival to any stationary site within the annual cycle may force the individual into relatively poor and unpredictable habitat or to queue for better habitats to be available (Rappole and Warner 1976, Studds and Marra 2007). This could potentially counteract later birds attempting to overtake earlier individuals in the migration race.

There were also negative relationships between annual events and duration of subsequent stationary periods from the winter and onwards. This indicates a time synchronisation when approaching the onset of breeding, and that each migrant may follow alternative spatiotemporal schedules throughout the nonbreeding season. Alternatively, the temporal synchronization in spring migration may simply be an effect of habitat improvement with season resulting in an increased relative fuelling efficiency in later migrating

birds. The positive correlation between departure from the wintering area and arrival to the breeding area reveals the occurrence of more distal time relationships in the annual cycle when approaching the breeding season. The effect seen across the spring may indicate a time constraint in late departing birds, which have knock-on effect on the fine-tuning of arrival time to the breeding area. The negative relationship between departure from the breeding area and arrival to the wintering area was not significant which indicates that the temporal setting of the autumn migration is relatively flexible.

To explore the consistency in individual space-time scheduling of the annual cycle and to evaluate the fitness consequences of events in the nonbreeding season we need to track individuals over multiple seasons (Vardanis et al. 2011, Stanley et al. 2012), as well as follow up on their breeding success (Béty et al. 2004). This is a goal of our future studies.

**Acknowledgements** – This is report 300 from Ottenby Bird Observatory. We are grateful for assistance during fieldwork from Urban Rundström and Olof Person.

**Funding** – The research received supported from the Swedish Research Council to SÅ (621-2013-4361) and AH (621-2012-3585) and the Centre for Animal Movement Research (CAnMove) financed by a Linnaeus grant (349-2007-8690) from the Swedish Research Council and Lund Univ.

## References

- Åkesson, S. and Hedenström, A. 2000. Wind selectivity of migratory flight departures in birds. – *Behav. Ecol. Sociobiol.* 47: 140–144.
- Åkesson, S., Klaassen, R., Holmgren, J., Fox, J. W. and 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.
- Åkesson, S., Bianco, G. and Hedenström, A. 2016. Negotiating an ecological barrier: crossing the Sahara in relation to winds by common swifts. – *Phil. Trans. R. Soc. B* 371: 20150393.
- Alerstam, T. 1979. Wind as selective agent in bird migration. – *Ornis Scand.* 10: 76–93.
- Alerstam, T. 1990. Bird migration. – Cambridge Univ. Press.
- Alerstam, T. 2001. Detours in bird migration. – *J. Theor. Biol.* 209: 319–331.
- Alerstam, T. 2009. Flight by night or day? Optimal daily timing of bird migration. – *J. Theor. Biol.* 258: 530–536.
- Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, E. (ed.), *Bird migration: physiology and ecophysiology*. Springer, pp. 331–351.
- Arizaga, J., Belda, E. J. and Barba, E. 2011. Effect of fuel load, date, rain and wind on departure decisions of a migratory passerine. – *J. Ornithol.* 152: 991–999.
- Bates, D., Maechler, M., Bolker, B. M. and Walker, S. C. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Berthold, P. 1996. Control of bird migration. – Chapman and Hall.
- Berthold, P. 2006. Bird migration: a general survey. – Oxford Univ. Press.
- Béty, J., Giroux, J. F. and Gauthier, G. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). – *Behav. Ecol. Sociobiol.* 57: 1–8.
- Botev, Z. I., Grotowski, J. F. and Kroese, D. P. 2010. Kernel density estimation via diffusion. – *Ann. Stat.* 38: 2916–2957.
- Bruderer, B. and Boldt, A. 2001. Flight characteristics of birds: I. Radar measurements of speeds. – *Ibis* 143: 178–204.
- Cleere, N. 1998. Nightjars: a guide to nightjars and related nightbirds. – Pica Press.
- Cohen, E. B., Moore, F. R. and Fischer, R. A. 2012. Experimental evidence for the interplay of exogenous and endogenous factors on the movement ecology of a migrating songbird. – *PLoS One* 7: e41818.
- Conklin, J. R., Battley, P. F. and Potter, M. A. 2013. Absolute consistency: individual versus population variation in annual-cycle schedules of a long-distance migrant bird. – *PLoS One* 8: e54535.
- Crampton, S. (ed.) 1985. The birds of the Western Palearctic. Vol. 4. – Oxford Univ. Press.
- Cresswell, B. and Edwards, D. 2013. Geolocators reveal wintering areas of European nightjar (*Caprimulgus europaeus*). – *Bird Study* 60: 77–86.
- Dänhardt, J. and Lindström, Å. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. – *Anim. Behav.* 62: 235–243.
- del Hoyo, J., Elliott, A. and Sargatal, J. (eds) 1999. Handbook of the birds of the World. Vol 5. – Lynx Edicions.
- Dingle, H. 1996. Migration: the biology of life on the move. – Oxford Univ. Press.
- Ekstrom, P. A. 2004. An advance in geolocation by light. – *Mem. Natl. Inst. Polar Res. Spec. Iss.* 58: 210–226.
- Erni, B., Liechti, F. and Bruderer, B. 2005. The role of wind in passerine autumn migration between Europe and Africa. – *Behav. Ecol.* 16: 732–740.
- Finch, T., Saunders, P., Miguel Aviles, J., Bermejo, A., Catry, I., de la Puente, J., Emmenegger, T., Mardega, I., Mayet, P., Parejo, D., Račinskis, E., Rodríguez-Ruiz, J., Sackl, P., Schwartz, T., Tiefenbach, M., Valera, F., Hewson, C., Franco, A. and Butler, S. J. 2015. A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. – *Divers. Distrib.* 21: 1051–1062.
- Fox, J. W. 2010. Geolocator manual v8. – British Antarctic Survey.
- Fransson, T., Österblom, H. and Hall-Karlsson, S. 2008. Swedish bird ringing atlas, vol. 2. Grouses – woodpeckers. – Naturhistoriska Riksmuseet, Stockholm.
- Fry, H. C., Keith, S. and Urban, E. K. (eds) 1988. Birds of Africa. – Academic Press.
- Fudickar, A. M., Wikelski, M. and Partecke, J. 2012. Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. – *Methods Ecol. Evol.* 3: 47–52.
- Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. – *J. Theor. Biol.* 189: 227–234.
- Hedenström, A. and Sunada, S. 1999. On the aerodynamics of moult gaps in birds. – *J. Exp. Biol.* 202: 67–76.
- Hedenström, A., Bensch, S., Hasselquist, D., Lockwood, M. and Ottosson, U. 1993. Migration, stopover and moult of the great reed warbler *Acrocephalus arundinaceus* in Ghana, west Africa. – *Ibis* 135: 177–180.
- Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. and Macdonald, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. – *J. Anim. Ecol.* 74: 455–463.
- Hill, C. and Braun, M. J. 2001. Geolocation by light level – the next step: latitude. – In: Sibert, J. R. and Nielsen, J. (eds), *Electronic tagging and tracking in marine fisheries*. Kluwer, pp. 315–330.



