

Repeated migration of a juvenile European Nightjar *Caprimulgus europaeus*

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Abstract Most of our current knowledge on migration strategies in juvenile light-weight birds originates from laboratory studies, displacement experiments and partial migration tracks. Here we report on the first recording of two consecutive migration cycles of one such light-weight migrant, the European Nightjar *Caprimulgus europaeus*. This bird visited the same stopover zones and wintering area in both years, but with earlier arrival times and less time spent at stopover zones in the second year. This unique dataset shows that adult nightjars seem to possess the capability to perform some form of navigation towards areas which are established during the juvenile migration.

Keywords Trans-equatorial solitary migrant · Stopover sites · Wintering areas · Naïve migration · Navigation · Geolocator

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Zusammenfassung

Wiederholter Zug eines juvenilen Ziegenmelkers *Caprimulgus europaeus*

Der größte Teil unseres derzeitigen Wissens über Zugstrategien bei juvenilen Vögeln mit geringem Körpergewicht stammt aus Laboruntersuchungen, Verfrachtungsexperimenten und teilweiser Verfolgung der Zugwege. Hier beschreiben wir die erste Beobachtung zweier aufeinanderfolgender Migrationszyklen eines solchen juvenilen leichtgewichtigen Zugvogels, eines Ziegenmelkers *Caprimulgus europaeus*. Der Vogel besuchte in beiden Jahren dieselben Rast- und Überwinterungsgebiete; dabei kam er im zweiten Jahr früher an und verbrachte weniger Zeit in den Rastgebieten. Dieser einzigartige Datensatz zeigt, dass adulte Ziegenmelker die Fähigkeit zu besitzen scheinen, durch eine Art von Navigation Gebiete aufzusuchen, die sie als Jungvogel auf dem Zug kennengelernt haben.

Introduction

The European Nightjar *Caprimulgus europaeus* (hereafter referred to as nightjar) is a light-weight (approx. 70 g), trans-equatorial, solitary migrant which mainly breeds in open semi-natural habitats closely associated with sandy soils (Evens et al. 2017). Western European nightjars migrate towards wintering areas in subtropical Africa and share common stopover zones (Evens et al. 2017). However, there are no published reports describing the first (naïve) migration of a juvenile nightjar.

Studies that compare migration strategies between juvenile and adult long-distance migrants are scarce, and those which do exist are mostly restricted to the use of remote tracking devices on larger, diurnal, soaring species (≥ 100 g) (e.g. Sergio et al. 2014). Investigations of the migration strategies of smaller birds (≤ 100 g) generally rely on small archival devices which require recapture in order to download migration data. As a result, it is uncommon to deploy such devices on small juvenile birds because high juvenile mortality, prominent natal dispersal and low philopatry increase the probability of loss of these tracking devices.

Larger species, such as storks, geese and cranes, share social information on migration routes in multi-age flocks (Beauchamp 2011). In contrast, many other species migrate alone at night (Willemoes et al. 2015), apparently without any social input from experienced conspecifics (Vega et al. 2016). It is presently assumed that naïve migrants rely on their innate clock-and-compass program during their first migration. In subsequent years, these birds are expected to re-use stopover sites and wintering areas from previous years, as such behavior promotes their survival (Cresswell 2014). Nevertheless, due to the lack of successful tracking studies and the absence of repeated tracks, most of our current knowledge on migration strategies in light-weight juvenile birds originates from laboratory studies or displacement experiments (Thorup et al. 2011).

In order to bridge this knowledge gap we deployed a geolocator on a juvenile nightjar. This bird was recaptured 2 years later as a territorial male, approximately 2 km from its birth place. To our knowledge, this is the first study to report on the results of two consecutive migration cycles in two life stages of a light-weight sub-Saharan migrant. Our findings demonstrate possible age-dependent differences in migration and contribute to furthering our understanding of the repeated migration of juvenile birds.

