Assessing the effects of global change on avian migratory pathways:
the case of the European Nightjar

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DOCTORAL DISSERTATION

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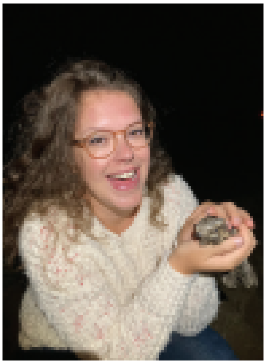



Foreword


Trying to describe the process of working on this thesis over the last few years in a coherent way seems like an impossible task. However, the one word that describes the experience the best to me is *fulfilling*. The opportunity to dedicate four years of my life to this research has been the most rewarding experience of my life. I can say I am proud of how I have grown and what I have achieved both on a personal and professional level and will look back on my journey as a PhD-student with nothing but satisfaction. What made the journey truly special though is the people who have been there to support me along every step of the way, all of whom I would sincerely like to thank.

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Of course, also a big thanks to my family, mostly for putting up with my absence from pretty much everything. Mama, thanks for making this possible. When your 6-year-old son was constantly pestering you with questions like "how it's possible that birds are able to fly?", you made the time to listen and encouraged that curiosity. Although it was not easy, thanks to you I was able to complete my studies and get where I am today, for which I will be forever grateful. Oma, your support has meant the world to me. Some of my fondest childhood memories are of us going out early in the mornings before school to go watch the local squirrels and jays foraging for acorns or spotting the local badger family crossing the road. Thanks for always being there and supporting me in every way possible. Sanne, even though I haven't been around as much as I would have liked in the last few years as I've missed some important milestones, you've consistently been the first to lift my spirits when things got tough and celebrate every success with me. I really want to thank you for always being there for me and being your cheerful self.

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Last but not least, Käthe, my girlfriend, my best friend, thanks for your immense support. I can’t really express into words what it has meant to me to have someone in my life who understands and supports my passion for this work in the way that you have. When I spent three consecutive weeks catching nightjars every evening without a break, your support may have understandably dwindled a little bit, but even from before the start of this crazy experience you’ve been there to encourage me to follow my dream. Your support was not “from the sidelines”, but over the years you’ve earned the title of honorary nightjar researcher, as you assisted with fieldwork, including recapturing a migration logger and sleeping in the back of the van. From helping out when I had my nervous breakdowns over filling in paperwork, to removing a dozen tick bites after a rough night in the field, you were always there for me. It has for sure not always been easy, you having your own PhD to worry about, trying to find a place to live together during the peak of the Nightjar fieldseason, while one of the many COVID lockdowns was in effect, trying to raise a tumultuous dog together, getting our first house together, but I wouldn’t have wanted it any other way and with anyone else but you. So, all I can say is thanks so much for everything, and cheers to our future together!

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Biodiversity in the Anthropocene

Human activities, resulting in misguided management of biological resources, are the most significant threat to species and ecosystems (McNeely et al. 1990). Because of this anthropogenic influence on the global environment it is often stated we have entered a new epoch: the Anthropocene (Williams et al. 2015). The aggregation of human actions aimed at satisfying needs and goals, such as fisheries, agriculture, logging, mining, infrastructure development, tourism, and transportation, have significant and often adverse impacts on nature, which the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) categorizes into five direct drivers: land-use/sea-use change, resource extraction, pollution, invasive and alien species, and climate change (IPBES 2019).

Anthropogenic influence directly affects more than 70% of the global land surface (IPCC 2019). For example, the extraction of biomass, fossil fuels, metal ores, and non-metallic minerals has doubled from 2005 to 2015, threatening biological dynamics and ecosystem functioning (Marín-Beltrán et al. 2022). Population growth, urbanization and the fact that our need for agricultural commodities continues to decrease (Tilman et al. 2011) have led to one third of the global land surface currently being used for cropping or animal husbandry resulting in major losses of forests, wetlands, prairies and many other natural land cover types (Zabel et al. 2019, Winkler et al. 2021, Potapov et al. 2022). Aside from direct loss, land-cover change has increasingly degraded and fragmented the remaining natural land cover types. Currently, an estimated 70% of the world's remaining forest is within one kilometre of the forest's edge (Haddad et al. 2015), and 20% of tropical areas still contain expansive forest areas larger than 500 km^2 (Potapov et al. 2017). This loss of surface area, increase of isolation, and greater exposure to human land uses along fragment edges initiate long-term changes to the structure and function of remaining fragments of valuable habitats (Lindenmayer and Fischer 2007).

Another result of human activities is the rising atmospheric concentration of greenhouse gasses (namely carbon dioxide, methane and nitrous oxide), which are causing worldwide increasing temperature trends exceeding natural variation (IPCC 2023). Human-induced warming reached 1°C above pre-industrial levels in 2017, with rises of 0.2°C per decade (IPCC 2018), resulting in long

term geophysical and biological changes such as retreating glaciers (Lutz et al. 2014), melting permafrost (Biskaborn et al. 2019) and changes in phenological responses across different taxa

(Cohen et al. 2018). Additionally, rising temperatures initiate a wide array of cascading effects such as changes in global precipitation patterns (Tabari et al. 2019) and the frequency and intensity of extreme weather events such as heatwaves, droughts, storms and floods (Cai et al. 2014, King et al. 2016, Wang et al. 2017). The effects of all of these changes can accumulate and interact resulting in further unexpected nonlinear change, with perhaps irreversible impacts on nature and nature's contributions to people and to society – including economic growth and food and water security (Burke et al. 2015, Friedrich et al. 2016, Pecl et al. 2017). Additionally, interaction with other direct drivers such as the spread of invasive species or disease may further exacerbate impacts on nature and society (IPBES 2019).

Biodiversity, defined by the 1992 United Nations Convention on Biological Diversity as "*the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems*", can be considered as the life support system for all life on earth, as all organisms depend on it for the air they breathe, the food they eat, and the water they drink (Tilman et al. 2014). People conceive of or relate to nature in multiple and often complementary ways: living from, with, in, and as nature. These different ways of valuing and relating to nature and biodiversity reflect people's different world-views (IPBES 2022).

Relational values, revolve around the meaningfulness of the relationships between nature and people, as well as among people within nature (Chan et al. 2018). These values emerge from the deep connections, responsibilities, and cultural identities associated with our interactions with the environment (Chan et al. 2018). They reflect the spiritual, emotional, and communal bonds that individuals and communities develop with nature, which are often rooted in traditions and cultural practices (Knippenberg et al. 2018). These values are especially prominent in non-Western cultures and are often closely intertwined with intrinsic values (Gould et al. 2019). The intrinsic valuation of biodiversity acknowledges the inherent worth of nature, emphasizing its significance for its own sake, independent of human interests. It recognizes that non-human entities deserve moral consideration in their own right (O'Connor and Kenter 2019). In contrast, biodiversity may be valued through its instrumental value in enabling the functioning of ecosystems and facilitating ecosystem services, defined as the processes and conditions of natural systems that support human activity (Singh et al. 2006).

However, as we are beginning to appreciate the variety and complexity of benefits that stem from nature and, more specifically, biodiversity, we are reaching a critical point in human history where biodiversity losses are accelerating due to increased human impacts. Currently, estimates of biodiversity loss suggest a contemporary extinction rate that is 100–1000 times greater than the pre-human background rate of approximately 1 extinction per 10 million species per year (De Vos et al. 2015, Lamkin and Miller 2016, Cowie et al. 2022). If human pressures on the environment remain as they are today, extinction rates could become 10 000 times higher compared to background levels (De Vos et al. 2015), paving the way towards the sixth mass extinction event in Earth’s history (Barnosky et al. 2011, Cowie et al. 2022).

A loss of biodiversity may not necessarily lead to a direct and equivalent loss of ecosystem functioning as more than one species may be involved in an ecological process or have the same functional niche (Rosenfeld 2002). However, when a species or its interactions are lost, this impacts the functioning and stability of the ecosystem this species is part of and, in turn, the services that this ecosystem provides to humanity (Cardinale et al. 2012, Hautier et al. 2015). It is essential to recognize that drivers of biodiversity loss often interact and amplify their effects, potentially leading to irreversible impacts on nature and society (Isbell et al. 2022). The complexity and the interconnectedness of these drivers necessitate a collective and comprehensive approach to address them (Wright et al. 2009, Moreno-Mateos et al. 2020). Preserving biodiversity, food security, and water resources necessitate collective efforts to mitigate and adapt to the underlying drivers of change. These efforts involve transformative changes across economic, social, technological, and environmental systems, incorporating sustainable practices, conservation strategies, and international cooperation. By actively addressing these drivers and developing a harmonious relation with nature, we can strive towards a future that simultaneously promotes human well-being and safeguards the long-term survival of ecosystems and species (Bulkeley et al. 2020, Coffey et al. 2022, Visseren-Hamakers et al. 2022).

As humans, we manipulate the Earth on a large scale (Deer 2019), distinguishing us from all other organisms (Meine et al. 2018). The necessity to reduce human impacts on biodiversity has received wide political recognition through e.g. The United Nations Convention on Biological Diversity (CBD), agreed at the 1992 UN Conference on Environment and Development and an increasing array of regional, national, and international policy mechanisms aimed at biodiversity conservation. Recognition by the general public is also widespread, with millions of people worldwide actively

supporting biodiversity conservation through membership of e.g. The Nature Conservancy in the United States, the Royal Society for the Protection of Birds in the United Kingdom or the World

Wide Fund for Nature (WWF).

However, despite all this support, current conservation of biodiversity is failing (Pattberg et al. 2019). Countries unite to set targets aimed towards the protection and conservation of natural systems, such as the Aichi Biodiversity Targets set in 2010, but the success in meeting these targets has been low and not uniform by region nor by target (Phang et al. 2020). While the vagueness and contradicting nature of such targets plays a role in this failure (Rees et al. 2018, Lemieux et al. 2019), the effectiveness of biodiversity conservation efforts is significantly hindered by numerous factors, including inadequate funding (Dempsey et al. 2021) and a lack mechanisms for prioritizing investment in endangered species management (Martin et al. 2018). However, there are also some success stories which indicate that when specific threats are removed, target species or populations may recover from being on the brink of extinction. For example, population trends of marine mammal species such as Northern Elephant Seal (*Mirounga angustirostris*) or Humpback Whale (*Megaptera novaeangliae*) have increased markedly following hunting bans (Lowry 2014, Bejder et al. 2016), and non-native predator control has helped the critically endangered endemic Kakï, or Black Stilt (*Himantopus novaezelandiae*), population in New-Zealand to recover from 23 to 169 adult individuals living in the wild (Keedwell et al. 2002). Even when species population declines are caused by a multitude of different factors, well thought out conservation programs, combining different actions such as rehabilitation, habitat restoration, reintroduction, population augmentation and invasive species eradication, can be effective (Sodhi et al. 2011, Bolam et al. 2023).

