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RESEARCH PAPER

Migration and daily flight activity patterns in the barred warbler *Curruca nisoria* over the annual cycle

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Abstract. The barred warbler, *Curruca nisoria*, is an Afro-Palearctic migrating bird with a wide breeding distribution across eastern Europe to central Asia. Ring recoveries and direct observations have suggested they migrate to non-breeding grounds in East Africa. However, little is known about their migration routes and flight behaviour during migration and on the non-breeding grounds. Using geolocators and multi-sensor loggers, we tracked three barred warblers from a Czech breeding site to document their migration routes, stopover and non-breeding sites, and flight activity patterns across the annual cycle. All three tracked birds took south-eastern autumn migration routes through the Levant, with a shared stopover in Syria before crossing the Arabian Desert, the Red Sea and eastern Sahara Desert and stopping in Sudan for ca. two months. After 109 days (average), birds arrived at their main non-breeding sites of W Kenya or S Ethiopia. A single stopover on the Red Sea coast of Saudi Arabia was used during the spring migration before continuing NW across the Mediterranean. Pressure and acceleration data showed that warblers migrated exclusively at night, with the longest flights crossing the Sahara and travelling from Sudan to non-breeding sites. Daily diurnal activity patterns were uniform across all stationary sites.

Key words: geolocation, tracking, nocturnal activity, diurnal activity, Afro-Palearctic bird migration system

Introduction

Knowledge of the annual cycle of migrating birds, including where and when they can be found at different times of the year, provides important information about the factors affecting bird movement, breeding and survival. For example, poor conditions (e.g. low rainfall and resulting decreased food availability) at tropical non-breeding sites have been shown to delay spring migration, resulting in later arrival at breeding grounds and lower reproductive success (Rockwell et al. 2012, Cooper et al. 2015). Similarly, cold weather conditions along migratory routes have also been shown to affect migratory performance in long-distance migrants, carrying over to late arrival and low return rates at breeding sites due to increased mortality *en route* (Briedis et al. 2017). These observations suggest that

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understanding avian migration routes and behaviour is fundamental to understanding the population dynamics of long-distance migratory birds.

The barred warbler, *Curruca nisoria*, is an Afro-Palaearctic long-distance migrant with an estimated world population of 4 to 7.8 million individuals across a breeding range of about 16 million km^2 from eastern Europe to central Asia (BirdLife International 2023). Barred warblers favour richly structured habitats consisting of bushes and shrubs, and as a result, their inconspicuous behaviour has made observations of their behaviour challenging. Ring recoveries have shown that warblers breeding in Europe migrate to East Africa, and the high concentration of recoveries in the Middle East suggests funnelling to Africa likely occurs via the Levant (Aymí et al. 2021, Spina et al. 2022). However, direct observations at non-breeding grounds are restricted to a small region in eastern Africa, namely parts of Kenya and northern Tanzania, and a few in eastern Uganda and Ethiopia from November to March. The only two available ring recoveries from the putative African passage and/or non-breeding range are recorded from the River Nile valley in Sudan (Spina et al. 2022). Still, no tracking study on individual barred warblers has been published to verify the migration routes used, and little is known about the flight behaviour of warblers during migration and the non-breeding period.

Thus, we aimed to unravel the migration tracks, stopover sites, non-breeding sites and daily activity patterns of individual barred warblers to better inform knowledge of their migration ecology during the annual cycle. We focus on spatial-temporal occurrences along the flyway and the presumably restricted non-breeding grounds, as those sites seem important for many populations across the Palaearctic breeding range.

Material and Methods

Study site

We studied barred warblers at Načeratický kopec, an abandoned military training area near Znojmo, Czech Republic (48.83 N, 16.10 E). The study area (ca. 130 ha) is a nature sanctuary with dominant open steppe grassland habitats. Thorny shrubs (especially the dog rose *Rosa* spp. and hawthorn *Crataegus* spp.), planted old fruit trees, and smaller wild trees form a minor part of the site.

Fieldwork

In 2017, we deployed 16 light-level geolocators (model SOI-GDL2, Swiss Ornithological Institute) and two multi-sensor loggers (model SOI-GDL3-PAM, Swiss Ornithological Institute) on ten males and eight females. In 2019, we deployed seven geolocators and ten multi-sensor loggers on nine males and eight females. The mean weight of geolocators was 0.68 g and of multi-sensor loggers 1.48 g. The mean body mass of adult males equipped with loggers was 22.7 g ± 1.3 SD (range 20.8-26.8 g), while the mean female body mass was 25.5 g ± 1.9 (range 22.3-29.8 g). In May and June, we trapped all adult birds with mist nets within their breeding territories. In the following breeding seasons, we retrieved one geolocator and two multi-sensor loggers (all from males; one logger was retrieved after two years). The return rate of logger-tagged birds was 15.8% (3/19) for males and 0% (0/16) for females. The return rate of control birds (ringed only) was 8.8% for males (5/57) and 7.9% for females (3/38) from 2016 to 2021. Thus, the odds ratio of tagged males returning compared to untagged males was 1.8 (95% CI: 0.4-8.3), while the odds ratio of tagged females returning compared to untagged females was 0.3 (0.01-6.8).