Materials and methods

Field work

We attached an archival geolocator (MK12 geolocator; Biotrack Ltd., Wareham, UK; weight 1.1 g, stalk length 15 mm) to one juvenile nightjar (fledgling, 74.1 g at time of logger placement) in Belgium (Bosland; 51.17°N, 5.34°E; August 2012). Our aim had been to capture the bird's parents, which failed, and therefore we tagged the fledgling. The bird was captured using ultra-fine mist-nets (Ecotone, Gdynia, Poland; 12 × 3 m, mesh size 20 × 20 mm) and fitted with a metal ring (Royal Belgian Institute for Natural Sciences). The device was attached with a full body harness (0.1–0.2 g; Teflon ribbon 3 mm;

Bally Ribbon Mills, Bally, PA) dorsally between the wings (Åkesson et al. 2012). The logger and harness represented 1.8% of the bird's body weight.

Light data analysis

Light data were processed similar to the methods described by Evens et al. (2017). To minimize latitudinal error at the bird's known location (breeding area 2012 and 2014), we used the sun-elevation angle in order to minimize latitudinal error (Fox 2010). During other stationary periods (breeding 2013, overwintering 2012 and 2013), the locations were calculated using sun-elevation angles, derived from Hill–Ekström calibrations (R package Geolight; Lisovski and Hahn 2012), as described in detail in the Electronic Supplementary Material (ESM) Appendix. Latitudinal data from 14 days before to 14 days after the vernal and autumnal equinoxes (22/23 September, 20 March, respectively) were not used for further analysis. Longitudinal data could be readily estimated throughout the year (ESM Appendix). We used the term “stopover site” to indicate the location where the individual interrupted migration for ≥ 3 days and the term “stopover zone” to describe regions that include stopover sites of other nightjars (Evens et al. 2017). We calculated cumulative tracks of 3-day mean positions to determine migration routes, distances and speed (Åkesson et al. 2012).

Results

The geolocator contained robust data covering two complete migration tracks, one track as a juvenile and the consecutive second as an adult. Analysis of the migration routes indicated a loop migration pattern of approximately 16,500 km between breeding periods. This bird crossed the Mediterranean, the Sahara and the Central African Tropical Rainforest on its way to wintering sites in sub-equatorial Africa (Fig. 1).

During both migration cycles, brief (3–4 days) stopovers were made in the Democratic Republic of Congo, Morocco and Spain (Fig. 1; Table 1). Prolonged stopovers (8–28 days) were made in stopover zones similar to those visited by other Western European Nightjars, i.e. Northern Africa, Central Africa and Western Africa (Evens et al. 2017). During the first migration an additional stopover was made in Central France (10 days). Spring crossing of the Sahara occurred further east in the first year compared to the second year (by 4–6°; approx. 280–420 km; maximal variation in longitude, calculated during stationary periods = 0.94° or approx. 100 km; see ESM Appendix) (Fig. 1). Longitudinal differences in the autumnal crossing of the Mediterranean Sea could not be determined due to an