Biotic and abiotic changes resulting from interconnected aspects of global change will not only impact ecosystems at a local level but also have far-reaching consequences for global distribution patterns, which further contribute to e.g. ongoing climatic changes (Geyer et al. 2011). Global change introduces new and additional stresses on biological diversity, exacerbating existing threats such as habitat loss and fragmentation (Pimm 2008, Segan et al. 2016). It amplifies the complexities already involved in conservation efforts, requiring a comprehensive consideration of its implications. Recognizing the imperative of protecting biological diversity in the long term, it becomes essential for conservation initiatives to incorporate global change considerations (Coenen et al. 2011, Munera Roldan et al. 2022, Saunders et al. 2023). While numerous ideas and approaches have been proposed in the literature to integrate global change into conservation practices, their practical implementation remains limited due to various challenges such as the limited knowledge capacity, including insufficient information on the biological impacts of regional and local global changes, and the high degree of uncertainty associated with projections of global change (Geyer et al. 2014, Wu et al. 2020, Farooqi et al. 2022). However, proactive and evidence-based strategies that anticipate and adapt to global change are often more cost-effective and efficient than reactive approaches (Drechsler et al. 2011, Walls 2018). Therefore, there is an urgent need to cover the knowledge gap related to global change, biodiversity, and ecosystem functioning across the globe (particularly in under-represented countries and regions) through interdisciplinary approaches, in order to provide a sound scientific basis for effective conservation measures.

In evidence-based practice and policy-making, rather than merely relying on personal experience or anecdotes, practitioners and policy-makers make decisions and take actions informed by systematic and critical analyses of both their own and the world's previous experiences (Salafsky et al. 2019). This is critical to ensure decisions and actions are timely, relevant, measurable, and have the desired impact. In conservation practice and decision-making, collecting, and analysing appropriate knowledge and evidence is ever more important as it can contribute to solving some of the world's greatest social, economic, and ecological challenges (Sutherland et al. 2004). Since its conception "Conservation science" has broadened and diversified to draw on many fields of research, most notably from the social sciences and humanities as well as natural sciences (Bennett et al. 2017). Because of changes in the framing and narratives of conservation (Louder et al. 2021), the importance of science has become deeply entrenched within the mainstream conservation community as the vast majority of conservationists agree that conservation goals should be based on scientific findings (Sandbrook et al. 2019). However, while the importance of science in conservation is undeniable and broadly recognized, there are still major knowledge gaps in our understanding. There are few data on the status, trends, or functional importance of underrepresented taxa such as micro-organisms, invertebrates, and many plant groups (Titley et al. 2017). Even our knowledge of relatively well-known groups, such as vertebrates, is heavily biased towards species of temperate regions, while species in the tropics or migratory species are less well understood (Runge et al. 2014, Titley et al. 2017). Additionally, we still barely understand how different components of biodiversity contribute and relate to the provisioning of ecosystem services and resilience to environmental change (Mastrángelo et al. 2019).

An additional challenge lies in maximizing utilization and impact of existing research (Fabian et al. 2019, Roche et al. 2022). Across disciplines such as restoration ecology, climate science, and ecosystem management, science has failed to influence the decision-making process in meaningful ways (Nguyen et al. 2022). Although the effective uptake of knowledge to inform conservation decisions and action around the world is hindered by multiple barriers, such as cultural and institutional differences between functional communities (e.g., science and policy), mismatches in scales, timelines and timing, lack of relevance, and applicability of research to practice, the low priority given to biodiversity conservation is still considered to be most important (Nguyen et al. 2022). Mainstreaming and communicating science clearly to the decision- and policy-making arenas are, therefore, of paramount importance to bridge the knowledge-implementation gap in conservation science (Sutherland et al. 2020).

Animal migration

As a result of limited time, funding and people available to combat the current biodiversity crisis, conservationists have suggested taxonomic or geographic priorities for action. This prioritization includes approaches based on selecting areas with both the highest diversity and highest threat level, e.g. the recognition of biodiversity hotspots (Myers et al. 2000), selecting species based on threat level and phylogenetic value (Isaac et al. 2007), taking into account taxonomic, phylogenetic and functional diversity (Brum et al. 2017), social and cultural values (Whitehead et al. 2014), persistence of investments and cost-efficiency (Pienkowski et al. 2021) and integrating ecosystem services in conservation planning (Qiu et al. 2022). Migratory organisms represent an important group in the context of biodiversity conservation. Migration, which can be defined as "*a seasonal to and-fro movement of populations between regions where conditions are alternately favourable or unfavourable"* (Dingle and Drake 2007), results in the movement of large numbers of animals from one region to another link nutrient sources which can enhance primary productivity, alters soil characteristics, and has widespread effects on organisms within the food webs (Varriano et al. 2020). In certain ecosystems, migrating animals, such as cyprinid fish migrating from their natal lakes into connected streams to overwinter, serve as crucial seasonal sources of nutrients that sustain the ecosystems throughout the year (Moore et al. 2007, Hansen et al. 2020). Moreover, the transfer of nutrients by migrating species leads to complex changes in ecosystem functioning, providing stability and resilience which preserve ecosystem services (Bauer and Hoye 2014, Subalusky et al. 2017).

Migration is a wide-spread phenomenon observed across all taxa of the animal kingdom. Insects, mammals, fish, and birds are prominent examples of taxa that exhibit migratory behaviour which can entail continent-wide movements, or occur within localized regions (Milner-Gulland et al. 2011). The evolution of migration is a result of natural selection favouring migrating individuals over those who remain resident through fitness benefits, referring to an individual's contribution to the gene pool of future generations (Fudickar et al. 2021). To be advantageous, migration must enable animals to maximize their chances of survival and reproductive success amidst seasonal environmental changes, which is accomplished through a wide array of different benefits. For instance, migration provides refuge from predation for species such as common bream (*Abramis brama*) (Skov et al. 2011), and offers a means to escape unfavourable environmental conditions (Newton 2008, Streby et al. 2015). Additionally, migration allows animals to gain access to higher quality or more abundant food resources and escape competition (Somveille et al. 2015). However, an extended migration does come with its costs, which include the energy expenditure involved in transportation (Wikelski et al. 2003) and increased vulnerability to predation during the journey (Béguer-Pon et al. 2012). Given the high fitness costs resulting from non-optimized behaviour, migration is assumed to be optimized in order to minimize travel duration, total energy expenditure and predation risk (Alerstam and Lindström 1990, Alerstam 2011) so that survival and future reproductive performance are maximized (Alves et al. 2013).

Large-scale variation in ecological factors such as local weather conditions, the quality and quantity of food resources, intra- and interspecific competition, predation and parasitism can result in differing energy costs and benefits for different species and populations, driving the evolution of a wide variety of migration strategies (Alerstam et al. 2003). In no taxonomic group is this more evident than in birds. Avian migrants have evolved extremely diverse migration strategies, varying on a spatial, temporal and behavioural scale. Migration distances range from the more than 80 000 km round trip from the high arctic to the Southern ocean and back in Arctic Tern (*Sterna paradisaea*; Egevang et al. 2010) to a mean of 10 kilometres which Blue Grouse (*Dendragapus obscurus*) migrate from their montane wintering grounds to breeding grounds in the valleys below. Additionally, Migrants may complete their migration on very different schedules. Alaskan Bar-tailed Godwits (*Limosa lapponica*), for example, spend 8 days flying non-stop to reach their wintering grounds in New Zealand (Gill et al. 2009), whereas most other long-distance migrants may rely on stopover or staging areas, where they interrupt their migration for several days or weeks to spend time replenishing their energy reserves (Schmaljohann et al. 2022). All aspects of migration strategies, such as flight altitude and the timing of daily migratory flights, represent a spectrum of behavioural choices that entail different costs and benefits, which may differ between species and populations, and under different environmental circumstances. For instance, many migratory species opt to travel at night to evade predation and minimize dehydration (Alerstam 2009). However, for species utilizing thermal updrafts for energy-efficient soaring flight, diurnal travel is advantageous (Katzner et al. 2015). Selecting the optimal flight altitude depends on factors like wind assistance, which reduces energy expenditure. Nevertheless, ascending to higher altitudes comes with its own costs, meaning the benefit of wind-assisted flight may only outweigh the costs for long journeys over ecological barriers (Erni et al. 2005).

As the match between availability of resources, and demand for such resources is so crucial in ensuring a successful migration, a significant proportion of phenotypic variance in migration behaviours is genetically hardwired and controlled by relatively rigid endogenous mechanisms which ensure that individuals engage in specific activities at the appropriate time and place in their annual cycle (Gwinner 1996a, Åkesson and Helm 2020). Support for innate endogenous programs controlling migration first came from observations of migratory restlessness, a pattern of directional movements in caged birds corresponding to orientation and the timing of the migration of their wild conspecifics (Eikenaar et al. 2014). This migratory restlessness under constant captive conditions occurs in a circannual cycle rhythm, but their period lengths are ca. 9–15 months, so that life-cycle stages usually drift to occur at earlier or later dates over progressive years (Gwinner 1996b, Karagicheva et al. 2016). In contrast, this drift does not occur under natural conditions, and life cycle stages recur annually at similar dates. Hence, it became clear that the circannual clock is able to function in interaction with other cues, such as fuel load, habitat availability or weather conditions that synchronize and modify its program (Cohen et al. 2012). Some degree of individual flexibility in decision-making about migratory scheduling, routes, or when and where to make stops is key as a means to respond to unpredictable or variable ecological conditions (Winkler et al. 2014, Åkesson and Helm 2020). Innate migration templates are therefore shaped into realised migration through a complex set of factors (Fig 1). Geographical location (Barboutis et al. 2022, López-Iborra et al. 2022), the kind of habitat (Buler and Moore 2011, Hadjikyriakou et al. 2020), food abundance and availability (Ferretti et al. 2019, Tattoni et al. 2019), the amount of fat stores (Gomez et al. 2017), density (Cohen et al. 2022), dominance status and competition (Stillman et al. 2021), predation risk (Skov et al. 2011), weather (Haest et al. 2018, Rüppel et al. 2023) and season (Nilsson et al. 2013) all work together to determine a migrants’ decision making process in optimizing its migration strategy through altering timing, altitude, speed and routes.