Analysis

Ambient air pressure was recorded every 15 min, while day light intensity and the bird's activity (accelerometer) were recorded every 5 min. Geographical position estimates of the warblers were calculated in one of two ways: from light-only data (logger 21DV; SOI-GDL2 tag) using the R package SGAT (Wotherspoon et al. 2013) or from the combination of pressure, light and activity data (loggers 22PO and 22PH; SOI-GDL3-PAM tags) using the R package GeoPressureR (v.3.1.2) (Nussbaumer & Gravey 2022). The light-only logger provided data on a complete annual cycle from the breeding to the non-breeding grounds and back, while the multi-sensor loggers contained data from the autumn migration and the non-breeding residence sites until 4 February and 13 March when the batteries depleted.

We analysed light-only data in similar steps outlined in Wong et al. (2022), and the light, pressure and activity data following the guidelines of the GeoPressure Manual (https://raphaelnussbaumer.com/GeoPressureManual/; Nussbaumer et al. 2023). In short, SGAT uses a Bayesian approach to estimate locations based on the twilight error distribution, the flight speed distribution (gamma distributed;

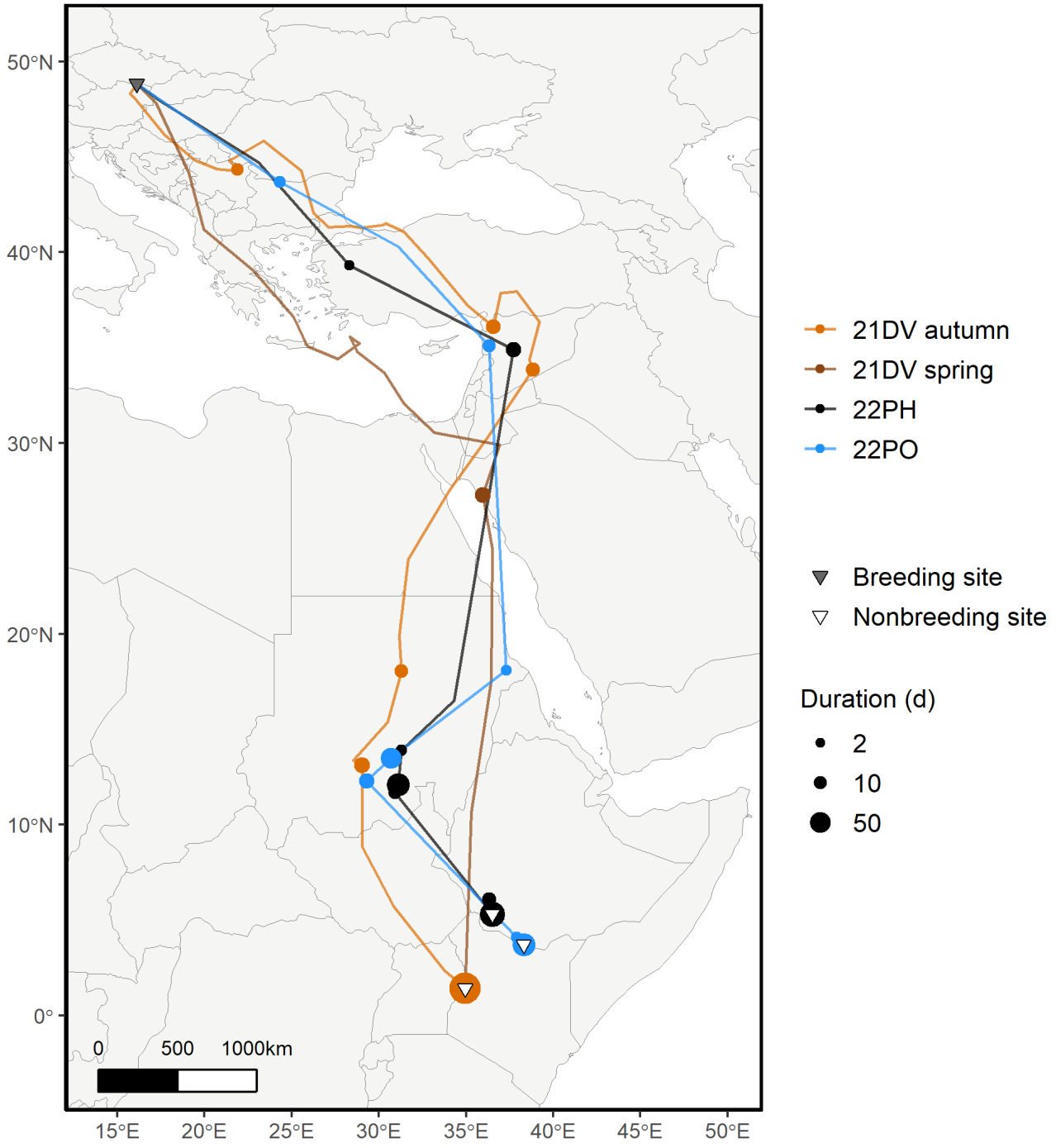

Fig. 1. Modelled autumn and spring migration tracks used by three barred warblers originating from a Czech breeding site. 21DV (orange/brown) was modelled using SGAT and shows the most likely median path, while 22PH (black) and 22PO (blue) were modelled using GeoPressureR and show the path that maximises the overall probability. Each dot represents a stopover site (≥ 2 days stop) used by the individual bird, and the size of the dot is scaled to the minimum duration of days spent at the site. Triangles represent the breeding site (grey) or the main non-breeding site (white). 22PH and 22PO tracks represent only autumn migration until tags stopped recording at the non-breeding site. Uncertainties associated with position estimates are presented per individual in Figs. S1-S3.