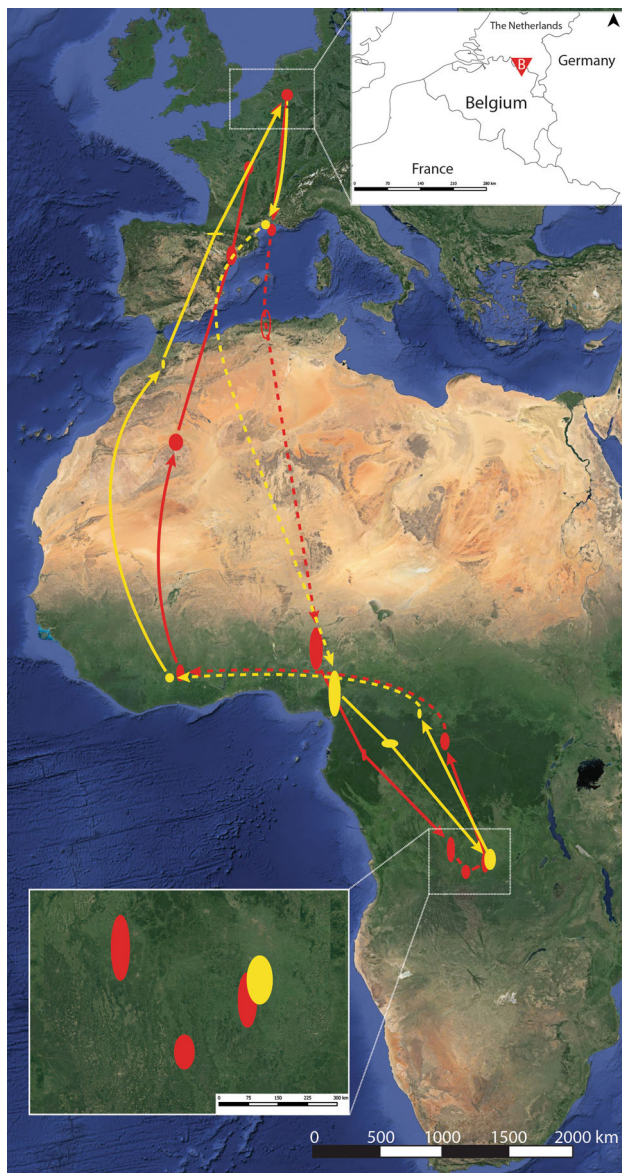


Fig. 1 The migration cycle of the studied European Nightjar *Caprimulgus europaeus* as a juvenile (red) and adult (yellow). *Inset top* Natal/breeding area in Bosland, *inset bottom* wintering areas in the Democratic Republic of Congo. Migration routes were constructed by simplifying 3-day cumulative tracks. *Solid lines* Actual routes, *dashed lines* assumed routes based on longitudinal data during equinox periods. *Solid symbols* Calculated average location of an individual's staging area, *open symbols* calculated average location of an individual's assumed staging area based on longitudinal data during equinox periods. Adult autumnal migration across the Mediterranean Sea is suggestive only due to insufficient accurate geolocator data. Visualized stopover sites are average coordinates of geolocator data with standard deviation represented in the *oval-shaped symbol*. *Arrows* Migratory direction

insufficient quality of geolocator data during the second migration cycle (Fig. 2). After arrival in subtropical Africa in November 2012, the juvenile bird stayed at two different wintering sites for 4 weeks before shifting to its final

wintering site in late December 2012. These separate wintering sites were approximately 200 km apart. In October 2013, during its second migration cycle, the nightjar immediately flew to the same region of its last wintering area from the previous winter and stayed there until the next spring migration (Fig. 1; see ESM for details concerning variation in wintering site). In the first year, i.e. the juvenile stage, arrival times at the stopover zones, wintering site and breeding area occurred later and time spent at stopover zones in Europe was longer (by approx. 10 days).

Discussion

We succeeded in recapturing a third-calendar-year nightjar that had been tagged 2 years earlier as a juvenile. To the best of our knowledge, these data provide a first insight into migration strategies between two different life stages of the same light-weight, solitary, sub-Saharan migrant. This nightjar showed remarkable capabilities during its first naïve migration to search for stopover zones and wintering areas similar to those used by adult Western European nightjars (Evens et al. 2017) and to locate specific areas again the next year.

During the second migration cycle, arrival times at stopover zones were earlier and stopover times in Europe were shorter. Based on the current data it is unclear whether the observed differences were caused by annual variations in physiological (Fusani et al. 2009) or environmental (Studds and Marra 2011) conditions *en route* or by optimization of migration timing (Sergio et al. 2014). Due to contradictory findings reported in earlier studies, it remains unclear whether optimized refueling at stopover sites reduces the residence time of adults (e.g., McKinnon et al. 2014; Sergio et al. 2014). In order to understand why this adult nightjar was able to reduce the time spent at stopover sites, it will be interesting to investigate annual arrival and departure times of migratory birds at these sites in the context of environmental conditions, body condition and annual food availability patterns.