Figure 1: Schematic overview of exogenous factors influencing the endogenous migration program to form the realized migration (Adapted from Bairlein (2003))

In the age of ongoing and accelerating climate change and habitat degradation across the globe, it is crucial to understand the complex interplay among physiological, ecological, and behavioural mechanisms allowing birds to perform successful migrations. An improved understanding can help guide mitigation programs and aid in conserving migratory birds that presently experience alarming population declines in almost all regions of the world (Bairlein 2016, Rosenberg et al. 2019, Burns et al. 2021). The continent-wide migration of many bird species inherently entails vulnerabilities, as these migrants’ reliance on resources found in geographically distinct areas throughout the annual cycle may leave them particularly vulnerable to human-induced threats (Wilcove and Wikelski 2008, Robinson et al. 2009). Infrastructure associated with human development poses significant mortality risks, particularly for nocturnally migrating birds which may be attracted and disoriented by artificial light of roads and urban centres resulting in a risk of collision with buildings and other structures (Van Doren et al. 2017, Colling et al. 2022, La Sorte et al. 2022). Additionally, bird mortality due to powerline collision or electrocution has been shown to have significant population-level effects

(Bernardino et al. 2018, D'Amico et al. 2019). Illegal hunting is among the most significant direct threats to birds (Kirby et al. 2008), linked to population declines (Balmori 2019, Jiguet et al. 2019b) with hotspots of hunting occuring in for example Mediterranean island nations where large-scale passerine hunting persists (Raine et al. 2015, Brochet et al. 2016, Sebastianelli et al. 2020). Indirect anthropogenic threats include the conversion of natural habitat. The expansion of agricultural land has been linked to declines in migratory birds (Vickery et al. 2014, Walther 2016, Zwarts et al. 2018), and in association, the use of agrochemicals (particularly pesticides and fertilizers) may also affect species through toxicity (Eng et al. 2019), reduction in prey availability (Sánchez-Bayo 2019) and habitat degradation (Vickery et al. 2001). Climate change further exasperates this anthropogenic habitat alteration and degradation through e.g. increasing temperatures, flooding and desertification (Ummenhofer and Meehl 2017). Additionally, populations that travel long distances may be unable to adapt the timing of departure and other migratory behaviours to rapid climatic changes that occur elsewhere, causing a phenological mismatch between energy demand and suitable environmental conditions to support this demand (Tøttrup et al. 2012, Maggini et al. 2020).

Migratory birds have become an emblematic case study of the decline of animal migrations in general (Wilcove and Wikelski 2008). Numerous academic papers and books, such as the evocatively titled "Where Have All the Birds Gone?" (Terborgh 1989), exemplify the high level of concern over the conservation of migratory birds over the last decades. Initially, this conservation concern was spurred by evidence for large-scale population declines, as shown by e.g. Berthold et al. (1998) where trapping data collected between 1972 and 1996 were shown to reflect significant declines in populations of central European migratory songbirds. This trend has been persisting ever since in the Afro-Palearctic migration system (Sanderson et al. 2006, Hahn et al. 2009, Vickery et al. 2014), and has also been shown for Neotropic migrants in America (Robbins et al. 1989, Rosenberg et al. 2019) as well as for Australasian migrants (Studds et al. 2017). These declines have led to responses in the form of large intergovernmental and interagency task forces and conservation programs to promote conservation of migratory birds. In the Afro-Palearctic migration system two policy instruments focus specifically on the conservation of migratory landbirds and raptors, namely the African–Eurasian Migratory Landbirds Action Plan (AEMLAP) and the Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia, both initiated by the Convention on the Conservation of Migratory Species of Wild Animals. These agreements were adopted under the United Nations Convention on Migratory Species and provide frameworks for cooperation between governments and with other key stakeholders (including nongovernmental organizations, industry, and funding agencies), in order to take actions against threats like habitat loss and degradation, taking and trade, disease and collision risk (Baldwin 2011, Hensz and Soberón 2018).

Due to the expansive geographic nature of migratory behaviour, the protection of migratory bird species necessitates conservation efforts of a comparable scale (Martin et al. 2007). Actions undertaken within one particular region are insufficient to safeguard species that spend significant portions of their lives in other areas (Schuster et al. 2019), and should account for migrants dependance on the condition of other sites that may be geographically and politically distant (Runge et al. 2014, Guilherme et al. 2023). Therefore, in order to effectively conserve migratory birds, a comprehensive understanding of the spatial and temporal distributions of distinct migratory populations is of paramount importance (Marra et al. 2015). Unfortunately, substantial gaps in knowledge of the abundance, distribution, behaviour and demography of most migratory species have hampered strategic planning and led to uncertainty about the optimal allocation of conservation effort (Runge et al. 2014, Vickery et al. 2014). Advances in remote sensing and tracking technologies have increasingly enabled the unraveling of complexities within the life cycles of migratory birds (López-López 2016, Vickery et al. 2023), and are facilitating high-resolution mapping of anthropogenic impacts (Corbane et al. 2015, Pettorelli and Pettorelli 2019). Consequently, such research provides valuable insights for the design of conservation strategies, which are essential for the protection of migratory birds in the Anthropocene epoch.

The European Nightjar

The European Nightjar (*Caprimulgus europaeus*) is a long-distance migratory bird with a temperate breeding distribution ranging from Northwest Europe to East Asia (Fig. 2). Belonging to Caprimulgiformes, which includes around 120 species, the European Nightjar, like its relatives, is well adapted to a nocturnal lifestyle, sallying for flying insects from a perch or hawking in mid-air during twilight (Cleere and Nurney 1998, Delaunay et al. 2020). Historically, Aristotle mistakenly referred to them as "aigothèlas" or "goat-suckers" (*aix*, *aigos* goat; *thèlázo* to suckle), as he saw “a *bird larger than a Blackbird yet smaller than a Cuckoo, living in the mountains, active at night, slow, laying two eggs and approaching goats at night to suck their udders dry*”. Even though what he observed is likely to have been Nightjars foraging for moths and beetles in the proximity of goats, to this day Nightjars are referred to as *goat-suckers* in various languages: *Caprimulgus* (Latin), *Succiacapre* (Italian), *Chotacabra* (Spanish), *Geitenmelker* (colloquial Dutch) or *Ziegenmelker* (German).

Breeding
Passage
Wintering

Figure 2: Breeding (yellow), wintering (pink) and passage (blue) distribution of European Nightjar (Caprimulgus europaeus). Adapted from Birdlife International 2023a

The family *Caprimulgidae* comprises 89 species and has long been divided into two subfamilies, *Caprimulginae*, or true Nightjars, and *Chordeilinae*, nighthawks, based on morphological characters such as e.g. the presence of rictal bristles (Cleere and Nurney 1998). Recent molecular work indicates that Nightjars originated from the region surrounding the Indian Ocean, and subsequently diversified into the New World before recolonizing and radiating into the Old-World (Han et al. 2010, White et al. 2016). Reassessments of the phylogenetic relationships within *Caprimulgidae,* however, are strongly at odds with the traditional, morphology-based classifications and do not support the traditional subfamilies of *Caprimulginae* (Nightjars) and *Chordeilinae* (nighthawks) (Larsen et al. 2007, Han et al. 2010, White et al. 2016). Currently, four geographically isolated clades are recognized corresponding to South American Nightjars (*Eleothreptus, Hydropsalis, Lurocalis, Macropsalis, Nyctidromus, Nyctiprogne,* and *Uropsalis*), Central American Nightjars (*Phalaenoptilus, Antrostomus, Nyctiphrynus* and *Siphonorhis*) Old World Nightjars (*Caprimulgus*) and New World Nighthawks (*Chordeiles* and *Podager*). *Caprimulgus* is one of the largest genera of birds, comprising 55–57 species, and has, therefore, long been recognized as likely polyphyletic with species possessing no remarkable morphological characteristics being "dumped" in this genus (Han et al. 2010). However, to this day limited taxon sampling has obstructed a comprehensive generic revision. The species in this genus are distributed across the African, Asian, Australian, and European continent (White et al. 2016) and are usually associated with dry scrub habitats (Langston et al. 2007, Camacho et al. 2014, Jackson 2015, Paliwal and Bhandarkar 2020). The European Nightjar likely originated from the Afrotropics (Day et al. 2023), as the most closely related extant species, Rufous-cheeked Nightjar (*C. rufigena*), is an Afroptropic resident (Han et al. 2010), before colonizing Eurasia where suitable breeding habitat would have been available (Ponti et al. 2020). Currently six subspecies are recognized (*C.e. europaeus, meridionalis, sarudnyi, unwini, plumipes* and *dementievi*), broadly following an East-West distribution (Cleere and Nurney 1998). The distinction between sub-species is based on morphological characteristics such as body size, colour and size of white wing spots in males. However, a recent phylogenetic analysis based on mtDNA has found little association between genetic variation and the current classification of subspecies (Schweizer et al. 2020).

The species is a typical long distance palearctic migrant with an annual cycle consisting of three major life-history events, breeding, moulting and migration, which are separated by time and location . Breeding Nightjars are closely tied to open semi-natural habitats with sparse trees, as well

as in plantations and other low-nutrient habitats, associated with sandy soils (Cramp et al. 1985; Conway et al. 2007; Langston et al. 2007a; Evens et al. 2017c). They belong to the guild of aerial insectivores, hunting for flying insects such as moths and beetles through sallying from a perch or during continuous flight (Cramp 1985, Delaunay et al. 2020). As they are visual hunters, spotting prey against the illuminated nocturnal sky, foraging is mainly restricted to the crepuscular periods of dusk and dawn. Recent evidence however has shown how nocturnal activity and foraging is linked to increased light levels as a result of the full moon (Evens et al. 2020), as well as atmospheric light pollution (Evens et al. 2023). Adult male European Nightjars exhibit sexually dimorphic white patches on their wings and tails, which are displayed during courtship and territorial defence (Cleere and Nurney 1998). As in other species, such as e.g. Rock Sparrow (*Petronia petronia*; Griggio et al. 2010), these ornaments may impose a handicap on individuals, as they increase visibility to predators and susceptibility to feather damage. Preliminary work we conducted quantifying the size of these ornamentations indicate they are subject to sexual selection and may play a key role in sexual interactions as signals of mate quality (Unpublished results; see Appendix V). Nightjars are ground-nesting birds which lay their eggs on bare substrate with little to no modification to their nest’s surroundings (Berry 1979). The female usually lays two white, densely speckled eggs which she incubates for approximately 17 days (Cramp 1985). Approximately ten days after hatching, the female can leave the chicks to start a second brood, which may be fathered by a different male (Cresswell and Alexander 1990). Males may contribute to parental care by relieving the female from incubation duties at dusk, and taking over the rearing of the chicks until they fledge approximately 16 days after hatching (Schlegel 1967). However, the extent of male parental care seems highly variable (personal observation), warranting further investigation of nightjar breeding habits.

After the breeding season nightjars start their long-distance migration to sub-Saharan Africa, which evolved as an adaptive response to seasonality, maximizing survival during the resource-depleted non-breeding season (Salewski and Bruderer 2007, Winger et al. 2019). This has long been thought to have taken place at the at the end of the last glacial maximum (Larsen et al. 2007), but recent work suggests that this migratory behaviour likely evolved prior to the last-glacial maximum, with long-distance migration seemingly persisting throughout the Pleistocene (Day et al. 2023). Other species of *Caprimulgus* are known to undertake similar migratory movements, such as e.g. the Red

Necked Nightjar (*C. ruficollis*) which breeds in south-west Europe and north-west Africa, and travels to west Africa for the winter (BirdLife International 2023c), or the Gray Nightjar (*C. jotaka*) breeding

in Southeast Siberia and northern China which is known to winter in Indonesia and the Philippines (BirdLife International 2023b). Another group of species may migrate over shorter distances, such as the Rufous-Cheeked Nightjar which migrates seasonally within Africa, or may remain largely resident, such as the Sombre Nightjar (*C. fraenatus*), although the movements of many Afrotropical species remain poorly described (Holyoak 2001).