shape: 2.2, rate: 0.08), and a land mask to give locations on land a higher prior. Meanwhile, GeoPressureR combines the additional pressure information to create a 1) likelihood map of positions from matching logger-recorded pressure data to global reference weather data and then enhances position estimates by constructing a 2) likelihood map from light data. From this, the path that maximises the overall probability is modelled between estimated stationary sites while taking into account a gamma-distributed flight speed distribution (shape: 7, scale: 7, low-speed fix: 15). Calibration was performed by deriving the median reference solar zenith angles from the breeding site. As the minimum duration for

Table 1. Migration timing, distance, and speed for three geolocators (21DV) and multi-sensor loggers (22PH, 22PO) tracked barred warblers. BS = Breeding site; NBS = Non-breeding site. Further details about individual distances travelled and duration between stationary sites are provided in Table S1.

	21DV	22PH	22PO
Autumn migration			
Departure from BS	1 Aug	30 Jul	12 Aug
Arrival to main NBS	29 Oct	5 Dec	24 Nov
Duration (days)	89	128	109
Travel duration (days)	21	24	20
Great circle distance (km)	5555	5196	5372
Site-to-site distance (km)	6486	6007	6588
# stopovers	5	5	5
Sum of stopover duration (days)	70	115	95
Migration speed great circle distance (km/day)	62	41	49
Migration speed site-to-site (km/day)	73	47	60
Travel speed (km/day)	309	250	329
Spring migration			
Departure from main NBS	1 Apr	-	-
Arrival to BS	1 May	-	-
Duration (days)	30	-	-
Travel duration (days)	10	-	-
Great circle distance (km)	5555	-	-
Site-to-site distance (km)	5804	-	-
# stopovers	1	-	-
Sum of stopover duration (days)	20	-	-
Migration speed great circle distance (km/day)	185	-	-
Migration speed site-to-site (km/day)	193	-	-
Travel speed (km/day)	580	-	-

physiological recovery in migratory songbirds is one day (Eikenaar et al. 2023), we defined stationary sites as stops ≥ 48 h (as in Adamík et al. 2024).

To understand the flight and activity patterns of barred warblers throughout the year, we analysed the activity data recorded by the multi-sensor loggers. We classified flapping activity using the function 'classify_flap' in the R package PAMLr (Dhanjal-Adams et al. 2022). This function determines the threshold between high and low activity using k-means clustering, and classifies continuous high activity (i.e. continuous flapping flight) over our set threshold of 20 min as migratory flight. We used the function 'classify_summary_statistics' to calculate the flight altitudes and duration of each migratory flight (Dhanjal-Adams et al. 2022).

Great circle distances were calculated between stationary sites to evaluate the total flight distance travelled by migrating birds using the 'distVincentyEllipsoid' function in the R package geosphere (Hijmans 2021). The total migration distance per season was calculated by summing the distances between stationary sites.

Results

Autumn migration

All three barred warblers departed from their Czech breeding grounds in late July/early August (mean: 4 August; range: 30 July-12 August) in a southeast direction circumventing the Mediterranean Sea (Fig. 1). Before crossing the Sahara, the birds made 2-3 stopovers from August to September in Romania (22PO), Serbia (21DV), Turkey (22PH) or Syria (all birds; mean stopover duration: 11.4 days). After flying over the Red Sea and crossing the Sahara at its eastern part between 31° E to 38° E, warblers stopped at 2-3 sites in Sudan, arriving in mid-September (mean stopover duration per site: 23 days; mean total stopover duration in Sudan: 63 days) and departing