We observed that the crossings of the Sahara (spring) occurred 4–6° (approx. 280–420 km) (Fig. 1) further to the east during the juvenile migration cycle. This observation may correspond to recent findings in larger migratory species, where juveniles follow straighter migration routes (Vega et al. 2016) and travel further to the east than do adults (Sergio et al. 2014). Information on the degree of within-individual flexibility during long-distance migrations is rare and open to interpretation (Stanley et al. 2012). Unfortunately, due to the lack of information on additional repeated migrations of other (juvenile) nightjars, uncertainty about age-related susceptibility to wind drift and

Table 1 Migration timing and stopover duration during the juvenile and adult migration cycle

Stopover site	Juvenile				Latitude (°N)				Longitude (°E)				Latitude (°N)			
	Arrival	Duration (days)	Calculation ^a		Average	SE			Average	SE			Average	SE		
Belgium	24-08-2012	n/a	3		6.4144	0.2655	47.3367	3.7255	09-06-2013	83	32		5.6556	0.2369	51.6341	0.1511
Southern Europe ^b	13-09-2012	4	2		4.2500	0.4525	42.0450	0.6718	10-09-2013	1	1		3.7300	–	43.4200	–
Algeria ^b	20-09-2012	12	2		3.7100	0.5515	36.7400	1.7536	?	?	?		?	?	?	?
Nigeria ^b	08-10-2012	19	13		8.2369	0.7305	10.4931	2.5266	26-09-2013	25	7		9.8971	0.6524	6.5357	2.7435
Congo	02-11-2012	3	2		12.5250	0.1768	1.1250	0.6435	21-10-2013	2	2		14.8250	0.9405	2.0950	0.4313
DRC 1	08-11-2012	22	9		20.4042	0.4039	–6.7339	1.2078	–	–	–		–	–	–	–
DRC 2	30-11-2012	27	10		21.8974	0.4464	–9.1475	0.8883	–	–	–		–	–	–	–
DRC 3	26-12-2012	66	32		23.3788	0.5993	–7.9618	1.1199	28-10-2013	120	42		23.6565	0.6574	–7.4844	1.2098
CAR/Northern DRC ^b	03-03-2013	16	2		19.6500	0.4808	2.1850	0.9970	26-02-2014	12	3		17.5067	0.1701	4.7533	0.5187
Ivory Coast/Ghana ^b	02-04-2013	26	4		–3.8750	0.4094	8.3475	0.9654	20-03-2014	29	1		–4.8900	–	7.9300	–
Morocco	04-05-2013	3	2		–4.2767	0.7943	27.8100	0.9615	29-04-2014	4	5		–5.4200	0.1281	33.8120	0.4825
Spain	09-05-2013	18	18		0.7022	0.5396	41.5056	1.0874	07-05-2014	8	2		–0.7600	0.9051	42.9100	0.0707
France	28-05-2013	11	5		2.1417	0.4807	47.0250	0.7240	–	–	–		–	–	–	–
Belgium	09-06-2013	83	32		5.6556	0.2369	51.6341	0.1511	20-05-2014	n/a	5		5.6243	0.1288	50.8833	0.1945

SE, Standard error; DRC, Democratic Republic of Congo; n/a, data not available

^a Calculation refers to the number of days used to calculate average longitude and latitude^b Uncertainty regarding in observed values 14 days before and 14 days after autumnal and vernal equinox (22/23 September, 20 March, respectively)^c “–”, No stopover occurred