Current maps show the possible wintering range of European Nightjar to extend along the eastern coast of Africa from Kenya to South Africa and in the western Sub-Saharan region from Senegal to Cameroon (Holyoak 2001, Cleere and Nurney 1998; Fig. 2). However, this distribution is based on extremely limited sightings and recovery rates of ringed individuals within Africa and data to confirm current distribution maps and migratory routes for the continent are lacking (Wernham et al. 2002, Franks 2022). Starting with the work of Cresswell and Edwards (2013), and later Evens et al. (2017c), Norevik et al. (2017) and Jacobsen et al. (2017), research projects in the UK, Belgium, France, Denmark and Sweden started fitting European Nightjars with miniaturized geolocators and archival GPS devices in order to provide detailed and accurate information on their migration and movements. Initial findings revealed that Nightjars in western and northern Europe start their migration in August, arriving in discrete wintering areas located in the scrub dominated grasslands south of the equatorial rainforests, primarily within the Democratic Republic of Congo, Angola and Zambia, outside of the previously estimated wintering range (Fig. 1). During their sedentary stay on the wintering site, Nightjar moult the flight feathers of their wings and tail (Cleere and Nurney 1998). As flight feathers are worn and damaged they need to be replaced, which is costly in terms of energy and time (Jenni and Winkler 1994) and may compromise aerodynamics, insulation or camouflage, thereby affecting survival (Jenni and Winkler 2020). Many migrants therefore moult during the wintering period in order to avoid conflict with other energetically costly annual cycle events, namely reproduction and migration (Svensson and Nilsson 1997, Hemborg 1999). Our unpublished data show how Nightjars, upon their return to the breeding sites, frequently show incomplete moult in their secondaries, while primary moult is fully completed. This could serve to preserve wing surface area under time- and energetic constraints on moult, limiting detrimental effects on flight performance during migration (Kiat et al. 2018). Our data also suggest that the frequency of incomplete and asymmetric moult is higher in younger individuals, and in males compared to females (Appendix VI). In other species this same discrepancy has been linked to foraging efficiency, which tends to increase with age, as well as potential differences in migration schedules among age groups and sexes (Zuberogoitia et al. 2016, Adekola et al. 2021) which remains to be formally investigated in Nightjars.

Spring departure from the wintering site takes place in February, after which individuals arrive back at the breeding site in April-May. Nightjars converge near stopover zones in Southern Europe, Northern Africa and the Sahel region, the same stopover sites as a large number of other Afro palearctic migrants (Vickery et al. 2014), where they stay for a few days up to 2–3 weeks. European populations follow a clockwise loop migration pattern, with routes in spring being more western than in autumn, which likely serves as an adaptation to take advantage of seasonally available food sources in west Africa (Tøttrup et al. 2012) and suitable wind conditions when crossing the Sahara and the Mediterranean sea (Norevik et al. 2020). Recent studies have shown how nightjars' migration schedules and behaviour are further optimized in response to e.g. the lunar cycle. Increase in foraging activity has been linked to moonlit nights, likely driven by an increase in light-dependent fuelling opportunities (Norevik et al. 2019). Atmospheric conditions have been shown to drive flight altitude selection during migratory flight, as nightjars select flight altitudes where the general airflow is expected to be supportive (Norevik et al. 2021). Knowledge of en route behaviour, habitat requirements during the non-breeding season or key threats is, however, far from complete, making it difficult to ascertain possible population bottlenecks or constraints to population growth.

Figure 3: representation of the annual cycle of the European Nightjar (*Caprimulgus europaeus*), breeding in Western Europe. Adapted from Evens, 2019

Although current population trends show local increases, linked to conservation efforts in restoring semi-open breeding habitats (Conway et al. 2007, Feys et al. 2020), the population numbers remain low compared to those of the late 19th century (Langston et al. 2007). In contrast, several other populations in e.g. Switzerland and Austria continue to decline (Sierro et al. 2001, Wichmann 2004).

Because of the current and historic declines, the European Nightjar is listed in Annex I of the European Birds Directive 2009/147/EC. The most recent Belgian population estimates indicate a positive trend, and estimate the population at 600-1000 breeding pairs (Feys et al. 2020), although

this may be a significant overestimation since the species is notoriously difficult to monitor with traditional survey methods (Zwart et al. 2014, Evens 2019). Historic declines have been linked to the extensive afforestation of heathlands throughout Europe with pine plantations which took place during the previous century (Morris et al. 1994, Gregory et al. 2002). Based on preliminary analyses of 11 years of capture-recapture data from our study population in Belgium we were able to estimate survival rates at 0.66 for males and 0.57 for females, pointing towards an effect of disturbance or predation of breeding females (Appendix VII). It has also been argued that unfavourable ecological conditions during the non-breeding period could play a key role for the decline of the European breeding population of the Nightjar (Evens et al. 2017b) as e.g. droughts in the Sahel region between 1970-1990 resulted in declining population numbers of many palearctic migrants through both carry-over effects on reproduction as well as direct mortality effects (Winstanley et al. 1974, Bruderer and Hirschi 1984, Zwarts et al. 2009). For migrants like the European Nightjar threats can therefore occur over a great number of geographic regions, be patchy or variable, and often inconsistent in how they impact the ecology of the affected species. In times of unprecedented global change there is therefore an urgent need for a full annual cycle approach in assessing the extent of the effects of these changes on avian long-distance migrants (Marra et al. 2015).

The European Nightjar presents an interesting model species in this context. In broad aspects they are typical of palearctic migrants in that they rely on temporally restricted food resources at discrete stopover sites in southern Europe, northern Africa, and the Sahel region, where many other migrants converge (Hahn et al. 2009, López-Iborra et al. 2022). Insights into how Nightjars are affected by environmental changes throughout their annual cycle can therefore provide a basis for conservation efforts relevant for a wide range of threatened migratory species. However, when looking past the superficial similarities between long-distance migrants, it becomes clear that the way in which migrants are able to cope with changing environments are likely to be highly species specific and may vary in different ecological contexts, reflecting the large variation in migration strategies among birds. The value of studying a species like the European Nightjar therefore can also be found in its species-specific traits related to migration. While the migration of nightjars might at first sight seem similar to that of other long-distance migratory insectivores like e.g. Common Cuckoo (*Cuculus canorus*) or Common Swift (*Apus apus*), as these three species show similar broad spatiotemporal migration patterns (Jacobsen et al. 2017), from a behavioural point of view there are many fundamental differences related to their basic biological traits. For example while most insectivorous

(near-) passerine migrants travel during the night and forage during the day, European Nightjars' activity is exclusively limited to night-time (Lathouwers et al. 2022a). Their strictly nocturnal habits, excluding exceptional diurnal flights during barrier crossings (Norevik et al. 2023), poses an interesting constrain on daily activity patterns. Additionally, their foraging style, hunting for flying insects against a lit nocturnal sky through sallying and hawking, imposes further constraints on daily activity patterns as well as fine scale habitat selection. The unique sets of species-specific traits related to foraging, orientation, physiology etc. result in shaping how nightjars optimize their migration strategies in relation to their environment. Therefore, an understudied species like the European Nightjar is an ideal model system to gain fundamental insights into how avian migrants are affected by global environmental change.

Thesis outline

The overall aim of this study is to gain further knowledge on migration ecology of long-distance migratory birds in light of global change, using the European Nightjar as a study species. I test hypotheses related to Nightjar's migration ecology, including aspects of route choice, phenology, behavioural strategies, and habitat associations, as well as how these may be impacted by future global change. All these aspects were investigated in order to enable increased effectiveness of future conservation efforts for avian migrants. My findings can be found in this thesis, which is divided into the following parts: *Introduction, General Methodology, Ch. 1: Migration routes and phenology, Ch. 2: Migration strategies, Ch. 3: Annual cycle habitat selection, Ch. 4: Future habitat suitability, Conclusions and future perspectives, Preliminary research and References and Annexes.*

- *Introduction*, outlines the background and framework of this thesis.
- *General Methods*, provides information on the methodology that has been used for data collection and analysis. Additionally, we describe a collaborative application of novel approach which improves upon the accuracy of traditional light-level geolocation methods through the use of barometric pressure- and acceleration data.
- **Chapter one**, *Migration routes and phenology*. Using multi-sensor geolocators we describe the migration of an unstudied population of European Nightjar at the easternmost edge of its breeding distribution in Mongolia. The migration routes and phenology are compared with studied populations in Europe, identifying key differences between populations. We test the hypothesis that the increased migration distance in the Mongolian population results in a decreased stopover duration in order to maintain the spatiotemporal migration schedule optimized in accordance with temporally restricted food resources. The differences between populations are discussed in the context of global change and possible carry-over effects on life-history aspects and population dynamics.
- **Chapter two**, *Migration strategies*. Here we test the hypothesis. We use archival GPS logging data in combination with multi-sensor geolocation data to study how flight speed, travel speed, altitude, and time budgeting of migratory flight bouts and periods of foraging activity vary throughout different biomes encountered *en route*. We hypothesize that Nightjars vary these behavioural aspects during active travel stages of their migration, in order to optimize their migration strategy when faced with contrasting local environmental conditions, and we discuss the implications this may have in terms of their ability to cope with unforeseen changes in resource availability.
- **Chapter three**, *Annual cycle habitat selection*. We present a multi-scale investigation into the resource selection decisions of Nightjars during their full annual cycle. we examine intra annual variation in habitat selection patterns, testing whether Nightjars exhibit a

higher degree of selectivity in their habitat use on the breeding grounds compared to their non breeding grounds. Additionally, we investigate the variation in habitat selection across spatial scales. We hypothesize that selection of stationary sites from the landscape during migration is largely driven by general indicators of habitat quality while habitat selection within stationary sites is closely linked with optimal foraging conditions determined by proximity and configuration of suitable foraging habitats.

- **Chapter four**, *Future habitat suitability.* In the last chapter I present the results of a species distribution model constructed using GPS-tracking data and remote-sensed land-use data as environmental input to assess habitat suitability for Nightjars throughout their Western European flyway. Using projections of land-use change under an array of socio-economic scenarios, we aim to predict how the spatial distribution and gross amount of suitable habitat may change in the near future. We test the hypothesis that global land-use change patterns will lead to significant declines distributed heterogeneously across the flyway, with non breeding habitat being altered significantly more. Based on these results I discuss which effects this may entail in the context of the migration ecology of Nightjars and other long distance migrants.
- *Conclusions and future perspectives*, summarizes the results from this study. More specifically, it outlines how this study has contributed to new knowledge on the migration ecology of Nightjars and attempts to provide a general overview and discussion of how global change will impact Nightjars and other long-distance avian migrants. Finally, this part lists ideas for further research, which can provide additional insights into potential global change effects and improve the conservation of this species during different parts of its annual cycle.
- *References and appendices*, includes all references and additional information related to the different parts of this thesis, such as additional documents, figures and tables. Furthermore, the appendices include the results of three research topics outside the scope of this thesis. Owing to their enigmatic lifestyle, European Nightjars are notoriously difficult to monitor and survey, thereby limiting our fundamental comprehension of various aspects of their biology. Therefore, we used the data gathered throughout this, and previous, research projects to further our understanding into three critical aspects of their ecology: sexual selection, moult strategies, and life history traits.