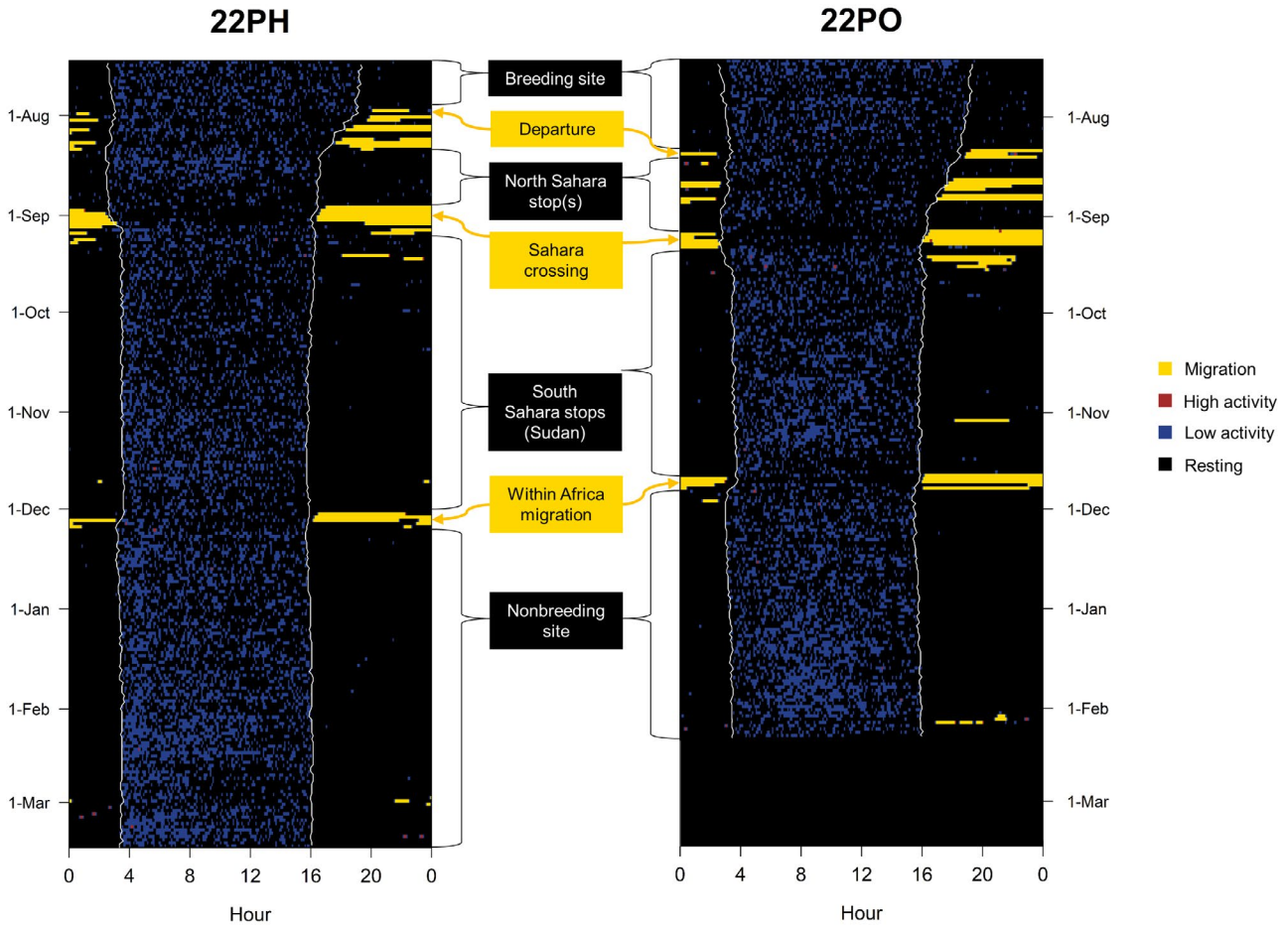

Fig. 2. Actograms showing the classified activity of two individuals (22PH and 22PO) from post-breeding (July) until the late non-breeding period (February and March) based on PAMLr classification by flapping activity. Sustained high activity for ≥ 20 min was classified as migration. White lines delineate sunrise and sunset times.

on average in mid-November. One individual (22PO) made an additional stopover in Ethiopia at the end of November (duration: 5 days). Warblers arrived at their final non-breeding sites on average around November 20 (range: 29 October-5 December) in W Kenya (21DV) or S Ethiopia (22PH, 22PO) after a total average autumn migration journey of 109 days (range: 89-128 days) (Table 1). After 91 days at its main Ethiopian non-breeding site, individual 22PH moved to a second site in Ethiopia on February 29, where it remained until the logger stopped recording on March 13. The site-to-site migration distance travelled by the birds in autumn averaged 6,360 km (range: 6,007-6,588 km), compared to an average direct great circle distance (not accounting for the route used by the birds) of 5,393 km (range: 5,196-5,555 km) between the breeding site and non-breeding site (Table 1). Overall, the longest travel distances occurred *en route* to Syria, Syria to Sudan, and Sudan to the final non-breeding sites of Kenya or Ethiopia (Table S1).

Spring migration

Spring migration information was only available for one individual (21DV), which departed its non-breeding site in W Kenya on April 1 and arrived at a stopover site in Saudi Arabia on April 3 (Fig. 1). There, the bird remained for 20 days before departure on April 23 in a NW direction. In contrast to autumn migration, this individual took a Mediterranean path through the Greek islands, returning to Czechia through the Balkans, Hungary and Slovakia, arriving on May 1 back at the breeding site (Fig. 1, Table 1). The total site-to-site distance of spring migration was 5,804 km, with similar distances travelled from Kenya to Saudi Arabia, and Saudi Arabia to Czechia (Table 1, Table S1).