- Hill, R. D. 1994. Theory of geolocation by light levels. – In: Le Boeuf, B. J. and Laws, R. M. (eds), *Elephant seals: population ecology, behavior and physiology*. Univ. of Calif. Press, pp. 227–236.
- Holyoak, D. T. 2001. *Nightjars and their allies: the Caprimulgiformes*. – Oxford Univ. Press.
- Jackson, H. D. 2000a. Food of the nightjars in Zimbabwe. – *Ostrich* 71: 404–407.
- Jackson, H. D. 2000b. The food of the Afrotropical nightjars. – *Ostrich* 71: 408–415.
- Jackson, H. D. 2003. A review of foraging and feeding behaviour, and associated anatomical adaptations, in Afrotropical nightjars. – *Ostrich* 74: 187–204.
- Jackson, H. D. 2008. Moults and ectoparasites of nightjars collected during two January expeditions across Zimbabwe. – *Ostrich* 79: 91–100.
- Klaassen, R. H. G., Strandberg, R., Hake, M., Olofsson, P., Tøttrup, A. P. and Alerstam, T. 2010. Loop migration in adult marsh harriers *Circus aeruginosus*, as revealed by satellite telemetry. – *J. Avian Biol.* 41: 200–207.
- Kokko, H. 1999. Competition for early arrival in migratory birds. – *J. Anim. Ecol.* 68: 940–950.
- Korner-Nievergelt, F., Jenni, L., Tøttrup, A. P. and Pasinelli, G. 2012. Departure direction, migratory timing and non-breeding distribution of the red-backed shrike *Lanius collurio*: do ring re-encounters and light-based geolocator data tell the same story? – *Ring. Migr.* 27: 83–93.
- Kranstauber, B., Weinzierl, R., Wikelski, M. and Safi, K. 2015. Global aerial flyways allow efficient travelling. – *Ecol. Lett.* 18: 1338–1345.
- Lemke, H. W., Tarka, M., Klaassen, R. H. G., Åkesson, M., Bensch, S., Hasselquist, D. and Hansson, B. 2013. Annual cycle and migration strategies of a trans-Saharan migratory songbird: a geolocator study in the great reed warbler. – *PLoS One* 8: e79209.
- Lindström, Å., Alerstam, T., Bahrenberg, P., Ekblom, R., Fox, J. W., Råghall, J. and Klaassen, R. H. G. 2016. The migration of the great snipe *Gallinago media*: intriguing variations on a grand theme. – *J. Avian Biol.* 47: 321–334.
- Lisovski, S. and Hahn, S. 2012. GeoLight-processing and analysing light-based geolocator data in R. – *Methods Ecol. Evol.* 3: 1055–1059.
- Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W. and Hahn, S. 2012. Geolocation by light: accuracy and precision affected by environmental factors. – *Methods Ecol. Evol.* 3: 603–612.
- Lopez-Lopez, P., Garcia-Ripolles, C. and Urios, V. 2014. Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors. – *Curr. Zool.* 60: 642–652.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. – *Science* 282: 1884–1886.
- Migrate Technology 2015. *IntiProc – Geolocation Processing Software*.
- Moreau, R. E. 1972. *The Palaearctic – African bird migration systems*. – Academic Press.
- Morel, G. 1973. The Sahel zone as an environment for Palaearctic migrants. – *Ibis* 115: 413–417.
- Nilsson, C., Klaassen, R. H. G. and Alerstam, T. 2013. Differences in speed and duration of bird migration between spring and autumn. – *Am. Nat.* 181: 837–845.
- Norevik, G. et al. 2016. Data from: Migration strategies and annual space-use in an Afro-Palaearctic aerial insectivore – the European nightjar *Caprimulgus europaeus*. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.m5g71>>.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. and Ratcliffe, L. M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. – *Proc. R. Soc. B* 271: 59–64.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedado, P. and Kassem, K. R. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. – *Bioscience* 51: 933–938.
