

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

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1 Migration routes and timing of European Nightjars (*Caprimulgus europaeus*) 2 breeding in eastern Mongolia

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23 24 25 **Abstract**

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

35 zones for nightjars associated with the crossing of an ecological barrier formed by the deserts and mountains of
36 the Iranian Plateau and the Arabian Peninsula.

37

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

40

41 **Zusammenfassung**

42 **Zugrouten und zeitlicher Zugverlauf Europäischer Ziegenmelker (*Caprimulgus europaeus*) in der östlichen** 43 **Mongolei**

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

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58

59

60 **Introduction**

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

72

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

93

94 Another such species with a wide distribution range is the European Nightjar (*Caprimulgus europaeus*, hereafter
95 referred to as “nightjar”). Nightjars are long-distance migrants in the Palearctic-Afrotropical system, breeding
96 across Eurasia in open semi-natural habitats (Cramp, 1985; BirdLife-International, 2021). Recent tracking
97 studies, using geolocation and GPS-loggers, show that Western European nightjars migrate along the East
98 Atlantic flyway or Mediterranean flyway to reach wintering areas in Central Africa (Cresswell and Edwards, 2013;
99 Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017). However, for populations from other parts of the
100 breeding range, migration routes, wintering areas, and timing remain largely unknown. Limited information
101 from observations in Africa, including two recoveries in Central Asia of nightjars ringed in Kenya (Pearson et al.,
102 2014), suggest that individuals from these populations may winter along the east coast of Africa (Cleere and
103 Nurney, 1998; Holyoak, 2001). Here we aim to ascertain the wintering locations and migration routes of nightjars
104 breeding in Mongolia, at the eastern edge of the species’ distribution range, using multi-sensor loggers. We
105 hypothesize, based on prior knowledge of habitat use of the species in wintering areas (Evens et al., 2017;
106 Jacobsen et al., 2017; Norevik et al., 2017), that individuals migrating from Mongolia may winter in semi-open
107 habitats from the East coast of Africa to southern Africa. Additionally, we compare our results with known
108 migration characteristics of individuals from Western European populations and discuss this in light of potential

109 time constraints faced by individuals migrating from the Mongolian population, and the possible results on the
110 timing and pace of their migration.

111

112

113

114 **Methods**

115 Field methods

116 We conducted fieldwork in eastern Mongolia (Binder sum, Khentii province; 48.57°N, 110.83°E; 2018-2019)
117 where we captured nightjars in presumed breeding territories using ultra-fine mist nets (Ecotone, 12 × 3m) and
118 song playback lures (Evens et al., 2017). We marked each individual with a unique alphanumeric ring and fitted
119 29 individuals (2018: 13 individuals; 2019: 16 individuals) with a 1.2 g SOI-GDL3pam data logger (hereafter multi-
120 sensor logger) dorsally between the wings (Evens et al., 2017; Evens et al., 2020). The multi-sensor loggers
121 contain sensors to record air pressure, ambient light intensity, air temperature and acceleration in five-minute
122 intervals and magnetic field in four-hour intervals.

123

124 Geolocation

125 From the recovered multi-sensor loggers, we derived position estimates using (1) light intensity measured every
126 5 minutes, (2) activity data measured as the sum of the difference in acceleration on the z-axis of 32
127 measurements taken at 10Hz (~3 sec) every 5 minutes, and (3) atmospheric pressure (hPa) measured at five
128 minute intervals, following the methods described in Nussbaumer et al. (2022b) using the R-package
129 “GeoPressureR” (Nussbaumer and Gravey, 2022). We briefly describe the main steps of the method here but
130 refer the reader to (Nussbaumer et al., 2022a; Nussbaumer et al., 2022b) for more details on the method.

131

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

137

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

141

142 Light intensity data were used to estimate the position of each stationary period, following the threshold
143 method (Lisovski et al., 2020). First, twilight times were automatically defined as the first and the last recorded
144 light of each day and then manually edited for outliers. Light measurements recorded at the breeding site were
145 used for in-habitat calibration, by fitting the distribution of zenith angle with a kernel smoothing function. Using

146 this calibration, a probability map was computed for each twilight and the maps of all twilights belonging to the
147 same stationary period are aggregated into a single probability map with the log-linear pooling aggregator.