Individual behaviour during migration and the non-breeding period

Accelerometery data showed that the two warblers migrated only at night and were less active during the day leading up to a nocturnal migratory flight (Fig. 2). The median time for both birds to start migratory flights was 0.9 h (54 min) after sunset (22PH: 2.2 h; 22PO: 0.8 h), and the median time of landing was 2.8 h before sunrise (22PH: 2.4 h; 22PO: 4 h) (Fig. 3). The start and end of migratory flights was primarily related to the duration of the

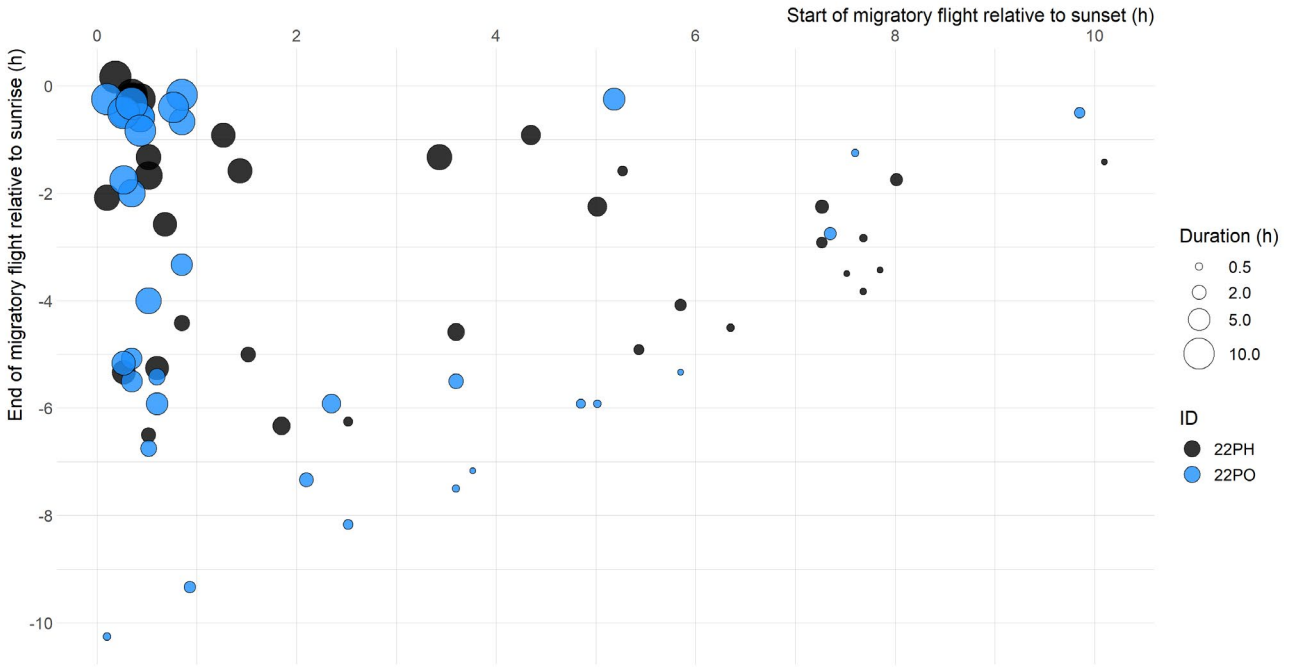

Fig. 3. Starts of migratory flights relative to sunset and the ends of migratory flights relative to sunrise, shown per individual (22PH and 22PO) across the annual cycle. Each circle represents a migratory flight, and the size of the circle represents the relative duration of that flight. Migratory flights ranged in duration from 0.3 to 11 hours.

flight, with longer duration flights starting closer to sunset and ending closer to sunrise (Fig. 3). Flight durations were remarkably similar between the two individuals, with the longest single migratory flights of 10.8 h (22PH: 2-3 September) and 10.4 h (22PO: 8-9 September), occurring during the crossing of the

