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# Migration routes and timing of European Nightjars (*Caprimulgus europaeus*) breeding in eastern Mongolia

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**Abstract**

The phenology and routes of long-distance migrations of European Nightjars are well-described for Western European individuals migrating within the East Atlantic and Mediterranean flyways, while little is known about populations from other parts of the Eurasian breeding range. We describe the route choice and timing of European Nightjars breeding in eastern Mongolia, migrating within the Asia-East Africa flyway in order to reach wintering destinations in South-East Africa. After covering about 15,000 km during autumn migration, Mongolian nightjars arrived one month later in their wintering grounds compared to nightjars breeding in Western Europe. A similar difference was also observed in the timing of their arrival back at their respective breeding grounds illustrating the differences in timing of migration events between the two populations. We identify the steppes of Central Asia and the savannah of the Horn of Africa and Eastern Africa as key stopover zones for nightjars associated with the crossing of an ecological barrier formed by the deserts and mountains of the Iranian Plateau and the Arabian Peninsula.

**Key words:** Bird migration, light-level geolocation, Asia-East Africa flyway, long-distance migrant, ecological barrier, stopover site

**Zusammenfassung**

**Zugrouten und zeitlicher Zugverlauf Europäischer Ziegenmelker (*Caprimulgus europaeus*) in der östlichen Mongolei**

Die Phänologie und die Zugrouten des Europäischen Ziegenmelkers *(Caprimulgus europaeus)* sind für westeuropäische Populationen, die innerhalb der ostatlantischen und mediterranen Zugrouten wandern, gut beschrieben, während über Populationen aus anderen Teilen des eurasischen Brutgebiets wenig bekannt ist. In dieser Arbeit beschreiben wir die Routenwahl und den zeitlichen Ablauf des Zuges von Europäischen Ziegenmelkern, die in der östlichen Mongolei brüten und innerhalb der asiatisch-ostafrikanischen Zugroute wandern, um ihre Überwinterungsziele in Südostafrika zu erreichen. Nachdem die mongolischen Ziegenmelker während des Herbstzuges etwa 15.000 km zurückgelegt hatten, kamen sie im Vergleich zu den in Westeuropa brütenden Ziegenmelkern einen Monat später in ihren Winterquartieren an. Ein ähnlicher Unterschied wurde auch bei der Ankunft in ihren jeweiligen Brutgebieten beobachtet, was die Unterschiede in der zeitlichen Abfolge der Wanderungen zwischen den beiden Populationen verdeutlicht. Wir konnten die Steppen Zentralasiens und die Savannen am Horn von Afrika und in Ostafrika als wichtige Rastgebiete identifizieren. Diese Rastgebiete dürften im engen Zusammenhang mit der Überquerung der bedeutenden ökologischen Barrieren, der Wüsten und Berge des iranischen Plateaus sowie der Sandwüsten der arabischen Halbinsel, stehen.

## Introduction

Most long-distance migratory birds breeding in Eastern Asia spend the non-breeding period in the temperate and tropical zones of Southern Asia or Australia, with only few exceptions of species known to migrate from East Asia to Africa instead (Yong et al., 2021) such as e.g. Northern Wheatear (*Oenanthe oenanthe*; Schmaljohann et al., 2017; Bairlein et al., 2012) or Willow warbler (*Phylloscopus trochilus;* Sokolovskis et al., 2018). Migrations along the Asia-East Africa flyway have therefore only been described in a limited number of studies, demonstrating some of the longest migrations among Asian land birds (Dixon et al., 2011). For species with breeding distributions extending across the Palearctic, there may be significant differences in migration distance as well as environmental conditions at the breeding grounds between populations at the extremes of the range (Newton, 2008). Differences in e.g. length of the seasons, weather and food availability may lead to different selection pressures to accomplish annual cycle events at favourable periods in order to coincide with changing conditions (Newton, 2011).

When migratory birds experience potential time constraints within the annual cycle, an expected response may be to maximize the speed of their migration in order to free up more time for e.g. breeding or molting (Alerstam and Lindström, 1990). These time constraints may arise, for example, when a population only has a short period suitable for reproduction due to climatic conditions at the breeding site, or if the duration of the migration period is extended due to increased migration distance, so that the time spent on migration competes with other activities (Hedenström and Alerstam, 1997). Similarly, migration speed is expected to be higher in spring than in autumn because of competition for arrival order at breeding grounds (Nilsson et al., 2013). Studies investigating intra-specific differences in timing and rate of migration between breeding populations at different latitudes have shown how northern populations depart later for autumn migration and arrive later in the wintering grounds (Briedis et al., 2016; Jahn et al., 2019). Subsequently, departure for spring migration and the arrival at the breeding grounds are also later (Briedis et al., 2016; Jahn et al., 2019; Schmaljohann, 2019). Additionally, these individuals, who experience shorter breeding seasons and migrate longer distances, have been found to increase their migration speed, to reach their destination as fast as possible, particularly during spring migration, compared to conspecifics breeding at more southerly latitudes (Dodge et al., 2014; Schmaljohann, 2019; Hedh et al., 2021), although contrary results have also been found (Monti et al., 2018; Jahn et al., 2019). Populations where breeding locations are separated longitudinally, for example Common Cuckoos (*Cuculus canorus*) at the extremes of the distribution range in Mongolia and the UK, may show similar differences in the timing of migration events. Individuals breeding in Mongolia and China start their autumn migration around one month later and arrive back at the breeding grounds around two months later when compared to individuals breeding in the UK (*Cuculus canorus;* Hewson et al., 2016; Townshend, 2018; 2019).