148

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

154

155 **Comparative migration data**

156 To compare migration characteristics of European Nightjars breeding at the longitudinal extremes of the
157 breeding range we extracted data available from studies investigating migration of European Nightjars in
158 Western Europe. We searched for these studies using the keywords “European Nightjar” and “Migration” on
159 *Web of Science* and *Google Scholar*, and selected publications reporting departure and arrival dates at the
160 breeding/wintering sites and the duration of stopover periods. The studies used for this purpose were Norevik
161 et al., 2017b, Jacobsen et al., 2017 and Evens et al., 2017b. Two studies, Cresswell and Edwards, 2013 and Evens
162 et al., 2017a, were excluded since the data examined in these studies were part of the dataset in Evens et al.,
163 2017b.

164

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

173

174 **Results**

175 From 13 deployments in 2018 we recovered two multi-sensor loggers in 2019, constituting a recovery rate of
176 15%. Of the 16 deployments in 2019, we were only able to recover one multi-sensor logger due to the COVID-
177 19 pandemic preventing the organization of extensive fieldwork in 2020 and 2021. The recovery rate of 15%,
178 although low, lies within the variation in recovery rates in Western European populations where trapping efforts
179 have been constant across years (Norevik et al., 2021), and can most likely be attributed to bad weather
180 conditions during a two-week trapping session in Mongolia (July 2019). The two loggers recovered in 2019
181 recorded partial migration cycles, stopping 17 days and 58 days after departure from the wintering site. The
182 logger recovered in 2021 recorded data for a full migration cycle, in addition to the start of the subsequent
183 autumn migration (42 days after departure from the breeding site). This resulted in one partial and three full

184 autumn migration tracks, and two partial and one full spring migration tracks. We did not observe the quality of
185 recorded data to be impacted by failure of the loggers.

186

187 Migration timing and distance

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

196

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

203

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

216

217 Migration routes and stopovers

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

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

226

227 All three individuals had a series of more extensive stopovers in Central Asia, lasting a total of 12, 11 and 5 days
228 respectively, where individuals possibly resided in the arid, alpine steppes covering the foothills of the Tian Shan
229 and Pamir mountains (Olson et al., 2001; Fig. 1 a,b,c). Following this, all individuals flew in a SW direction towards
230 Eastern Africa, crossing the Iranian plateau, the Persian Gulf/Gulf of Oman and the Arabian Peninsula (Fig. 1
231 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
232 individuals stopped over on several occasions, for a total of 16, 33 and 12 days respectively (Fig. 1 a,b,c).
233 Hereafter they continued their way south along the East African coast, where two of the three individuals
234 stopped over for 13 and 3 days in the region of Tanzania, Kenya and Mozambique (Fig. 1 a,b), before continuing
235 to their respective wintering grounds in Zambia and South-Africa (Fig. 1 a,b,c).

236

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

249

250 **Discussion**

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

259

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

274
275 From the stopover zone in Central Asia, nightjars migrate east of the Caspian Sea towards the Arabian Peninsula.
276 Here, we observe that nightjars likely follow a mountainous region subjected to relatively mild conditions during
277 autumn (Dolnik, 1990), and not the lowland deserts between ca. 65° E and the Caspian Sea. This route towards
278 the Arabian Peninsula differs from the route described for passerines migrating from Asia to Africa, which follow
279 a route further to the west, flying north and west of the Caspian Sea (Bolshakov, 2002; Bulyuk and Chernetsov,
280 2005; Heiss et al., 2020). This detour is suggested as a strategy to avoid crossing the deserts and mountains east
281 of the Caspian Sea, which may form a major ecological barrier for avian migrants (Chernetsov et al., 2007).