Study areas

The European Nightjar has a wide breeding distribution spanning across the entire Palearctic region. In Belgium, we collected data in several study sites across the Campine region in the north-east of the country, which forms the core breeding area (Fig. 4). As part of a longstanding collaboration with the British Trust for Ornithology, data were shared from the British Trust for Ornithology’s Nightjar tracking project from populations in the United Kingdom (Fig. 4). Additionally, through a collaboration with the Mongolian Wildlife Science and Conservation Centre we were able to gather data from a Nightjar breeding population in east Mongolia (Fig. 4). Data gathered in Belgium and the UK were used in analyses of Chapter 2-4. Data from the Mongolian population were used in Chapters 1-2.

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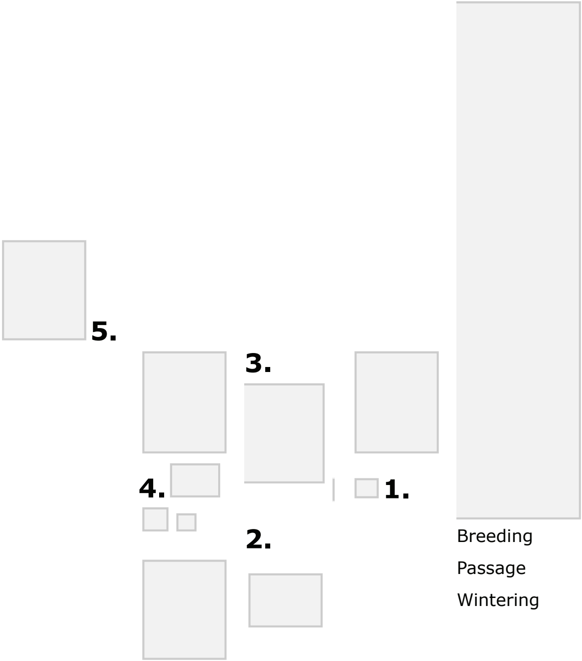


Figure 4: map showing study sites in Belgium (1-5), the UK (6-7) and Mongolia (8)

- **1. BELGIUM - National Park Hoge Kempen (Lat: 50.974336, Lon: 5.640367)** NPHK is located in the east of the province of Limburg and has recently expanded to an area of 12742 ha. The national park harbours a wide area of habitats including deciduous- and coniferous forests, grasslands and wetlands. Our activities were focused on the central part, specifically the Mechelse Heide and the Valley of the Ziepbeek. These represent the largest areas of continuous heathlands in the national park, which are interspersed and surrounded with extensively grazed grasslands, meadows, and pine forests. Management in these areas focusses on maintaining a mosaic of diverse structure through grazing, mowing, sod cutting and burning.

- **2. BELGIUM – Duinengordel (Lat: 51.064911, Lon: 5.596280)** In the central part of the province of Limburg the duinengordel forms a chain of land dunes, the largest of which is called the Oudsberg. This area, which has recently become part of the National Park Hoge Kempen, forms an important breeding site for Nightjars and comprises recently restored heathlands and sand dunes, surrounded by large pine plantations. Nearby, the military area of Meeuwen-Gruitrode is another main breeding site for Nightjars in Limburg, which is made up of large continuous heathland and remnants of extensively grazed grasslands in the surrounding intensively cultivated lands. Through sheep grazing, heathland habitat is maintained.

- **3. BELGIUM – Bosland (Lat: 51.174048, Lon: 5.331691)**
  Bosland is a 10000-ha nature reserve in the north-west of the province of Limburg, part of which has recently been assigned the status of National Park. The area holds a key corridor function, connecting heathlands in Belgium and the Netherlands. Our activities were focused on the center of Bosland, Domeinbos Pijnven and forests of the municipality Hechtel-Eksel, which is covered by a 2500-ha forest with open patches surrounded by other land use types, such as farmland, extensively cultivated grasslands and recreational areas. Recent management actions are aimed at restoring and connecting new heathland and sand-dune habitats. An additional study site in Bosland was Kattenbosserheide, a heathland area surrounded by pine plantations located near the valley of the Molse Nete.

- **4. BELGIUM – Kempense Heuvelrug (Lat: 51.210229, Lon: 4.875462)** Situated centrally in the Flemish Campine region, in the municipalities of Retie, Kasterlee, Herentals, Lille and Grobbendonk, the kempense heuvelrug is a 15 km long remnant of a large inland dune flanked by the valleys of the Aa river in the north and the Kleine Nete in the south. The area is dominated by pine plantations, surrounded by grasslands and agricultural land. Recent efforts to restore sand dunes and heathland patches in the area between Kasterlee and Herentals, where we focused our efforts in the region, have resulted in the return of breeding Nightjars after their absence caused by afforestation.

- **5. BELGIUM - Kalmthoutse Heide (Lat: 51.388281, Lon: 4.426500)** Kalmthoutse heide is located in the north-west of the province of Antwerp and is part of the larger Grenspark De Zoom - Kalmthoutse Heide which covers additional areas in the Netherlands. The site contains a varied landscape, consisting mainly of dry heathlands interspersed with sand dunes, wet heathlands, fens, and forest. We focused our activities near the Oude Gemeentebossen and Hazeduinen. which are comprised of large continuous heathland habitat managed through grazing with sheep and Galloway cows, sod cutting and mowing, preventing dominance of grasses and tree growth.

- **6. UK – Cloceanog Forest (Lat: 53.069281, Lon: -3.4728997)**

  Cloceanog Forest, located in northern Wales, supports large stands of plantation coniferous woodland of various ages, dominated by Sitka spruce *Picea sitchensis*, and interspersed with significant areas of non-forested habitats. It is part of the Welsh Government Woodland Estate, and is managed through felling and grazing, maintaining the mosaic of open and closed habitats. Coniferous plantation woodlands in Wales host approximately 9% of the U.K. population indicating the key importance of this site to Nightjars in both Wales and the U.K.

- **7. UK – Thetford Forest (Lat: 52.450000, Lon: 0.666667)**

  Thetford Forest is the largest lowland commercial forest in the UK, covering 185 km2 of Breckland, eastern England. This region is characterized by a semi-continental climate and sandy soils, and supports many species associated with heathland and ruderal land-uses. The forest constitutes part of the Breckland Forest Special Protection Area (SPA), designated under the EC Birds Directive (EC 1979) in 2006 for its internationally important breeding populations of Nightjar. The area is divided into discrete managed blocks of pine forests, surrounded by predominantly agricultural land and heathland.

- **8. MONGOLIA – Onon (Lat: 48.597944, Lon: 110.690167)**

  The village of Onon, named for the river Onon, is located in north-east Mongolia, in the Binder district of the Khentii province. The banks of the Onon river support diverse vegetation types, including willow groves, floodplain and riparian forests. The site near the village of Onon comprises steppe and forest steppe habitats which supports an assemblage of specialized species such as the European Nightjar.

Fieldwork

We captured Nightjars from 2009 until 2023 using ultra-thin mist nets and tape lures. We used

Ecotone Ultra-Thin mistnets with 0.08 mm black monofilament netting. These nets have a 20x20 mm mesh size and are 3.2 m high with four shelves. Depending on the terrain we used nets with a length of 15 m or 12 m. The tape lures used were Tronsmart Groove wireless speakers with a frequency range of 115 Hz to 15 KHz and 95 db sensitivity. During each ringing event, two nets were placed on four separate locations within the study site, which allowed us to catch individuals on four locations simultaneously. On each of the four locations, nets were set up in a 90°angle and placed near the edge of open habitats or in between high (2-5m) vegetation in open habitats. All nets were placed before dusk or dawn. In the former case, when nets were placed before dusk, tape lures were activated when the first Nightjar was heard. In the latter case, when nets were placed before dawn, tape lures were activated at least one hour before dawn. Capture sessions were ended within 60-90 minutes after the tape lures were activated. A combination of churring, calling and wing clapping sounds were used as tape lures, which were downloaded from www.xeno-canto.org and loaded onto a micro-SD card.

All (re)captured birds were removed from the mist nets as quickly as possible and bagged individually. Each new individual was marked with a unique alphanumeric ring from the Royal Belgian Institute of Natural Sciences (RBINS), with a diameter of 4.2 mm. Adult birds were also ringed with a plastic alphanumeric colour ring (inner diameter: 4.2 mm, height: 8 mm; www.colour-rings.eu) to facilitate the identification of birds on cameras or pictures and to aid in communicating about individuals. Subsequently biometric measures characteristics of each individual were recorded. The sex of the birds was determined based on the presence or absence of white markings, their presence being characteristically a male trait. As a result, the sex of 1CY, i.e. juvenile, birds could not yet be determined as they did not yet possess these markings. The age of each individual was determined based on moult patterns. Three distinct age groups can be identified: Juvenile (1CY), second calendar year individuals (2CY) and older than second calendar year individuals (>2CY). Calendar year (CY) refers to the age relative to the breeding season when the individual hatched i.e. a juvenile individual of class 1CY is an individual that hatched in the year when it was assigned to this category. Juveniles (1CY) do not yet possess the characteristically male white markings on their wing primaries and tail rectrices, and so they resemble the adult females. The juveniles were recognizable by the new plumage they possess, in which all wing feathers are of single age. In this juvenile plumage, the alula, primary covert and secondaries possessed a thin buff edge at the tips, while the tail rectrices possessed arrow-shaped dark marks. After moulting their plumage in the wintering grounds, adult individuals usually retain some feathers from the previous plumage, which can be recognized by their worn and sun-bleached appearance. When the feathers retained from the previous plumage were juvenile feathers, i.e. possessing the previously described thin buff edge or arrow-shaped mark, individuals were identified as second calendar year (2CY). Older than second calendar year were identified when feathers retained from the previous plumage were lacking the juvenile characteristics. When adult individuals had not retained any feathers from the previous plumage it was not possible to distinguish between 2CY and >2CY. These individuals were classified as >1CY, i.e. adult. Additionally, we recorded weight (using an electronic scale to the nearest 0.1 gram), wing length (the distance from the distal portion of the carpus to the tip of the longest primary feather with the wing chord flattened and straightened, measured with a stopped ruler to the nearest millimetre), stomach content (the volume of the stomach scored by feeling the area below the sternum; 0 [empty] – 5 [filled]), status of brood patch (presence of feathers on the abdomen scored by assessing moult state of the brood patch after blowing to lift the body coverts; 0 [absent] – 5 [fully developed]) and fat reserves (the presence of subcutaneous fat deposits in the furcular region and on the abdomen scored by assessing shape and colour after blowing to lift the body coverts; 0 [absent] to 5 [fully developed]). Finally, we scored moult (see Appendix VI) and photographed white wing and tail patches of adult males to be able to digitally quantify their size at a later stage (see Appendix V).