Another such species with a wide distribution range is the European Nightjar (*Caprimulgus europaeus,* hereafter referred to as "nightjar"). Nightjars are long-distance migrants in the Palearctic-Afrotropical system, breeding across Eurasia in open semi-natural habitats (Cramp, 1985; BirdLife-International, 2021). Recent tracking studies, using geolocation and GPS-loggers, show that Western European nightjars migrate along the East Atlantic flyway or Mediterranean flyway to reach wintering areas in Central Africa (Cresswell and Edwards, 2013; Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017). However, for populations from other parts of the breeding range, migration routes, wintering areas, and timing remain largely unknown. Limited information from observations in Africa, including two recoveries in Central Asia of nightjars ringed in Kenya (Pearson et al., 2014), suggest that individuals from these populations may winter along the east coast of Africa (Cleere and Nurney, 1998; Holyoak, 2001). Here we aim to ascertain the wintering locations and migration routes of nightjars breeding in Mongolia, at the eastern edge of the species' distribution range, using multi-sensor loggers. We hypothesize, based on prior knowledge of habitat use of the species in wintering areas (Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017), that individuals migrating from Mongolia may winter in semi-open habitats from the East coast of Africa to southern Africa. Additionally, we compare our results with known migration characteristics of individuals from Western European populations and discuss this in light of potential time constraints faced by individuals migrating from the Mongolian population, and the possible results on the timing and pace of their migration.

## Methods

### Field methods

We conducted fieldwork in eastern Mongolia (Binder sum, Khentii province; 48.57°N, 110.83°E; 2018-2019) where we captured nightjars in presumed breeding territories using ultra-fine mist nets (Ecotone, 12 × 3m) and song playback lures (Evens et al., 2017). We marked each individual with a unique alphanumeric ring and fitted 29 individuals (2018: 13 individuals; 2019: 16 individuals) with a 1.2 g SOI-GDL3pam data logger (hereafter multi-sensor logger) dorsally between the wings (Evens et al., 2017; Evens et al., 2020). The multi-sensor loggers contain sensors to record air pressure, ambient light intensity, air temperature and acceleration in five-minute intervals and magnetic field in four-hour intervals.

### Geolocation

From the recovered multi-sensor loggers, we derived position estimates using (1) light intensity measured every 5 minutes, (2) activity data measured as the sum of the difference in acceleration on the z-axis of 32 measurements taken at 10Hz (~ 3 sec) every 5 minutes, and (3) atmospheric pressure (hPa) measured at five minute intervals, following the methods described in Nussbaumer et al. (2022b) using the R-package "GeoPressureR" (Nussbaumer and Gravey, 2022). We briefly describe the main steps of the method here but referee the reader to (Nussbaumer et al., 2022a; Nussbaumer et al., 2022b) for more details on the method.

First, we used the activity data to determine stationary periods, defined as periods of minimum 12 hours during which a bird stays within the same location. As nightjars use flapping flight for migration (Norevik et al., 2021) we used an automated k-means classification algorithm to classify periods of flapping flight as migratory flight. Since the pressure analysis relies on high precision of this classification, we manually edit the activity and the pressure timeseries following the recommendation from (Nussbaumer et al., 2022b).

Subsequently, we used the pressure data recorded by the multi-sensor loggers to construct a probability distribution map of the position of each stationary period using GeoPressureR. The maps are generated with a resolution of 0.5° and an extent of latitude from 50 to -35 and longitude from 20 to 120.

Light intensity data were used to estimate the position of each stationary period, following the threshold method (Lisovski et al., 2020). First, twilight times were automatically defined as the first and the last recorded light of each day and then manually edited for outliers. Light measurements recorded at the breeding site were used for in-habitat calibration, by fitting the distribution of zenith angle with a kernel smoothing function. Using this calibration, a probability map was computed for each twilight and the maps of all twilights belonging to the same stationary period are aggregated into a single probability map with the log-linear pooling aggregator.

We model the trajectory of a bird with a graphical model (Nussbaumer et al., 2022a) combining the pressure and light probability maps computed above together with a movement model defining the possible distance traveled between consecutive stationary periods. For each geolocator track, we (1) compute the most likely path, (2) produce the posteriori (marginal) probability map of position at each stationary periods and (3) simulate 10 possible trajectories.

Comparative migration data

To compare migration characteristics of European Nightjars breeding at the longitudinal extremes of the breeding range we extracted data available from studies investigating migration of European Nightjars in Western Europe. We searched for these studies using the keywords “European Nightjar” and “Migration” on *Web of Science* and *Google Scholar*, and selected publications reporting departure and arrival dates at the breeding/wintering sites and the duration of stopover periods. The studies used for this purpose were Norevik et al., 2017b, Jacobsen et al., 2017 and Evens et al., 2017b. Two studies, Cresswell and Edwards, 2013 and Evens et al., 2017a, were excluded since the data examined in these studies were part of the dataset in Evens et al., 2017b.