282
283 Given the longer migration distance and similar migration speed, the duration of autumn migration was one
284 month longer for Mongolian Nightjars compared to Western European nightjars. Mongolian nightjars stayed in
285 their wintering sites for approximately four months, similar to the wintering period of Western European
286 individuals (Table 1). The one-month difference in arrival at the wintering grounds subsequently translates into
287 a similar difference in departure for spring migration (March vs. April). Mongolian nightjars arrive at the breeding
288 grounds in June, which coincides with benign environmental conditions at the Mongolian breeding site.
289 Mongolia is characterized by a strong continental climate with cold, dry winters and moderately warm summers
290 which start in June when the average temperature reaches 16 °C (Goulden and Goulden, 2013). In April-early
291 May, when Western European nightjars arrive in their breeding sites (Cresswell and Edwards, 2013; Evens et al.,
292 2017; Jacobsen et al., 2017; Norevik et al., 2017), the average temperature in Mongolia is still between 3 and 10
293 °C (Climate Risk Country Profile: Mongolia, 2021) while in Western Europe the average temperature has reached
294 10-15 °C. The observed differences in the timing of migration events between nightjars from Western European
295 and Mongolian populations are seemingly similar to those found in Common Cuckoo. Common Cuckoos arrive
296 in their east Asian breeding grounds in late May-early June, approximately two months later than individuals
297 breeding in the UK (Hewson et al., 2016; Townshend, 2018; 2019). This suggests that the dependence on

298 continent-wide seasonally changing food supplies, for both nightjars and Common Cuckoos, leaves limited room
299 for spatiotemporal flexibility during the migration period (Jacobsen et al., 2017).

300

301 With a spring arrival in June, the breeding season of Mongolian nightjars lasts about three months (cfr. autumn
302 departure in August), which is significantly shorter than the four-month breeding season of Western European
303 nightjars (Table 1). This difference in length of the breeding season could potentially be associated with
304 differences in breeding success through variability in the time available for replacement clutches following nest
305 loss, or for rearing multiple broods (Morrison et al., 2019). In Western Europe, nightjars raise a facultative second
306 brood (Cramp, 1985). To our knowledge, there are currently no studies describing the occurrence of double
307 broods in Asian populations of European Nightjars, so this remains to be investigated. However, in other species,
308 such as a Eurasian Hoopoe (*Upupa epops*) and Black-throated Blue Warblers (*Dendroica caerulescens*), shorter
309 breeding seasons have been linked to lower rates of double brooding individuals (Nagy and Holmes, 2005;
310 Hoffmann et al., 2015). Additionally, other nightjar species have been shown to adjust their breeding phenology
311 in response to potential mismatches in environmental conditions (English et al., 2018). The shorter breeding
312 season in the Mongolian population could limit individuals' flexibility in breeding phenology (Halupka et al.,
313 2021). Therefore, it may be advantageous for Mongolian nightjars to arrive early at the breeding grounds, in
314 order to increase individual fitness (Nilsson et al., 2013). In line with other studies on long-distance migrants (La
315 Sorte et al., 2013; Dodge et al., 2014; Nilsson et al., 2014), this may support our observation that Mongolian
316 nightjars, travelling longer distances than Western European individuals, increase spring migration speed in
317 order to reach their breeding sites as quickly as possible.

318

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

328

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

333

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340

341 **Declarations**

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346 **Competing interests**

347 The authors declare that they have no competing interests

348 **Ethics approval**

349 Research protocols were approved by the Mongolian Ministry of Environment and Tourism, license numbers:
350 06/2564 and 06/2862.