In an effort to maximize recapture rates, tracking devices (see below) were attached to adult male individuals. We selected individuals known to have established a breeding territory, or to have done so in preceding years, as male Nightjars return to the same territories between years (Cramp 1985, Raymond et al. 2020). This is an important bias to acknowledge in our results, as evidence points towards differential migration schedules between sexes and age classes (Cramp 1985, Evens et al. 2017a) this means our conclusions are not representative for females and juvenile individuals. Various attachment types are available to deploy tracking devices on birds, ranging from full-body harnesses to leg loops, tail mounts and neck-bands, with the species and the tracking device in question determining which attachment type is most suitable (Thaxter et al. 2014). Based on the methods of Evens et al. (2017b) we attached tracking devices dorsally between the wings with a full body harness made of Teflon ribbon or 2mm nylon string. However, even with a suitable attachment type, tracking devices should always be deployed with caution and reasoning as there is ample evidence that their use can impact birds’ survival, breeding success and behaviour (Lameris et al. 2018, Lopez et al. 2024). We employed the commonly used rule of thumb stating that the weight of the tracking device and attachments should not exceed 3-5% of a bird’s body mass (Kenward 2000). Nevertheless, there is still much debate and uncertainty concerning the ideal weight of tracking devices (Bodey et al. 2018). Depending on several factors such as the number of people present, the total number of caught individuals and the specific actions needed for each individual, birds remained in captivity for a range of 10 to 90 minutes. Birds were continuously monitored for signs of excessive stress such as gasping, laboured, or open-mouthed breathing. Severely distressed or injured individuals were taken into care with the wildlife rehabilitation centre of Oudsbergen where they were monitored and treated if necessary.

Tracking devices

For over 60 years, researchers have been using electronic tracking devices attached to individual birds to study various aspects of avian biology (Lord et al. 1962). The first technique used to track the movement of individual animals was VHF telemetry. In this method, a transmitter is attached to an individual, which emits a radio wave signal that can be detected by researchers using a radio receiver to determine the location. This practice started in the 1960s with large birds, able to carry heavy tracking devices, such as greater prairie chicken (Cebula 1966). Today, these radio transmitters may weigh as little as 0.2 g, meaning they can be used to study all but the smallest bird species, those weighing more than 7 g as, to avoid negative impacts on the tagged animals, tracking systems are limited to 3% of an individual's body mass (Kenward 2000). Conventional VHF tracking systems consist of a handheld receiver that the operator tunes to the frequency of the tag, and manually rotate an antenna until the audible tone was detected (McCurdy et al. 2019). The operator then moves to a new position and use triangulation to estimate the position of the individual. However, this is time intensive, requires detections from at least two locations to triangulate the tag position, and can be inaccurate, especially when the bird with the transmitter is in flight (McCurdy et al. 2019). The goal of gathering novel and unique data has continuously pushed tracking technology which has led to considerable advancements in terms of capabilities, size, and weight. Recently, telemetry systems have been automated, allowing for simultaneous tracking of a large number of birds (McCurdy et al. 2019). Using this technological advance, the Motus network was developed to track movement of birds using an array of detection stations, which, coupled with the low weight of VHF loggers, makes this a viable option for tracking large scale movements of small birds (Crewe et al. 2017).

Another development in avian tracking came in the form of satellite telemetry, which followed in the early 1970s (Craighead et al. 1971) and uses a transmitter linked to one or more satellites. Satellite telemetry incorporates the widely used Argos satellite receiver system. When the Argos satellites are within range of a transmitter, geographical positional fixes are calculated using Doppler shift; the signal frequency varies as the satellites approach or move away from the transmitter which allows locations to be calculated using the known position of the Argos satellites (Wilson et al. 2002). Raw location data are then sent by the Argos system to receiver station. Satellite tracking allows for more precise positional information than those derived from radio telemetry, and considerably reduces the effort involved in gathering these data (Miller et al. 2011). Nevertheless, there are weight limitations to this technology to mitigate negative effects on wildlife, necessitating a trade off between battery life, device capacity, weight, and applicability. Initial transmitters weighed up to 11 kilograms, limiting their use to the study of large mammals (Gillespie 2001). To allow for research on smaller species, geolocators were developed. These devices do not emit a signal but continuously measure the ambient light intensity. With the help of an internal clock, these geolocators gather information about the timing of sunset/sunrise and the duration of daylight and darkness, which can be used to determine longitude and latitude (Hill 1994). Although this technique is less accurate than satellite tracking, with error margins ranging from tens to hundreds of kilometres (Lisovski et al. 2012), the lower weight of geolocators revolutionized the study of birds (Bridge et al. 2011).

The accessibility of the GPS satellite network for non-military applications has led to another major improvement in satellite telemetry. Rather than sending signals from the GPS device to the satellite (as with Argos), a GPS device receives signals from minimum three satellites. As each satellite has a known position in space, and the timing and speed of the signal are known, GPS devices can calculate their position based on the signals they receive (Tomkiewicz et al. 2010). One advantage of GPS over Argos is that the positional fixes are more accurate, with an error of about 5 m (Wilson et al. 2002). A major drawback of GPS, however, is that GPS tags must be able to be reliably recovered from the animal, as the data are stored on board the tag (Wilson et al. 2002). Advancements in battery and solar power technology have reduced the device weight to around 1 gram, and if weight can be decreased, current models can be equipped with remote downloading or real-time data viewing capabilities through the Argos (Scarpignato et al. 2016) or GSM networks (Urios et al. 2015). Location determination through satellite telemetry or geolocation can now also be combined with other sensors such as a thermometer, microphone, barometer, heart rate monitor, accelerometer, etc., which can work in a complementary manner to increase the accuracy of the geolocator method or provide additional dimensions for research possibilities (Kays et al. 2015, Hofman et al. 2019) by shedding light on aspects of individual behaviour throughout the year such as daily patterns of categorized behaviour like flying, foraging and resting, and altitudes during flight (Liechti et al. 2018) or physiological responses of free-living individuals relative to the environmental conditions to which they are exposed (Linek et al. 2021).

In recent decades, the rapid evolution of these tracking devices has generated new scientific insights, especially concerning avian migration ecology. Much of what is known about bird migration has relied

on bird banding and re-sighting (Cohen et al. 2014a, Thorup et al. 2014). The ability to track individual birds' exact movements and locations improves the ability of conservation biologists and wildlife managers to protect birds and the places they rely on, through elucidating aspects such as migratory connectivity (Fraser et al. 2012, Hahn et al. 2013), phenology (Stanley et al. 2012, Sjöberg et al. 2015) or route choice (Evens et al. 2017c, Sokolovskis et al. 2018). During the course of this study, we used two different types of tracking devices:

Archival GPS-loggers

Archival Global Positioning Systems (GPS) record information from GPS satellites to determine latitude and longitude to a high degree of accuracy (i.e. within 10 m). These positions are subsequently stored on-board of the logger, requiring recovery, and downloading to acquire the data. We used the PinPoint 10 (Lotek) and nanoFix® GEO-Mini (PathTrack). These products have a weight of 1g which means they can safely be deployed on birds weighing more than 33 g. We programmed GPS-loggers to record 1-3 points per night, when Nightjars were presumed to be active, during active migration periods in September-November and February-April. During sedentary periods in December-January and May-August, they were programmed to record one position per week. These archival GPS-loggers additionally record altitude values, which are corrected for the height of the geoid above the ellipsoid using internal calculations, in order to estimate a flight altitude above mean sea level. Archival GPS data was used in analyses of Chapter 2-4.

Multi-sensor geolocators

Newly developed miniaturized multi-sensor loggers monitor light for geolocation, and simultaneously record a series of additional environmental variables. We used the SOI-GDL3pam loggers developed by the Swiss Ornithological Institute in collaboration with Bern University of Applied Sciences. The loggers consist of sensors for measuring ambient light intensity, air pressure, acceleration, temperature and magnetic field strength, and they weigh 1.4 g. We used multi-sensor geolocator data in analyses of Chapter 1-2.

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 a novel approach according to 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 refer the reader to Nussbaumer et al. (2023) 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 edited 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.

Remote sensing of the environment

Remote sensing techniques have become indispensable tools in the field of global change research. Their ability to provide large-scale, spatially explicit data on Earth's surface characteristics has revolutionized our understanding of complex and interconnected phenomena such as climate change and land-use change (Yang et al. 2013, Agilandeeswari and Sam Navin 2020).

The first step involved in remote sensing process is acquiring data. This can be accomplished with various sensors, including satellites, airborne platforms, and ground-based instruments which capture electromagnetic radiation across different wavelengths, ranging from visible to microwave, reflected or emitted by Earth's surface (Rycroft 2013). Once the data are acquired, pre-processing techniques are applied to ensure data quality and remove any artifacts or errors. These pre processing steps include geometric correction, atmospheric correction, radiometric calibration, and image registration (Agilandeeswari and Sam Navin 2020). After pre-processing, through image classification remote-sensed images can be used to classify e.g. land cover, as in the physiographical characteristics of the surface environment (Aplin 2004). Additionally, remote sensing allows for researchers to estimate measurements of ecosystem functions, such as the derivation of leaf area index (LAI) and net primary productivity (NPP) based on the normalized difference vegetation index (NDVI), which track dynamics in vegetation productivity (Kogo et al. 2019). The application of near continuous, long-term remote sensing measurements of key ecological parameters has emerged as an indispensable tool for monitoring ecosystems over significant spatial extents and temporal scales, facilitating comprehensive assessments of ecological dynamics in the context of climate change and land-use change (Yang et al. 2013, Potapov et al. 2017). By combining historical remote sensing data with socio-economic and demographic information, researchers can e.g. identify the drivers of land-use change and project future scenarios to inform land management and climate change mitigation strategies (Fasona et al. 2014).

Remote sensing has revolutionized the fields of ecology, biodiversity and conservation science, as it enables access to global, long-term, reliable information on spatio-temporal changes in the distribution of direct and indirect anthropogenic pressures to biological diversity; in the distribution, structure, composition, and functioning of ecosystems; as well as evidence of the effectiveness of various management actions (Pettorelli et al. 2014). Long-term satellite missions, like Landsat, Terra, Aqua Earth Observing System satellites, the Joint Polar Satellite System (JPSS) series or the

Copernicus satellite program, produce regional to global products characterizing land cover and atmospheric properties, offering a cost-effective and reliable means of obtaining comprehensive spatial information for large areas in a consistent manner and with regular updates (Schäfer et al. 2019).