From these studies we extracted the following parameters characterising both autumn and spring migration: departure date, arrival date, duration, minimum distance, number of stopover days, number of travel days, migration speed (distance divided by total duration of migration) and travel speed (distance divided by number of travel days). Additionally, we extracted the duration of the wintering and breeding seasons. Using our own results, we calculated these same parameters. For the sake of comparison, we defined stopovers as stationary periods of > 24 hours, and subsequently calculated the number of stopover and migration days by only considered stationary periods of more than 24 hours, since this is the resolution available in the existing studies where activity data were not available.

## Results

From 13 deployments in 2018 we recovered two multi-sensor loggers in 2019, constituting a recovery rate of 15%. Of the 16 deployments in 2019, we were only able to recover one multi-sensor logger due to the COVID-19 pandemic preventing the organization of extensive fieldwork in 2020 and 2021. The recovery rate of 15%, although low, lies within the variation in recovery rates in Western European populations where trapping efforts have been constant across years (Norevik et al., 2021), and can most likely be attributed to bad weather conditions during a two-week trapping session in Mongolia (July 2019). The two loggers recovered in 2019 recorded partial migration cycles, stopping 17 days and 58 days after departure from the wintering site. The logger recovered in 2021 recorded data for a full migration cycle, in addition to the start of the subsequent autumn migration (42 days after departure from the breeding site). This resulted in one partial and three full autumn migration tracks, and two partial and one full spring migration tracks. We did not observe the quality of recorded data to be impacted by failure of the loggers.

Migration timing and distance

Mongolian nightjars started autumn migration in late August and reached the wintering grounds in southeast Africa (Zambia and South-Africa; Fig. 1) at the end of November and the beginning of December, comprising on average 102 days between departure at the breeding site and arrival at the wintering site (Table 1). Spring migration started in March-April resulting in an average wintering period of 114 days (Table 1). During autumn migration the individuals remained at stopover sites for 41 days and actively migrated for 61 days (Table 1). The one individual for which spring migration was fully recorded arrived in the breeding grounds on the 1st of June, after a spring migration lasting 70 days, of which 20 days were spent stationary and 50 were spent on active migration.

The minimum autumn migration distance, calculated as the sum of great circle distances between the stationary sites, was on average 14546 km. In spring, the single recorded complete migration route had a minimum length of 15234 km (Table 1). The average autumn migration speed, calculated as minimum migration distance divided by the number of days in the migration period, was 143 km per day in autumn and 218 km per day in spring, while the average travel speed, the minimum migration distance divided by the number of migration days excluding the days spent on stopovers, was 201 km per day in autumn and 306 km per day in spring (Table 1).

Based on the activity data from three complete autumn tracks and one complete spring track, nightjars spent on average 312 (SD = 26; n = 3; range = 283 – 334) hours performing active migratory flight in autumn, and 316 hours in spring. During autumn this migratory flight was divided in, on average, 58 (SD = 6; n = 3; range = 53 – 64) separate flight bouts with an average length of 5.4 (SD = 3.6; n = 173; range = 0.6 – 11.3) hours in autumn. In the one complete spring migration track we observed 60 separate flight bouts with an average length of 5.3 (SD = 3.4; n = 60; range = 0.6 – 11.3) hours. By dividing the minimal migration distance by the hours spent on active migration, this gives an estimated average ground speed of 46.7 (SD = 2.3; n = 3; range = 44.1 – 48.6) km/hour in autumn and 48.2 km/h in spring. According to the definition of stationary periods as periods of >12h during which no migration activity was recorded, as used in our geolocation method, we observed a total of 66.3 (SD = 16.3; n = 3; range = 47.9 – 78.8) stationary days during autumn migration and 32.3 days during spring migration. This time was divided in 48 (SD = 21; n = 3; range = 24 – 61) separate stationary periods in autumn and 23 periods in spring.

Migration routes and stopovers

Daily position estimates show similar migration routes and stopovers, defined as stationary sites where individuals remained for more than 24 hours, for all three Mongolian nightjars (Fig. 1). Two of the three complete autumn migration tracks, as well as the single incomplete track, show how individuals stopped over within a few days after departure, no further than a few hundreds of kilometers south or southwest from the breeding site

(Fig. 1 a,c,d). These stopovers in Mongolia were relatively short, lasting between 1 and 3 days. After this, along with the individual which did not stopover in Mongolia, all individuals flew in a western direction, taking a relatively direct route towards Central Asia by flying north of the Gobi- and Taklaman deserts (Fig. 1 a,b,c). During this migration leg, two individuals had another short stopover, both lasting 2 days (Fig. 1 a,b).

All three individuals had a series of more extensive stopovers in Central Asia, lasting a total of 12, 11 and 5 days respectively, where individuals possibly resided in the arid, alpine steppes covering the foothills of the Tian Shan and Pamir mountains (Olson et al., 2001; Fig. 1 a,b,c). Following this, all individuals flew in a SW direction towards Eastern Africa, crossing the Iranian plateau, the Persian Gulf/Gulf of Oman and the Arabian Peninsula (Fig. 1 a,b,c). Either before or after the crossing of the Gulf of Aden/Red Sea, in Yemen or in the Horn of Africa, all three individuals stopped over on several occasions, for a total of 16, 33 and 12 days respectively (Fig. 1 a,b,c). Hereafter they continued their way south along the East African coast, where two of the three individuals stopped over for 13 and 3 days in the region of Tanzania, Kenya and Mozambique (Fig. 1 a,b), before continuing to their respective wintering grounds in Zambia and South-Africa (Fig. 1 a,b,c).