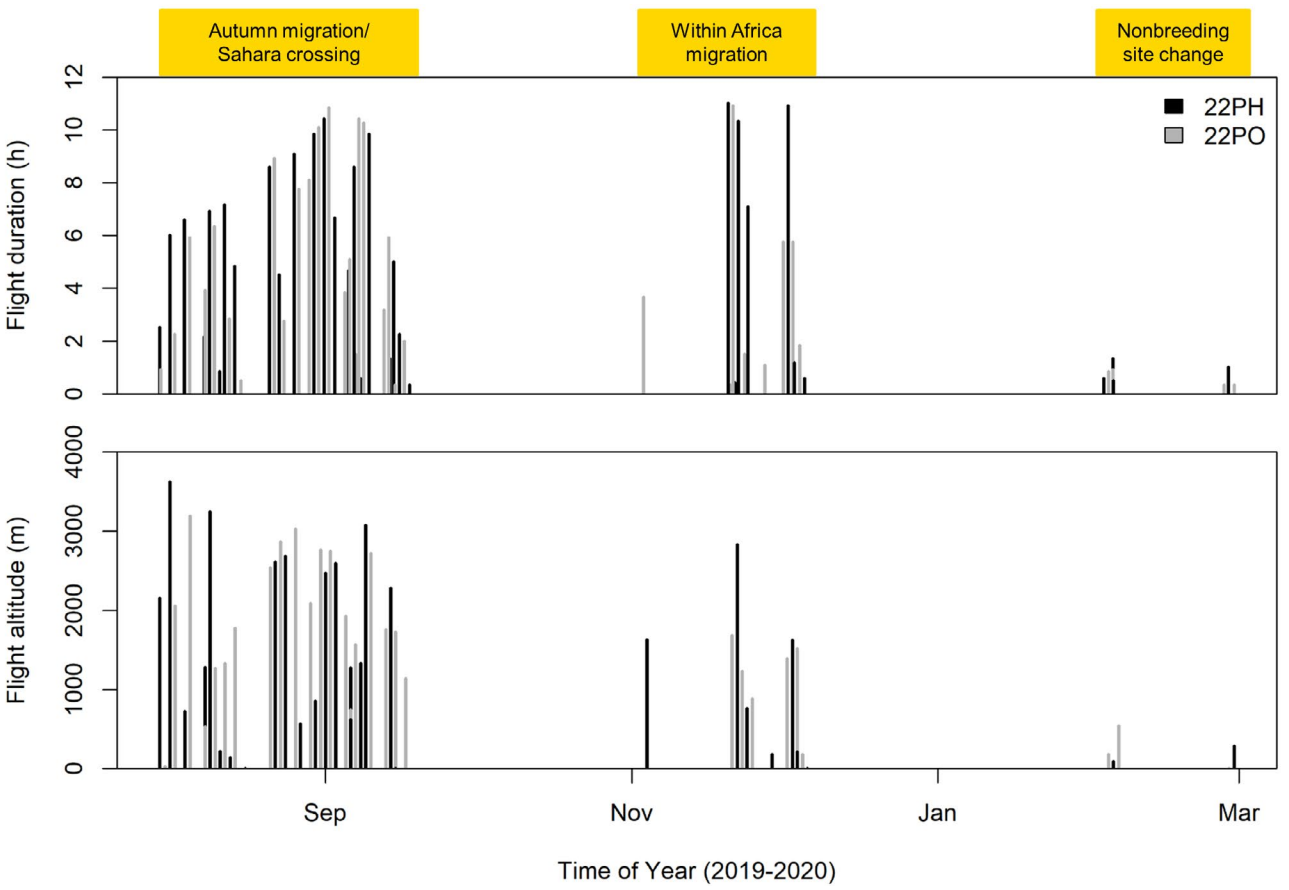

Fig. 4. Migratory flight durations and altitudes (based on PAMLr classification by flapping activity) for two individuals (22PH and 22PO) during autumn migration and when itinerant between non-breeding residence sites in Africa.