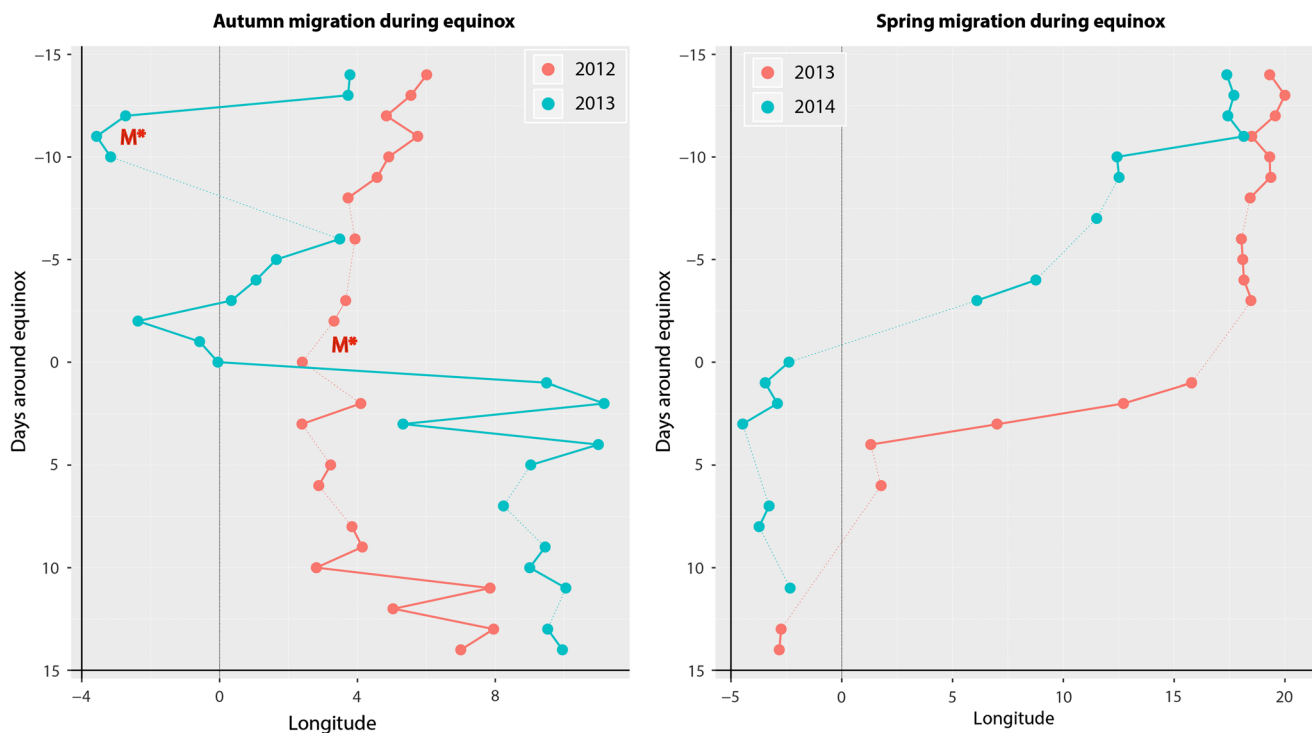


Fig. 2 Longitudinal movement 14 days before and 14 days after autumnal and vernal equinox (22/23 September, 20 March, respectively). *M** moment when Mediterranean Sea was crossed during autumnal equinox

uncertainty regarding any between-year variation caused by environmental conditions we were unable to evaluate the age-related degree of route flexibility.

In both years, this tracked nightjar visited similar stopover zones to those visited by GPS-tracked, adult, Belgian nightjars. During the autumnal Sahara crossing in the first year, the nightjar followed a similar trajectory to that of other adult birds, which cross the Sahara on a rather broad front. The juvenile nightjar crossed the vernal Sahara more easterly than did adult birds reported by Evens et al. (2017). Finally, the latitude of its wintering area was comparable to those of other Western European nightjars (Evens et al. 2017). The current belief is that naïve migrants learn cues and acquire skills to fine-tune an endogenous clock-and-compass program during their first autumn migration (Gwinner 2003). Experienced migrants can subsequently rely on true navigation (Willemoes et al. 2015) in order to follow a unique, but fixed, series of spatially and temporally linked sites to complete their annual migration (i.e. serial residency hypothesis sensu Cresswell 2014). In line with these expectations and similar to the findings of a recent comparative study between migration strategies in juvenile and adult cuckoos (Vega et al. 2016), our results suggest that the innate migration program of juvenile nightjars allows them to reach species-specific stopover zones and wintering grounds during their first migration and that experience allows them to fine-tune this program in order to re-use them the next year.

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