From the two incomplete and one complete spring migration tracks we observe that all individuals started their spring migration northwards through East-Africa, following roughly the same route as during autumn migration (Fig. 1 e,f,g). The logger of the first individual stopped recording 17 days after departure from the wintering site, when it was located on a stopover on the East coast of Africa (Fig. 1 e). The second individual stopped over on the East coast of Africa in the region of Mozambique for 6 days, after which it continued north (Fig. 1 f). In the Horn of Africa, both individuals had a stopover stopped over on several occasions for a total of 8 and 12 days respectively, before the crossing the Red Sea/Gulf of Aden (Fig. 1 f,g). After traversing the Arabian Peninsula and crossing the Persian Gulf/Gulf of Oman), one individual had a brief stopover of 1 day in the region of the Iranian plateau, before the route continued to Central Asia (Fig. 1 f), where the logger of the second individual stopped recording. The third individual stopped over in southern Kazakhstan, where it stayed for 4 days (Fig. 1 g,). This was followed by a flight in an eastern direction and two more stopovers in Mongolia for 5 days and on1e day (Fig. 1 g), before continuing northeastwards to the breeding grounds (Fig. 1 g).

**Discussion**

Nightjars breeding in eastern Mongolia migrate along the Asia-East Africa flyway to spend the boreal winter in South-East Africa. The minimum migration distance for Mongolian nightjars is around two times longer than the migration distance described for nightjars breeding in Europe (Table 1). The average migration speed, as well as ratio of time spent on stopovers versus active migration, are similar to those of individuals from the Western European populations (Table 1). Departure from the breeding grounds occurs in late August, similar to Western European nightjars, yet Mongolian nightjars arrive in their wintering grounds almost a month later (Table 1). Our data further suggest that Mongolian nightjars arrive later in the breeding grounds (Table 1), which may result in differences in the timing of migration events between the two populations.

During autumn migration, Mongolian nightjars travel between stopover zones in Central Asia, the Horn of Africa and the east coast of Africa, before reaching their wintering grounds in South-East Africa. This route concurs with the passage of nightjars in Kenya during early-mid November (Pearson et al., 2014). It is also in line with earlier suggestions that nightjars winter along the eastern coast of Africa, from Kenya to South Africa (Cleere and Nurney (1998); Holyoak (2001). Although only based on a single complete track, our data suggests that the spring migration route is similar to the autumn migration route. This spring migration route also concurs with the two ring recoveries from southern Kazakhstan and southern Iran and is in line with the timing of the ring recovery in southern Kazakhstan (May; Pearson et al., 2014). When departing the eastern Mongolian breeding site, all four tracks started with a flight westward to a stopover zone in Central Asia. In contrast, routes described for Common Cuckoos (*Cuculus canorus*; Townshend, 2019) and Amur Falcons (*Falco amurensis;* Clement and Holman, 2001; Dixon et al., 2011) also originating from eastern Mongolia show how these species initiate autumn migration in a southern direction towards South-East Asia, coinciding with the "mainland" route of the East Asian or East Asian-Australasian flyway (Yong et al., 2021). Subsequently, both species turn westwards, to cross the Indian subcontinent and the Indian ocean before arriving in Eastern Africa.

From the stopover zone in Central Asia, nightjars migrate east of the Caspian Sea towards the Arabian Peninsula. Here, we observe that nightjars likely follow a mountainous region subjected to relatively mild conditions during autumn (Dolnik, 1990), and not the lowland deserts between ca. 65° E and the Caspian Sea. This route towards the Arabian Peninsula differs from the route described for passerines migrating from Asia to Africa, which follow a route further to the west, flying north and west of the Caspian Sea (Bolshakov, 2002; Bulyuk and Chernetsov, 2005; Heiss et al., 2020). This detour is suggested as a strategy to avoid crossing the deserts and mountains east of the Caspian Sea, which may form a major ecological barrier for avian migrants (Chernetsov et al., 2007).

Given the longer migration distance and similar migration speed, the duration of autumn migration was one month longer for Mongolian Nightjars compared to Western European nightjars. Mongolian nightjars stayed in their wintering sites for approximately four months, similar to the wintering period of Western European individuals (Table 1). The one-month difference in arrival at the wintering grounds subsequently translates into a similar difference in departure for spring migration (March vs. April). Mongolian nightjars arrive at the breeding grounds in June, which coincides with benign environmental conditions at the Mongolian breeding site. Mongolia is characterized by a strong continental climate with cold, dry winters and moderately warm summers which start in June when the average temperature reaches 16 °C (Goulden and Goulden, 2013). In April-early May, when Western European nightjars arrive in their breeding sites (Cresswell and Edwards, 2013; Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017), the average temperature in Mongolia is still between 3 and 10 °C (Climate Risk Country Profile: Mongolia, 2021) while in Western Europe the average temperature has reached 10-15 °C . The observed differences in the timing of migration events between nightjars from Western European and Mongolian populations are seemingly similar to those found in Common Cuckoo. Common Cuckoos arrive in their east Asian breeding grounds in late May-early June, approximately two months later than individuals breeding in the UK (Hewson et al., 2016; Townshend, 2018; 2019). This suggests that the dependence on continent-wide seasonally changing food supplies, for both nightjars and Common Cuckoos, leaves limited room for spatiotemporal flexibility during the migration period (Jacobsen et al., 2017).