Researchers are now combining wildlife-tracking and remote-sensing data to create models showing how individuals, animal groups, and species respond to interact with their environment (Edrén et al. 2010, Gschweng et al. 2012). In Chapter 3-4 we utilized a series of remote-sensed products to integrate with wildlife tracking data, aiming to draw inferences on the behavioural and ecological aspects of Nightjars' migration.

Adapted from:

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

Lathouwers, M., R. Nussbaumer, F. Liechti, B. Davaasuren, T. Artois, N. Beenaerts, N. Dendoncker, E. Ulenaers, & R. Evens. (2022). Journal of Ornithology. DOI: 10.1007/s10336-022- 02000-4

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 to reach wintering destinations in South-East Africa. After covering about 15,000 km during autumn migration, Mongolian Nightjars arrived 1 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.

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 2023a). 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. 2017c, 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. 2017c, 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.

Material and 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. 2017c). 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. 2017c, 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). This method reduces the uncertainty associated with geolocation solely based on light intensity data, allowing us to estimate positions more accurately throughout the annual cycle, even during the periods around the equinoxes.

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 of minimum 30 minutes (6 consecutive readings of flapping flight at 5 min recording interval) as migratory flight. Since the pressure analysis in the next step relies on high precision of thisclassification, we used TRAINSET (Kapoor et al. 2022) to manually edit the activity classification and the pressure timeseries to be matched

Subsequently, we used ERA-5 atmospheric surface pressure reanalysis data (Hersbach 2018) at a resolution of 0.50°, combined with pressure data recorded by the multi-sensor loggers, to construct a probability distribution map of the position of each stationary period. To do this we computed a raster for each stationary period, with an extent of latitude from 50 to -35 and longitude from 20 to 120, containing the mean square error between the pressure timeseries and ERA-5 data (MSE). We then computed a raster of identical extent containing the proportion of datapoints in the pressure timeseries which correspond to an altitude that falls between the min and max altitude of each grid cell (z_{thr}). These rasters were then combined to form a probability map according to the following formula:

where represents the standard deviation in pressure (set to two hPa) and is the threshold mask (set to one). Since the autocorrelation of the timeseries is not accounted for in this equation, we used a log-linear pooling weight =log()−1, where is the number of datapoints in the timeseries (Nussbaumer et al. 2022b).

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. These twilight times were then manually edited with TRAINSET based on a comparison with the theoretical twilight at the best match location. Light measurements recorded at the breeding site were used for in-habitat calibration, by modelling the zenith angle. We fitted the distribution of zenith angle of all twilights during the calibration period with a kernel smoothing function in order to account for possible bias. Twilights were grouped by stationary periods, as defined using the activity data, and a probability map was computed to indicate probability of observing the zenith angle of each twilight using the calibrated error function for each cell within the same grid as used for the pressure probability map. The probability distribution maps of all twilights belonging to the same stationary period are aggregated into a single probability map. Because consecutive twilight estimates cannot be assumed to be independent due to shading effects (e.g., topography, weather, vegetation), we use a log-linear pooling aggregator with weight = 0.1 to combine the probability maps of consecutive twilights for each stationary period (Nussbaumer et al. 2022b)

Based on the pressure and light probability maps, we used the shiny app GeoPressureViz (Nussbaumer 2022) to ensure that the recorded pressure data and light data were coherent for each stationary period. Furthermore, all nodes, i.e. points with a unique latitude, longitude and stationary period as derived from the previous steps, were filtered to only select nodes which are within reach of all other nodes based on flight durations and a realistic flight speed of 40-150 km/h. Additionally, only nodes within the 99% percentile were kept. We then computed the probability of transitions between stationary sites, implementing a gamma distribution (shape = 7, scale = 7) to model the probability of groundspeeds. By weighting the transitions between nodes associated with each stationary site, so called edges, with the minus of the log of their probability, we simulated 10 paths between the stationary sites and define the most likely trajectory as the shortest path i.e. the simulated path between stationary sites with the lowest summed weights of the nodes.

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% (Appendix I Table S1). 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.

40
Cumulative Probability

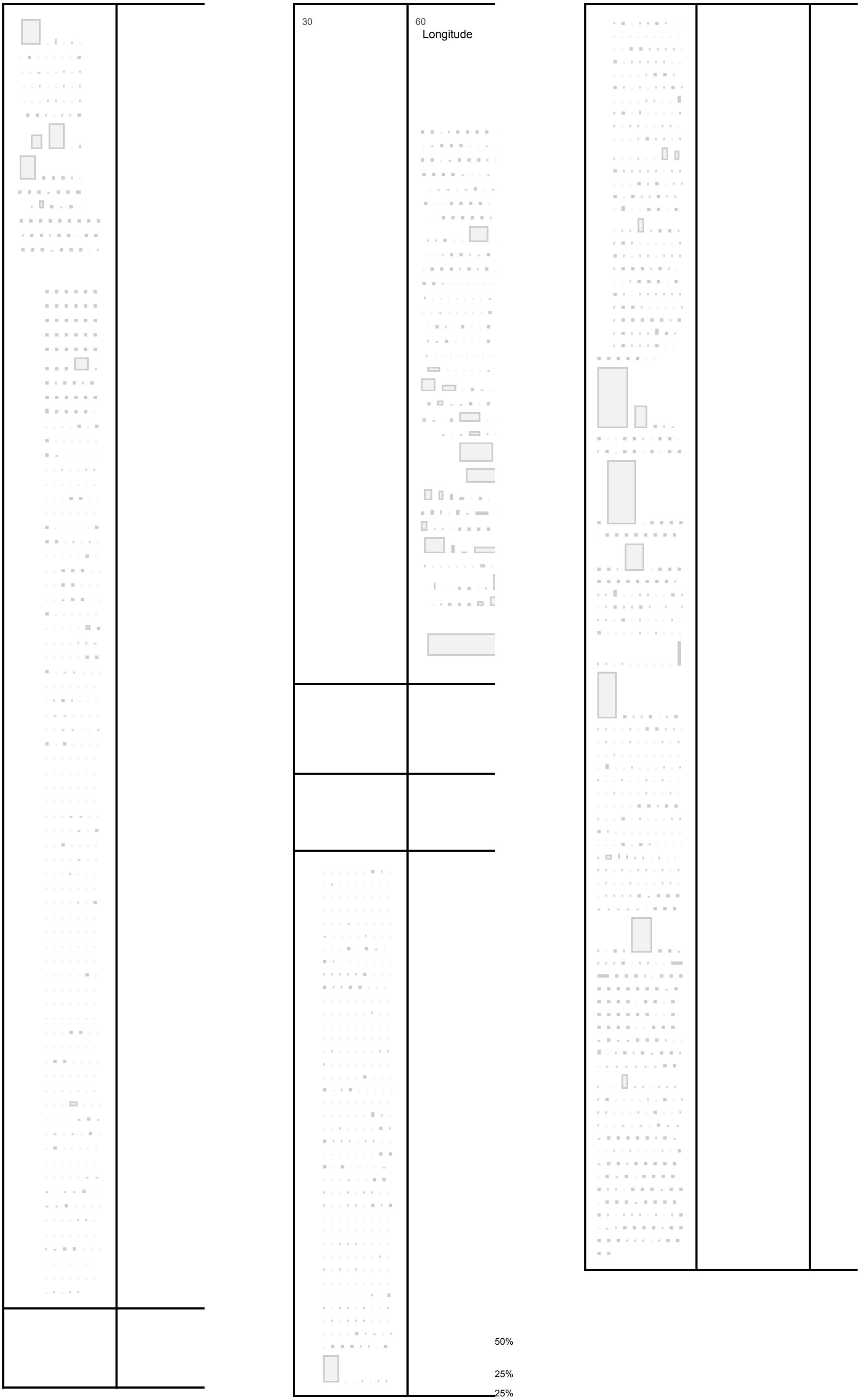
75%

40
Cumulative Probability

75%

50%

Latitude


30
60
Longitude
50%
25%
25%


20
20
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0
0
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120
Cumulative Probability
75%
40
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30 60 90 120 Longitude
Cumulative Probability
75%
50% 25%
50% 25%


Latitude
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20 0
Latitude
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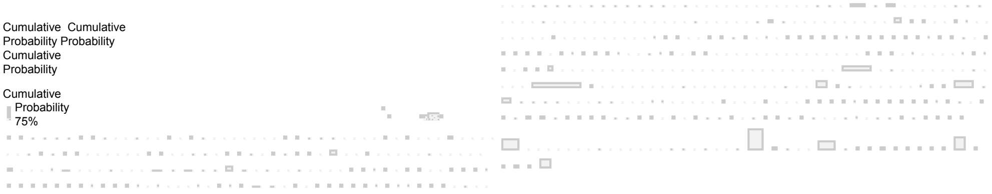
f)
30 60 90 120 Longitude
30 60 90 120 Longitude


Cumulative Cumulative
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Probability
Cumulative
Probability
75%

Latitude Latitude
40

40
75%

50%

Latitude
0

0

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Longitude
60
Longitude

30
30

75%

75%
50%

25%
40

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20

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Latitude
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120 120

40
50%
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25%

Cumulative
Probability

Cumulative
Probability
75%

20

Latitude Latitude
40

40

20

Latitude
0

−20

30 60 90 120
Longitude
30 60 90 120 Longitude

Cumulative
Probability

75%
50%
25%

−20

b) f)

d)

30 60 90 120 Longitude
30 60 90 120 Longitude
30 60 90 120 Longitude

Figure 5: Migration routes and stopover sites (stationary periods>24 h) 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 additional simulated paths (transparent lines) and stopover locations (stationary locations longer than 1 day; crosses), with corresponding cumulative probabilityestmates 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

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. 5) 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.

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,
End	29/11(27/11)	5	26/11-05/12	3	16/10 (28/10)	22	21/09 - 30/10	31 [1,
Duration	102	3	100-105	3	59	9	52-69	31 [1,
Travel days	61	8	54-69	3	22	1	21-23	18 [2
Stopover days	41	6	35-47	3	39	11	31-46	18 [2

Minimum migration distance (km)	14546	1121	13763-15830	3	7760	561	7133 - 8215	31 [1,
Migration speed (km/day)	143	12	134-157	3	135	23	119-162	31 [1,
Travel speed (km/day)	244	47	201-293	3	377	20	363-391	18 [2
Spring								
Start	23/03 (23/03)	9	14/03 - 01/04	3	23/02 (23/02)	7	16/02 - 02/03	31 [1,
End	01/06	/	/	1	01/05 (16/05)	27	01/04 - 18/05	31 [1,
Duration	70	/	/	1	71	14	55-82	31 [1,
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. 2017c) **2: (Jacobsen et al. 2017)** **3: (Norevik et al. 2017)**			

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. 5). 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 kilometres south or southwest from the breeding site (Fig. 5 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. 5 a,b,c). During this migration leg, two individuals had another short stopover, both lasting 2 days (Fig. 5 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. 5 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. 5 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 respectively (Fig. 5 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. 5 a,b), before continuing to their respective wintering grounds in Zambia and South-Africa (Fig. 5 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. 5 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. 5 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. 5 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. 5 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. 5 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. 5 g). This was followed by a flight in an eastern direction and two more stopovers in Mongolia for 5 days and on1e day (Fig. 5 g), before continuing north-eastwards to the breeding grounds (Fig. 5 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 assume 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 east, 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 (Asian Development Bank 2021). In April-early May, when Western European Nightjars arrive in their breeding sites (Cresswell and Edwards 2013, Evens et al. 2017c, Jacobsen et al. 2017, Norevik et al. 2017), the average temperature in Mongolia is still between 3 and 10 °C while in Western Europe the average temperature has reached 10-15 °C (Asian Development Bank 2021). 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 currently there are 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.