351 **Availability of data and materials**

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

354

355 **Authors' contribution**

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

359

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361 **References**

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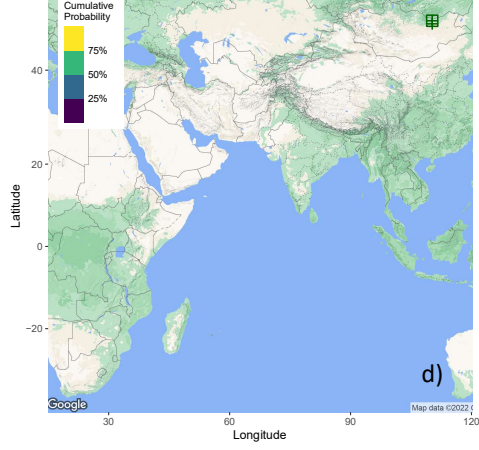
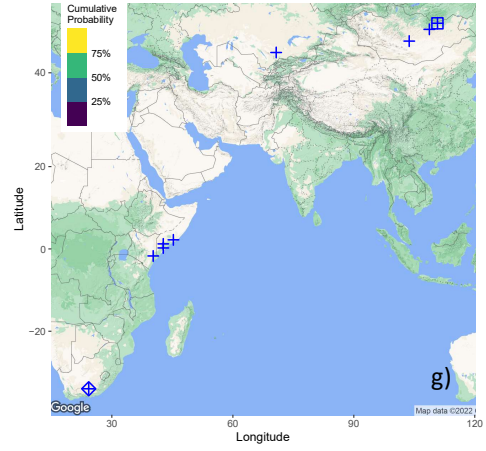
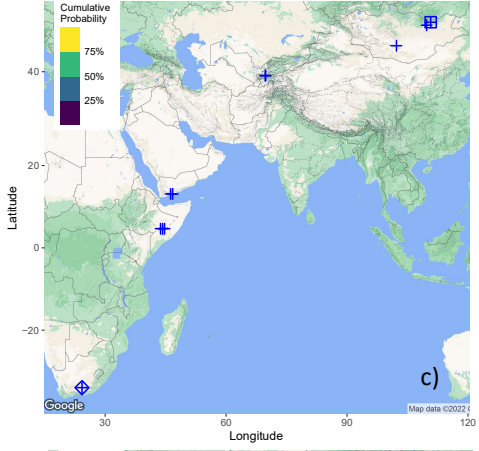
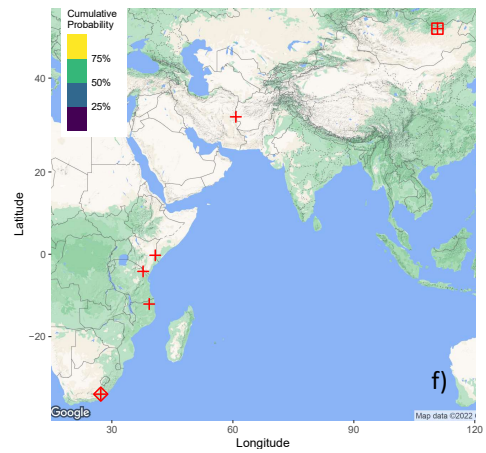
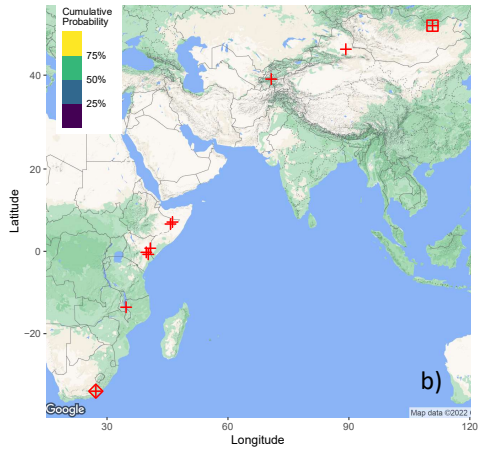
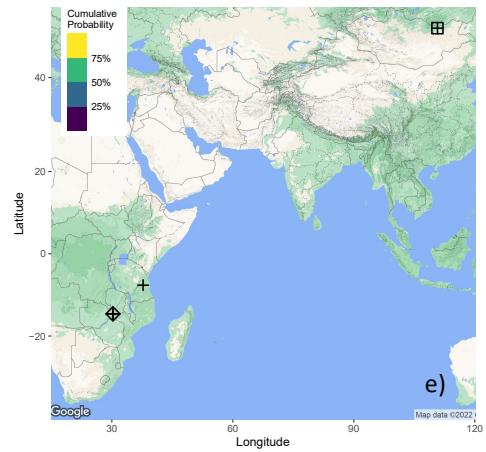
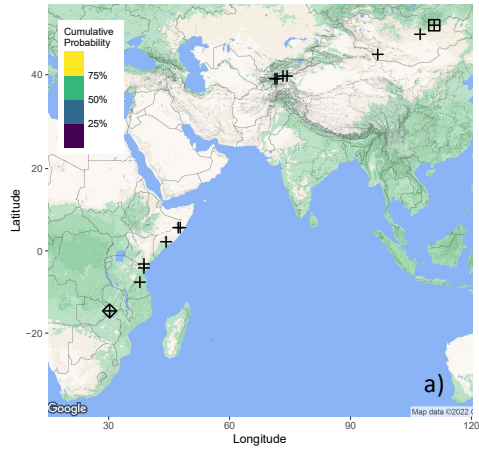
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497 **Figure 1:** Migration routes and stopover sites (stationary periods > 24 hours) of three European Nightjars
498 breeding in Eastern Mongolia. Maps show the shortest path modelled for autumn (a-d) and spring (e-g)
499 migration (bold lines), as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

504



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

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