With a spring arrival in June, the breeding season of Mongolian nightjars lasts about three months (cfr. autumn departure in August), which is significantly shorter than the four-month breeding season of Western European nightjars (Table 1). This difference in length of the breeding season could potentially be associated with differences in breeding success through variability in the time available for replacement clutches following nest loss, or for rearing multiple broods (Morrison et al., 2019). In Western Europe, nightjars raise a facultative second brood (Cramp, 1985). To our knowledge, there are currently no studies describing the occurrence of double broods in Asian populations of European Nightjars, so this remains to be investigated. However, in other species, such as a Eurasian Hoopoe (*Upupa epops*) and Black-throated Blue Warblers (*Dendroica caerulescens*), shorter breeding seasons have been linked to lower rates of double brooding individuals (Nagy and Holmes, 2005; Hoffmann et al., 2015). Additionally, other nightjar species have been shown to adjust their breeding phenology in response to potential mismatches in environmental conditions (English et al., 2018). The shorter breeding season in the Mongolian population could limit individuals' flexibility in breeding phenology (Halupka et al., 2021). Therefore, it may be advantageous for Mongolian nightjars to arrive early at the breeding grounds, in order to increase individual fitness (Nilsson et al., 2013). In line with other studies on long-distance migrants (La Sorte et al., 2013; Dodge et al., 2014; Nilsson et al., 2014), this may support our observation that Mongolian nightjars, travelling longer distances than Western European individuals, increase spring migration speed in order to reach their breeding sites as quickly as possible.

We are aware that data on spring migration are still sparse, and our findings based on this single migration track remain speculative. Nevertheless, the observed migration speed (migration distance/number of migration days) during spring is seemingly higher than in autumn, as well as being higher than the migration speeds observed for Western European nightjars (Table 1). As suggested by previous studies, we argue that this is likely caused by a difference in use of stopover zones *en route* (Table 1; Kölzsch et al., 2016) rather than increased ground speed, which we observed to be similar between seasons (autumn: 46.7 km/h, spring: 48.2 km/hour), illustrating how adjustments in stopover schedules may act as a primary mechanism for ensuring timely arrival (Schmaljohann, 2018). Whether and how these migration speeds and stopover schedules might be influenced by fuelling strategies before departure from the wintering grounds remains to be investigated.

In conclusion this work provides a first insight into the migration route and timing of migration events in a European nightjar population at the eastern edge of the global distribution range and may serve as a basis for future research investigating the interactions between migratory strategies, breeding conditions and demographic effects in this long-distance avian migrant.

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## Declarations

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### Competing interests

The authors declare that they have no competing interests

### Ethics approval

Research protocols were approved by the Mongolian Ministry of Environment and Tourism, license numbers: 06/2564 and 06/2862.

### Availability of data and materials

The code and parameters used to produce these results and allowing to reproduce the analysis are available at https://github.com/Rafnuss/MongolianNightjar.

### Authors' contribution

The study was conceptualized by ML and RE. RE acquired funding, FL provided resources and BD collected the data, which were curated and analyzed by RN and ML.  ML and RE wrote the original draft which was reviewed by RN, FL, BD, TA, NB, ND, and EU.

## References

Alerstam T, Lindström Å (1990). Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety. In: Gwinner, E (Ed.) Bird Migration. Springer, Berlin. pp. 331-351.

BirdLife-International (2021) Species factsheet: *Caprimulgus europaeus*.

Bolshakov C (2002) The Palaearctic-African bird migration system: The role of desert and highland barrier of western Asia. 3rd Conference of the European Ornithologists Union, Wageningen, Netherlands.

Briedis M, Hahn S, Gustafsson L, Henshaw I, Träff J, Král M, Adamík P (2016) Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. Journal of Avian Biology 47. 743-748.

Bulyuk V N, Chernetsov N (2005) Nocturnal passage of passerines in Western Kazakhstan in autumn. Journal of Arid Environments 61. 603-607.

Chernetsov N, Bulyuk V N, Ktitorov P (2007) Migratory stopovers of passerines in an oasis at the crossroads of the African and Indian flyways. Ringing & Migration 23. 243-251.

Cleere N, Nurney D (1998) A Guide to the Nightjars and Related Nightbirds Pica Press, Robertsbridge, UK.

Climate Risk Country Profile: Mongolia (2021) The World Bank Group and the Asian Development Bank

Cramp S (1985) The Birds of the Western Palearctic. Oxford University Press, Oxford.

Cresswell B, Edwards D (2013) Geolocators reveal wintering areas of European Nightjar (*Caprimulgus europaeus*). Bird Study 60. 77-86.