- Pearson, D. J. 1990. Palaearctic passerine migrants in Kenya and Uganda: temporal and spatial patterns of their movements. – In: Gwinner, E. (ed.), *Bird migration*. Springer, pp. 44–59.
- Pearson, D. J. and Backhurst, G. C. 1976. Southward migration of palaearctic birds over Ngulia, Kenya. – *Ibis* 118: 78–105.
- Pearson, D. J. and Lack, P. C. 1992. Migration patterns and habitats use by passerine and near-passerine migrant birds in eastern Africa. – *Ibis* 134: 89–98.
- Pearson, D. J., Backhurst, G. C. and Jackson, C. 2014. The study and ringing of Palaearctic birds at Ngulia Lodge, Tsavo West National Park, Kenya, 1969–2012: an overview and update. – *Scopus Spec. Suppl.* 4: 1–80.
- Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. and Briggs, D. R. 2004. Accuracy of geolocation estimates for flying seabirds. – *Mar. Ecol. Prog. Ser.* 266: 265–272.
- Rappole, J. H. and Warner, D. W. 1976. Relationships between behaviour, physiology and weather in avian transients at a migration stopover site. – *Oecologia* 26: 193–212.
- Schmidt-Nielsen, K. 1972. Locomotion: energy cost of flying, swimming and running. – *Science* 177: 222–228.
- Silverman, B. W. 1986. *Density estimation for statistics and data analysis*. – Chapman and Hall.
- Sinclair, A. R. E. 1978. Factors affecting food-supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savannah. – *Ibis* 120: 480–497.
- Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A. and Stutchbury, B. J. M. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. – *PLoS One* 7: e40688.
- Studds, C. E. and Marra, P. P. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. – *Clim. Res.* 35: 115–122.
- Svensson, L. 1992. *Identification guide to European passerines*. – Stockholm.
- The IUCN red list of threatened species 2014. Ver. 2014-3. – <[www.ioucredlist.org](http://www.ioucredlist.org)>, accessed 5 February 2014.
- Tøttrup, A. P., Thorup, K., Rainio, K., Yosef, R., Lehtonen, E. and Rahbek, C. 2008. Avian migrants adjust migration in response to environmental conditions en route. – *Biol. Lett.* 4: 685–688.
- Tøttrup, A. P., Klaassen, R. H. G., Strandberg, R., Thorup, K., Kristensen, M. W., Jørgensen, P. S., Fox, J. W., Afanasyev, V., Rahbek, C. and Alerstam, T. 2012. The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. – *Proc. R. Soc. B* 279: 1008–1016.
- Trierweiler, C., Klaassen, R. H. G., Drent, R. H., Exo, K. M., Komdeur, J., Bairlein, F. and Koks, B. J. 2014. Migratory connectivity and population-specific migration routes in a long-distance migratory bird. – *Proc. R. Soc. B* 281: 20132897.
- Vardanis, Y., Klaassen, R. H. G., Strandberg, R. and Alerstam, A. 2011. Individuality in bird migration: routes and timing. – *Biol. Lett.* 7: 502–505.
- Waliser, D. E. and Gautier, C. 1993. A satellite-derived climatology of the ITCZ. – *J. Clim.* 6: 2162–2174.

- Weber, T., Alerstam, T. and Hedenström, A. 1998. Stopover decisions under wind influence. – *J. Avian Biol.* 29: 469–477.
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. and Holmes, R. T. 2002. Links between worlds: unravelling migratory connectivity. – *Trends Ecol. Evol.* 17: 76–83.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis.* – Springer.
- Willemoes, M., Strandberg, R., Klaassen, R. H. G., Tøttrup, A. P., Vardanis, Y., Howey, P. W., Thorup, K., Wikelski, M. and Alerstam, T. 2014. Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. – *PLoS One* 9: e83515.
- Zwarts, L., Bijlsma, R. G., van der Kamp, J. and Wymenga, E. (eds) 2009. *Living on the edge: wetlands and birds in a changing Sahel.* – KNNV Publishing.

Supplementary material (Appendix JAV-01071 at <[www.avianbiology.org/appendix/jav-01071](http://www.avianbiology.org/appendix/jav-01071)>). Appendix 1.