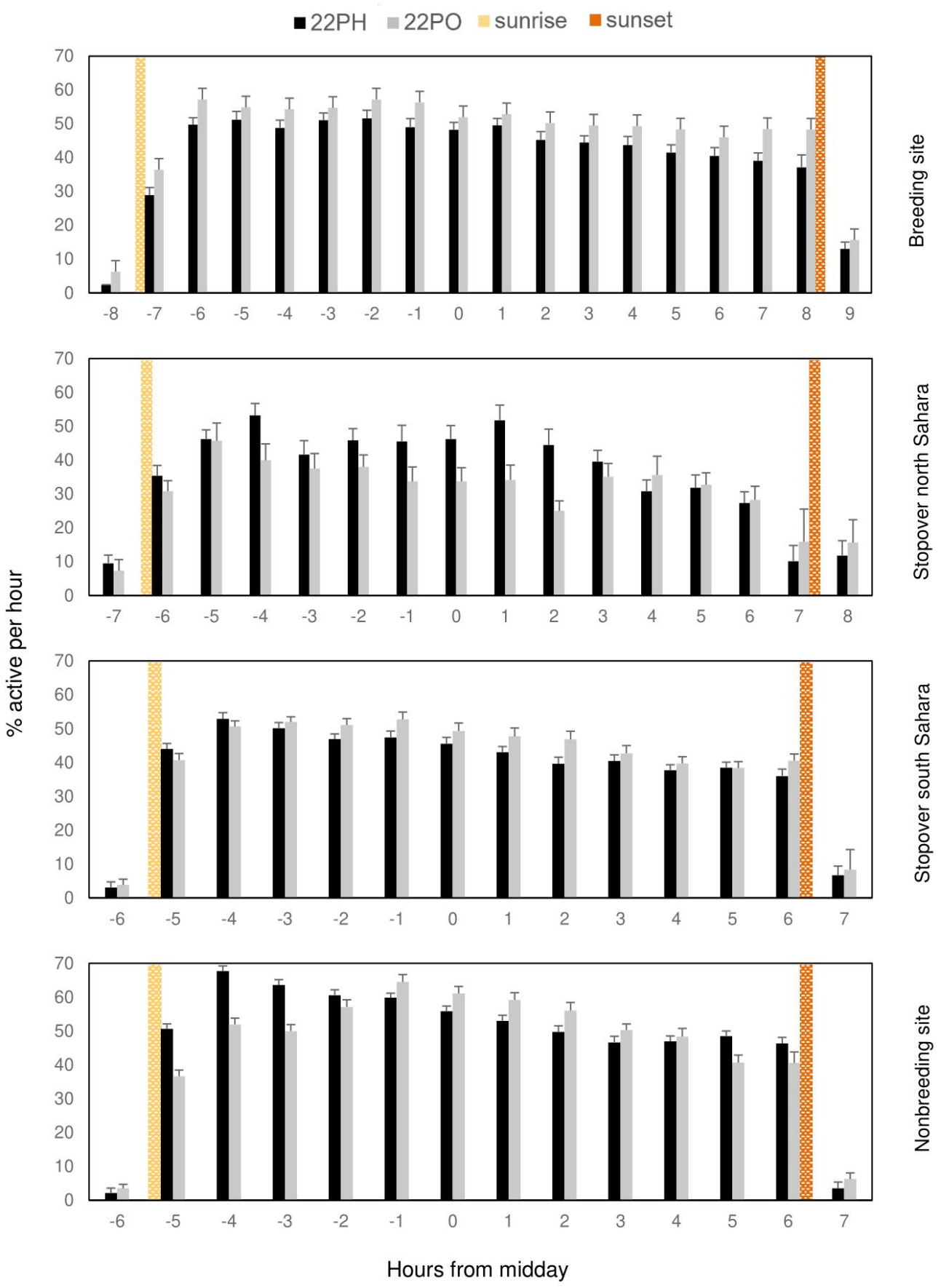

Fig. 5. Average proportion of activity (> resting, as classified by PAMLr) by individual (22PH and 22PO) per hour relative to sunrise and sunset, across the four main stationary periods. Variation in day length across the periods accounts for differences in sunrise and sunset across different stationary periods, as recorded by the light data.

Sahara (22PH: 29 August-8 September; 22PO: 6-11 September) and 10.9 h (22PH: 3-4 December) and 11 h (22PO: 22-23 November) between the migratory period from Sudan to their final non-breeding sites (22PH: 2-5 December; 22PO: 21-24 November) (Fig. 4). The Sahara crossing flight of 22PH was the only flight to extend into sunrise, by 0.16 h (3 September), but actograms showed that all remaining migratory endurance flights were not extended into the day (Figs. 2, 3). The median flight duration per individual was 3.0 h (22PH; range: 0.3-10.9 h) and 4.7 h (22PO; range: 0.3-11 h) (Fig. 3). The median altitude across migratory flights per individual was 1,273.7 m (22PH; range: 0-3,622.8 m) and 1,303.6 m (22PO; range: 0-3,070.7 m) (Fig. 4). The total cumulative flight hours for each bird to reach their main non-breeding sites were 140.3 h (22PH) and 167.8 h (22PO).

In contrast to migration, warblers were active almost exclusively during the day during annual periods of residency (Figs. 2, 5). Although birds appeared to be less active in the hour after sunrise, analysis of the hourly activity during residency periods showed no distinguishable patterns in daytime activity across sites (breeding sites, stopovers, non-breeding sites) nor daylight hours (Fig. 5).

Discussion

Our tracking study confirms that barred warblers from the Czech breeding site spend the main non-breeding residency period in W Kenya and S Ethiopia, and in addition, use migration routes through the Levant and Middle East during autumn and pass through the Mediterranean during spring migration. These findings correspond with the presumed autumn migration corridor of barred warblers, in which most known western Palaearctic breeding populations are thought to bypass the Mediterranean on their southward journey (Moreau 1961). The use of and arrival at non-breeding sites in Kenya and S Ethiopia are also within expected regions and timing (Raz et al. 2023), with former records detailing arrivals from late October/early November onwards to Kenya (21DV arrived October 29), and arrivals to inland Ethiopian sites from late-September to mid-December (22PO arrived November 24, 22PH arrived December 5) (Cramp 1985, Urban et al. 1997). We identified several important stopover sites and provide the first data on stopover durations.

Notably, all three birds utilised a ca. 19-day stopover in Syria before crossing the Sahara in autumn. The Levant is well known as a funnel between the Mediterranean Sea and the Arabian Desert for many long-distance migrants. In barred warblers, 26 out of 29 long-distance ring recoveries during migration were made in this region (Spina et al. 2022). Stopping here appears to be the last option for refuelling before crossing the Sahara, which requires substantial accumulated fuel for nocturnal endurance flights (see Fig. 2).

Following the Sahara crossing, all three birds stopped in Sudan for a long ca. two-month stopover. This halt is similar to long residencies detected in shrikes after crossing this significant barrier (Adamík et al. 2024). There may be several environmental conditions like food and shelter availability and physiological needs that favour the use of such a long stopover. One possibility is the recovery from long-endurance flights and replenishing exhausted body reserves for further migration, which might take several days but not such an extended residency period. Another explanation for the long stopover is post-breeding moult, which occurs when passerine birds renew flight feathers and usually avoid large movements. Interestingly, barred warblers are known to have a seasonally split wing-moult pattern in which, before autumn migration, they interrupt the regular moult of flight feathers after the renewing of primaries and complete the moult of secondaries at African non-breeding sites (Hasselquist et al. 1988, Lindström et al. 1993). Whether the Sudanese stopover sites are used to complete a wing feather moult awaits future investigations. A candidate for resource tracing is the steep gradient in stable sulphur isotopes between Sudanese sites and the warblers' main non-breeding grounds (Brlík et al. 2022), which allows quantification of site-specific contributions.