Dixon A, Batbayar N, Purev-Ochir G (2011) Autumn migration of an Amur Falcon *Falco amurensis* from Mongolia to the Indian Ocean tracked by satellite. Forktail 27. 86-89.

Dodge S, Bohrer G, Bildstein K, Davidson S C, Weinzierl R, Bechard M J, Barber D, Kays R, Brandes D, Han J, Wikelski M (2014) Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. Philosophical Transactions of the Royal Society B 369. 20130195.

Dolnik V R (1990). Bird migration across arid and mountainous regions of Middle Asia and Kasakhstan. In: Gwinner, E (Ed.) Bird Migration. Springer, Berlin. pp. 368-386.

English P A, Nocera J J, Green D J (2018) Nightjars may adjust breeding phenology to compensate for mismatches between moths and moonlight. Ecology and Evolution 8. 5515-5529.

Evens R, Conway G J, Henderson I G, Cresswell B, Jiguet F, Moussy C, Sénécal D, Witters N, Beenaerts N, Artois T (2017) Migratory pathways, stopover zones and wintering destinations of Western European Nightjars *Caprimulgus europaeus*. Ibis 159. 680-686.

Evens R, Kowalczyk C, Norevik G, Ulenaers E, Davaasuren B, Bayargur S, Artois T, Akesson S, Hedenström A, Liechti F, Valcu M, Kempenaers B (2020) Lunar synchronization of daily activity patterns in a crepuscular avian insectivore. Ecology and Evolution 10. 7106-7116.

Goulden C E, Goulden M N (2013). Adaptation to a Changing Climate in Northern Mongolia. In: Goldman, C R, Kumagai, M, Robarts, R D (Eds.) Climatic Change and Global Warming of Inland Waters: Impacts and Mitigation for Ecosystems and Societies. John Wiley & Sons, Ltd., New Jersey.

Halupka L, Borowiec M, Neubauer G, Halupka K (2021) Fitness consequences of longer breeding seasons of a migratory passerine under changing climatic conditions. Journal of Animal Ecology 90. 1655-1665.

Hedenström A, Alerstam T (1997) Optimum Fuel Loads in Migratory Birds: Distinguishing Between Time and Energy Minimization. Journal of Theoretical Biology 189. 227-234.

Hedh L, Dänhardt J, Hedenström A (2021) Population specific annual cycles and migration strategies in a leap-frog migrant. Behavioral Ecology and Sociobiology 76.

Heiss M, Gauger K, Himmel C, Fetting P, Haraldsson T A, Caucal G, Fərəcli Z, Sultanov E (2020) The development of the Besh Barmag Bird Migration Count in Azerbaijan and its importance for the monitoring of Eurasian migrant birds. Sandgrouse 42. 29-45.

Hewson C M, Thorup K, Pearce-Higgins J W, Atkinson P W (2016) Population decline is linked to migration route in the Common Cuckoo. Nature Communications 7. 12296.

Hoffmann J, Postma E, Schaub M (2015) Factors influencing double brooding in Eurasian Hoopoes *Upupa epops*. Ibis 157. 17-30.

Holyoak D T (2001) Nightjars and their Allies Oxford University Press, Oxford.

Jacobsen L B, Jensen N O, Willemoes M, Hansen L, Desholm M, Fox A D, Tøttrup A P, Thorup K (2017) Annual spatiotemporal migration schedules in three larger insectivorous birds: European nightjar, common swift and common cuckoo. Animal Biotelemetry 5. 4.

Jahn A E, Cereghetti J, Cueto V R, Hallworth M T, Levey D J, Marini M A, Masson D, Pizo M A, Sarasola J H, Tuero D T (2019) Breeding latitude predicts timing but not rate of spring migration in a widespread migratory bird in South America. Ecology and Evolution 9. 5752-5765.

Kölzsch A, Müskens G J D M, Kruckenberg H, Glazov P, Weinzierl R, Nolet B A, Wikelski M (2016) Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. Oikos 125. 1496-1507.

La Sorte F A, Fink D, Hochachka W M, DeLong J P, Kelling S (2013) Population-level scaling of avian migration speed with body size and migration distance for powered fliers. Ecology 94. 1839-1847.

Lisovski S, Bauer S, Briedis M, Davidson S C, Dhanjal-Adams K L, Hallworth M T, Karagicheva J, Meier C M, Merkel B, Ouwehand J, Pedersen L, Rakhimberdiev E, Roberto-Charron A, Seavy N E, Sumner M D, Taylor C M, Wotherspoon S J, Bridge E S (2020) Light-level geolocator analyses: A user's guide. Journal of Animal Ecology 89. 221-236.

Monti F, Grémillet D, Sforzi A, Dominici J M, Bagur R T, Navarro A M, Fusani L, Klaassen R H G, Alerstam T, Duriez O (2018) Migration distance affects stopover use but not travel speed: contrasting patterns between long- and short-distance migrating ospreys. Journal of Avian Biology 49. e01839.

Morrison C A, Alves J A, Gunnarsson T G, Thornorisson B, Gill J A (2019) Why do earlier-arriving migratory birds have better breeding success? Ecology and Evolution 9. 8856-8864.

Nagy L R, Holmes R T (2005) To double-brood or not? Individual variation in the reproductive effort in Black-throated Blue Warblers (*Dendroica caerulescens*). The Auk 122. 902-914.

Newton I (2008) The Migration Ecology of Birds Academic Press, London.

Newton I (2011) Migration within the annual cycle: species, sex and age differences. Journal of Ornithology 152. 169-185.

Nilsson C, Bäckman J, Alerstam T (2014) Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants. Behavioral Ecology and Sociobiology 68. 1799-1807.

Nilsson C, Klaassen R H, Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. The American Naturalist 181. 837-845.

Norevik G, Akesson S, Andersson A, Backman J, Hedenström A (2021) Flight altitude dynamics of migrating European nightjars across regions and seasons. Journal of Experimental Biology 224. jeb242836.

Norevik G, Åkesson S, Hedenström A (2017) Migration strategies and annual space-use in an Afro-Palaearctic aerial insectivore - the European nightjar *Caprimulgus europaeus*. Journal of Avian Biology 48. 738-747.

Nussbaumer R, Gravey M (2022) GeoPressureR: Location from Reanalysed Pressure.

Nussbaumer R, Gravey M, Briedis M, Liechti F (2022a) Inferring bird's trajectory from multi-sensor geolocators and remote sensing with a graphical model. Preprint available at Research Square. https://doi.org/10.21203/rs.21203.rs-1693751/v1693751.

Nussbaumer R, Gravey M, Liechti F (2022b) Global positioning by atmospheric pressure retrieved from multi-sensor geolocators. Preprint available at Research Square https://doi.org/10.21203/rs.21203.rs-1381915/v1381911.

Pearson D, Backhurst G, 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 33. 1-80.

Schmaljohann H (2019) The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. Movement Ecology 7. 25.

Schmaljohann H, Lisovski S, Bairlein F (2017) Flexible reaction norms to environmental variables along the migration route and the significance of stopover duration for total speed of migration in a songbird migrant. Frontiers in Zoology 14. 17.

Townshend T (2018) The Beijing Cuckoo Project. https://birdingbeijing.com/beijing-cuckoo-project/.

Townshend T (2019) The Mongolia Cuckoo Project. https://birdingbeijing.com/the-mongolia-cuckoo-project/.

Yong D L, Heim W, Chowdhury S U, Choi C-Y, Ktitorov P, Kulikova O, Kondratyev A, Round P D, Allen D, Trainor C R, Gibson L, Szabo J K (2021) The State of Migratory Landbirds in the East Asian Flyway: Distributions, Threats, and Conservation Needs. Frontiers in Ecology and Evolution 9. 10.3389/fevo.2021.613172.

**Figure 1:** Migration routes and stopover sites (stationary periods > 24 hours) of three European Nightjars breeding in Eastern Mongolia. Maps show the shortest path modelled for autumn (a-d) and spring (e-g) migration (bold lines), as well as five additional simulated paths (transparent lines) and stopover locations (stationary locations longer than one day; crosses), with corresponding cumulative probability estimates based on light and pressure probability maps. Black, red and blue each represent different individuals. Green represents a partial track from the blue individual tracked the year before. The cross inside the square indicates the breeding site and crosses inside diamonds indicate wintering areas.