Optimal habitat conditions are a prerequisite to accomplishing keratin synthesis and feather development within a reasonable time and without interruptions that could substantially weaken feather quality. The elongated Sudanese stopovers used by the barred warblers in our study range between 29° E and 32° E longitude, i.e. the longitudinal range wherein the River Nile flows in this region. The Sudanese portion of the Nile flood plains is associated with several important wetland areas and is also known to harbour a great diversity of plants and insects, which provide suitable conditions for insectivorous migratory species (Paltenea et al. 2008). The rainy season occurs in Sudan from June or July to September when the Intertropical Convergence Zone lies over the northern tropics of the Sahel region, resulting in a resource peak for insectivorous birds (Pearson & Lack 1992). This seasonal pattern of rainfall in the southern part of Sudan coincides

well with the timing of the arrival and departure of warblers in our study.

Favourable environmental conditions likely also dictate the choice of the main non-breeding site. Not only do the non-breeding sites of our tracked birds in north-western Kenya and southern Ethiopia correspond to the currently documented non-breeding distribution in Kenya and Ethiopia from November to March (https://ebird.org/species/barwar1), but they also fall within the wider Great Rift Valley area. The wider Great Rift Valley region is known to support a high diversity of birds and other animals (Lemma & Desta 2016), and barred warblers have been known to frequent the Valley in autumn and spring (Cramp 1985, https://ebird.org/species/barwar1). Rainfall in the presumed non-breeding regions occurs in southern Ethiopia from October to November and in Kenya from November to December (Pearson & Lack 1992). This finding suggests warblers likely select sites based on precipitation or proximity to a water body, which contributes to high insect availability, and likely depart when resource conditions deteriorate following the end of the rainy season.

Insight into the activity of barred warblers during migration and the non-breeding period was also revealed. Warblers generally took off on migratory flights within an hour after sunset and landed less than four hours before sunrise. In contrast to other songbirds (Adamík et al. 2016), barred warblers generally showed no elongation of flights into the day during barrier crossing, suggesting these birds may instead utilise optimal flight conditions (i.e. tailwinds) or have some flexibility in their choice of stopover sites (i.e. stopping anywhere before sunrise), which allow the avoidance of diurnal flights.

The actograms (Fig. 2) and the hourly proportion of activity (Fig. 5) indicate that warblers forage for diurnally active prey but show slightly lower foraging activity in the first hour after sunrise. Interestingly, the daily activity of barred warblers at the Sudanese sites was similarly high compared to breeding and subsequent non-breeding residence sites, indicating the same diurnal pattern of foraging and rest across stationary sites. This result may suggest that all stationary sites used present equal foraging opportunities.

Spring migration is the final step to complete the annual cycle, for which we provide data for the first time. The departure of 21DV from Kenya on April 1 is within the late March to early April range for which previously recorded departures of barred warblers (of unknown origin and fate) were recorded (Urban et al. 1997, Aymí et al. 2021). Using a single long, 20-day stopover at a site near the Red Sea coast in northern Saudi Arabia also matches records of barred warblers in high numbers in the southern Levant in April (Cramp 1985). The Red Sea coast of Saudi Arabia is a highly biodiverse region with a high prevalence of vegetation and invertebrates (Price et al. 1998), which suggests migratory warblers likely use this area as a primary refuelling site after a long flight from Africa and in preparation for another long flight across the Mediterranean. However, the spring passage through the Mediterranean and the southern Balkan peninsula has not been previously documented, as ring recoveries suggested warblers also return north using a Middle Eastern, Levantine route. The detailed flight activity and altitudes of this Mediterranean crossing flight remain unexplored as the bird carried a light-only geolocator tag.

Here, we provide a first look at the migration routes, stationary sites and daily flight behaviour of barred warblers. Despite data from just three individuals, our findings fit the expected non-breeding range and provide evidence for the Balkan and Levant migratory path speculated for this species. As species distributions are expected to shift with changes in climate and food availability, documenting the natural history of migratory birds is valuable to increase our understanding of their annual cycle and flight behaviour.

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Author Contributions

J.P. Wong, P. Adamík and S. Hahn designed the study, P. Adamík and M. Bažant conducted fieldwork, J.P. Wong analysed the data, and J.P. Wong and S. Hahn wrote the manuscript. All authors commented and agreed on the manuscript.

Data Availability Statement

The geographic positions and multisensory logger data supporting this study's findings are archived at Movebank (www.movebank.org, ID 3146197948) and Zenodo (http://doi.org/10.5281/zenodo.10209430).

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Supplementary online material

Table S1. Great circle distances (km) and durations from departure to arrival (days) between stationary sites on the autumn and spring migration, including the total great circle migration distance travelled per individual per season. Values have been rounded to the nearest km.

Fig. S1. Modelled track and stationary site position estimates for 21DV with associated uncertainty from analysis of light data using SGAT.

Fig. S2. Marginal probability of modelled track and stationary site position estimates for 22PH from analysis of pressure data using GeoPressureR.

Fig. S3. Marginal probability of modelled track and stationary site position estimates for 22PO from analysis of pressure data using GeoPressureR.

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