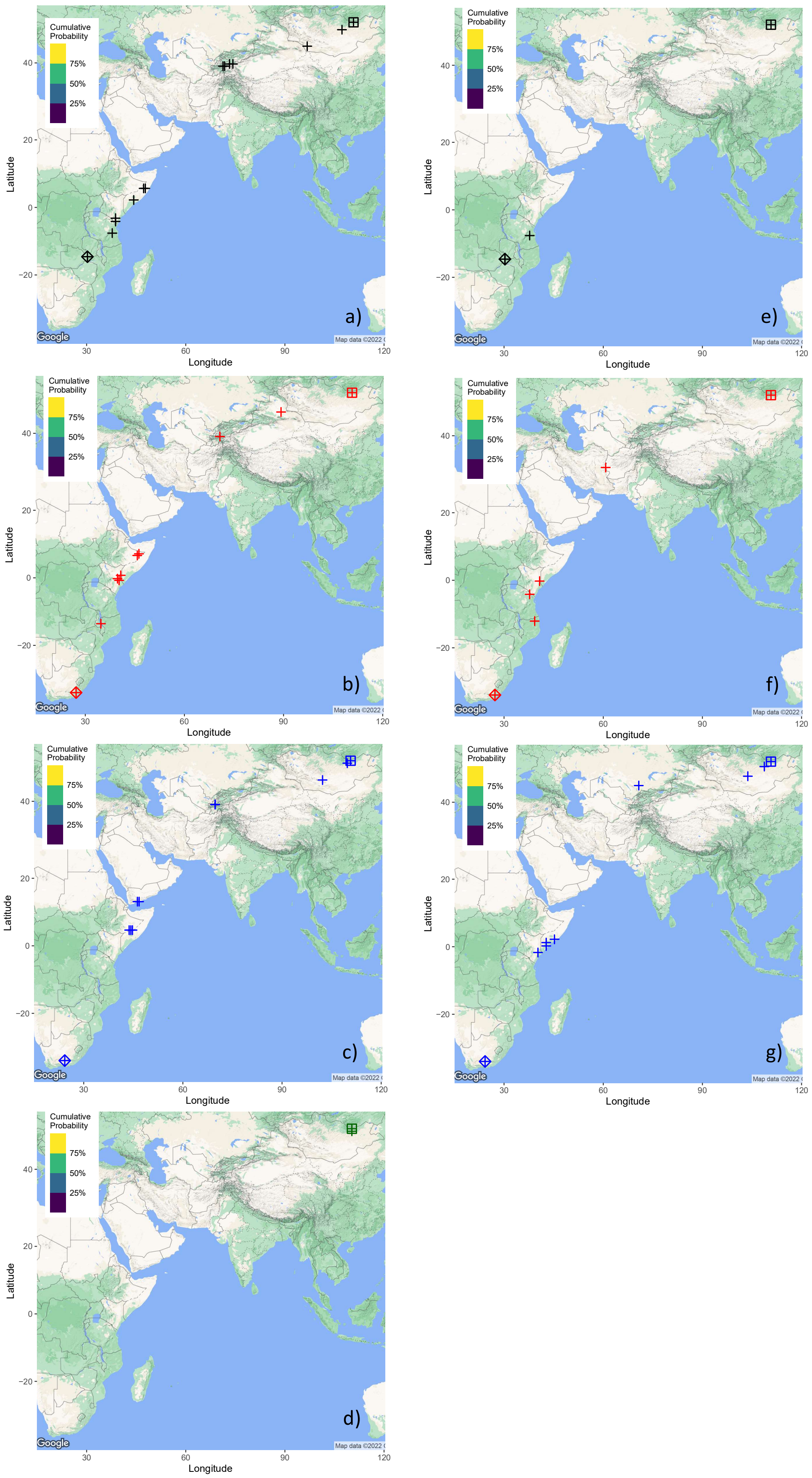
Cumulative Probability
75%
50%
25%
Latitude
Longitude
40
20
0
−20
30
60
90
120
a)
b)
c)
d)
e)
f)
g)
Google
Map data ©2022

**Table 1:** Autumn and spring migration characteristics of Mongolian nightjars, compared with migration characteristics of Western European nightjars from peer-reviewed literature

| | Mongolia | | | | Western Europe | | | |
|---|---|---|---|---|---|---|---|---|
| **Autumn** | **Mean (Median)** | **SD** | **Range** | **n** | **Mean (Median)** | **SD** | **Range** | **n** |
| Start | 18/08 (18/08) | 5 | 13/08 - 26/08 | 4 | 18/08 (20/08) | 17 | 01/08 - 03/09 | 31 [1,2,3] |
| End | 29/11(27/11) | 5 | 26/11- 05/12 | 3 | 16/10 (28/10) | 22 | 21/09 - 30/10 | 31 [1,2,3] |
| Duration | 102 | 3 | 100-105 | 3 | 59 | 9 | 52-69 | 31 [1,2,3] |
| Travel days | 61 | 8 | 54-69 | 3 | 22 | 1 | 21-23 | 18 [2,3] |
| Stopover days | 41 | 6 | 35-47 | 3 | 39 | 11 | 31-46 | 18 [2,3] |
| Minimum migration distance (km) | 14546 | 1121 | 13763- 15830 | 3 | 7760 | 561 | 7133 - 8215 | 31 [1,2,3] |
| Migration speed (km/day) | 143 | 12 | 134-157 | 3 | 135 | 23 | 119-162 | 31 [1,2,3] |
| Travel speed (km/day) | 244 | 47 | 201-293 | 3 | 377 | 20 | 363-391 | 18 [2,3] |
| **Spring** | | | | | | | | |
| Start | 23/03 (23/03) | 9 | 14/03 - 01/04 | 3 | 23/02 (23/02) | 7 | 16/02 - 02/03 | 31 [1,2,3] |
| End | 01/06 | / | / | 1 | 01/05 (16/05) | 27 | 01/04 - 18/05 | 31 [1,2,3] |
| Duration | 70 | / | / | 1 | 71 | 14 | 55-82 | 31 [1,2,3] |
| Travel days | 50 | / | / | 1 | 22 | 10 | 15-29 | 18 [2,3] |
| Stopover days | 20 | / | / | 1 | 47 | 9 | 40-53 | 18 [2,3] |
| Minimum migration distance (km) | 15234 | / | / | 1 | 8116 | 977 | 7180 - 9130 | 31 [1,2,3] |
| Migration speed (km/day) | 218 | / | / | 1 | 116 | 16 | 99-131 | 31 [1,2,3] |
| Travel speed (km/day) | 306 | / | / | 1 | 386 | 131 | 293-479 | 18 [2,3] |
| **Breeding** | | | | | | | | |
| Duration | 77 | / | / | 1 | 109 | 13 | 96-122 | 31 [1,2,3] |
| **Wintering** | | | | | | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Duration | 114 | 6 | 107-117 | 3 | 126 | 19 | 113-148 | 31 [1,2,3] |
| **1: (Evens et al., 2017)** | | | | | | | | |
| **2: (Jacobsen et al., 2017)** | | | | | | | | |
| **3: (Norevik et al., 2017)** | | | | | | | | |