Adapted from:

Rush or relax: migration tactics of a nocturnal insectivore in response to ecological barriers.

Lathouwers, M., T. Artois, N. Dendoncker, N. Beenaerts, G. Conway, I. Henderson, C. Kowalczyk,
B. Davaasuren, S. Bayrgur, M. Shewring, T. Cross, E. Ulenaers, F. Liechti & R. Evens. (2022).
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Abstract

During their annual migration, avian migrants alternate stopover periods, for refuelling, with migratory flight bouts. We hypothesise that European Nightjars (Caprimulgus europaeus) adapt their daily migration tactics in association with biomes. We tracked the autumn migration of 24 European Nightjars, from breeding populations in Mongolia, Belgium and UK, using GPS-loggers and multi

sensor data loggers. We quantified crepuscular and nocturnal migration and foraging probabilities, as well as daily travel speed and flight altitude during active migration in response to biomes. Nightjars adopt a rush tactic, reflected in high daily travel speed, flight altitude and high migration probabilities at dusk and at night, when travelling through ecological barriers. Migration is slower in semi-open, hospitable biomes. This is reflected in high foraging probabilities at dusk, lower daily travel speed and lower migration probabilities at dusk. Our study shows how Nightjars switch migration tactics during autumn migration, and suggest Nightjars alternate between feeding and short migratory flight bouts within the same night when travelling through suitable habitats. How this may affect individuals' fuel stores and whether different biomes provide refuelling opportunities en route remains to be investigated, to understand how future land-use change may affect migration patterns and survival probabilities.

Introduction

Many animals show seasonal cyclical movement patterns between key habitats located thousands of kilometres apart. This behaviour allows migratory species to exploit high quality and abundant resources during different periods of the annual cycle, maximizing their survival and/or reproductive success (Alves et al. 2013). Because long-distance migrations are energetically demanding (Alexander 1998, Alerstam et al. 2003, Wikelski et al. 2003), it is critical that individuals balance their available energy reserves *en route*. Hence, migrants will attempt to optimize their energy budgets in response to resource availability by employing a range of different migration tactics (Alerstam 2011).

Among long-distance migratory birds, many species alternate stopover periods, for refuelling, with migratory flight bouts (Hedenström and Alerstam 1997). An individual's migration schedule is most likely endogenously controlled, but fine-tuned by external cues (Åkesson and Helm 2020). During migratory flight bouts, flight tactics can be shaped by resource availability and refuelling opportunities (Mellone et al. 2013, Jiguet et al. 2019a, Senner et al. 2020), which in turn is determined by environmental drivers, such as local weather conditions (Chevallier et al. 2010), topography (Verhelst et al. 2011) and habitat (Klaassen et al. 2008). When refuelling opportunities are limited, for example in deserts, over extended water crossings or ice sheets (Alerstam 2001), individuals may choose to undertake longer flight bouts and travel faster with unidirectional movements to minimize the time spent in these unsuitable areas (Alerstam and Hedenström 1998). Conversely, migrants may minimize energy costs by undertaking shorter, slower movements when suitable habitats for refuelling are available (Alerstam and Hedenström 1998). Additionally, avian migrants further minimize their energy expenditure by optimizing their flight altitude (Liechti et al. 2000), in response to wind, temperature, topography and other factors (Senner et al. 2018). This optimization involves a trade-off between energy spent on forward movement against climbing to a specific altitude at the beginning of a flight bout In order to reduce the total cost of transport by selecting an altitude with favourable conditions (Norevik et al. 2021). The majority of empirical studies on individuals' flexibility in migratory flight behaviour is focused on large-bodied migratory species, able to carry heavy tracking devices. Several species of raptors, for example, have been shown to migrate rapidly over unsuitable ecological barriers and travel slower in more suitable areas

(Strandberg and Alerstam 2007, Klaassen et al. 2008, Strandberg et al. 2009b, Mellone et al. 2013, Hadjikyriakou et al. 2020).

The miniaturization of biologging technologies has revolutionized animal tracking, allowing research on endogenous factors (e.g., behaviour, physiology, and orientation) and external factors (e.g., ambient temperature, barometric pressure) influencing bird migration for even the smallest migratory passerines and near-passerine species (Backman et al. 2017, McKinnon and Love 2018). Here, we aim at investigating how biomes affect migratory flight tactics in a small-bodied (<100 g), crepuscular insectivore, the European Nightjar (*Caprimulgus europaeus*, hereafter referred to as Nightjar). We hypothesise that individuals spend less time per day on active migration (i.e relaxed migration) in biomes which may provide foraging opportunities at dusk or dawn. Conversely, we expected more time to be invested in active migration (i.e., rushed migration) in biomes where such foraging opportunities are lacking. Using multi-sensor loggers of five individual Nightjars, we quantified daily migration and foraging probabilities during dusk, night, and dawn as well as daily altitude change. Additionally, using archival GPS-logger data we quantified daily travel speed and flight altitude. Investigating how these migration parameters are associated with biomes will provide us with insights into individual migration tactics in response to the landscape.

Material and Methods

Field methods

We conducted fieldwork in Mongolia (48.6°N, 110.8°E; 2018), Belgium (51.1°N, 5.5°E; 2015-2019) and the UK (52.5°N, 0.7°E; 2015-2018, 53.1°N, -3.5°E; 2018-2019). These sites were selected to include individuals from longitudinal extremes of the global distribution range of the species. We captured Nightjars in breeding areas using ultra-fine mist nets (Ecotone, 12 × 3m) and tape lures (Evens et al. 2017b), marked each individual with a unique alphanumeric ring and fitted a data logger dorsally between the wings (Evens et al. 2017b, Evens et al. 2020). In total, we tagged 114 adult individuals, with 1.8 g Pathtrack Ltd. nanoFix or Biotrack Ltd. PinPoint-40 archival GPS-logger (Belgium and the UK) or a 1.2 g SOI-GDL3pam (Liechti et al. 2018) multi-sensor logger (Mongolia and Belgium; hereafter multi-sensor logger; for a list of deployments see Appendix II Table S1). The multi-sensor loggers contain sensors that recorded air pressure, ambient light intensity, air temperature and acceleration in 5-minute intervals and magnetic field in 4-hour intervals. The GPS-loggers record longitude, latitude, and altitude at 24-hour intervals at 00:00 GMT, when the birds were likely to be in flight (for specific settings see Table S1).

Estimation of migration routes from multi-sensor loggers.

From the recovered multi-sensor loggers, we estimated migration routes by combining flight activity data with light measurements. Multi-sensor loggers measure flight activity as the sum of the absolute differences in acceleration along the z-axis (Liechti et al. 2013), which allows the detection of flapping flights (Liechti et al. 2018). As such, we used an automated k-means classification algorithm to classify activity data into three categories: inactivity, low and high activity. This allowed us to define migratory flight bouts as periods (minimum 60 minutes) of uninterrupted high activity and the delineation of stopovers as periods of one day or longer where migration was interrupted, i.e. where no migratory flight activity was recorded (Dhanjal-Adams 2020).

We analysed light measurements using a threshold method to provide daily position estimates for the migration period (*sensu* (Lisovski et al. 2020)) with the R-package PAMLr (Dhanjal-Adams 2020). Initial position estimates were obtained by identifying sunset and sunrise events from the light intensity data. We used Hill-Ekstrom calibration, based on light-intensity measurements from the sedentary wintering period, to model the error in defining these sunrise/sunset events caused by shading of the light sensor (Lisovski et al. 2012). Initial position estimates during periods of stopover were grouped together and treated as a single location. Final position estimates were obtained using an Estelle model in SGAT (Wotherspoon et al. 2021) to refine initial location estimates based on Markov chain Monte Carlo (MCMC) simulations and provide a probability distribution around each estimate (two locations per day). In this model we included the following priors: the location where the tags were deployed, the model describing the error in twilight times, a distribution of probable flight speeds (relaxed gamma distribution of shape = 2.2 and rate = 0.08) and a spatial probability mask where stationary positions over water were not possible. We ran this model for 250 iterations to initiate, before tuning the model with the aforementioned priors (three runs with 300 iterations). Finally, to obtain the final position estimates the model was run for 2000 iterations to ensure convergence. Subsequently, we calculated the 97.5% credible intervals around these final position estimates.

Calculation of migration parameters

We only considered migratory flight bouts during autumn migration because most loggers only partially recorded spring migration. Autumn migration was defined as the period between the departure at the breeding areas and the arrival at the wintering areas (Evens et al. 2020). From the multi-sensor loggers, we excluded data from stopover days. For days containing migratory flight bouts, activity data (inactivity, low activity, high activity, migrating) were categorized into two binary variables: “migrating” (yes/no) and “activity” (yes/no). From previous studies, we know that high and low activity levels are likely associated with foraging behaviour (Evens et al. 2020). Hence, “activity” will subsequently be referred to as “foraging activity”. For each position estimate, information on the timing of day, night, and twilight (i.e., sunset and sunrise) were extracted using the “classify_DayTime” function from the R-package RchivalTag (Bauer 2020). We subdivided the daily activity into four time groups: day (from sunrise to sunset), night (from astronomical dusk to astronomical dawn) dusk (from sunset to astronomical dusk) and dawn (from astronomical dawn to sunrise).

Air pressure data recorded by the multi-sensor loggers, measured in hectopascals, were converted to estimated flight altitudes above sea level using the atitudeCALC function in the PAMLr R-package (Dhanjal-Adams 2020), according to the International Standard Atmosphere model (International Organization for Standardization 1975: ISO 2533:1975) utilising the following formula:

Where H = flight altitude above sea level (m), T_0 = temperature at sea level (K), L = lapse rate (temperature change per meter increase in altitude, deg/m), P = pressure recorded by the sensor (HPa), P_0 = pressure at sea level (HPa). We used the standard assumptions of P_0 = 1013.25 HPa, T_0 = 288.15 K and L = – 0.0065 deg/m (Sjöberg et al. 2018). These data on estimated flight altitude above sea level were subsequently used to calculate daily altitude change by subtracting the daily maximum and minimum estimated flight altitude above sea level.

GPS tracks were visually inspected and periods wherein directional movement was interrupted for at least one day were removed, in order to retain only travel segments (Evens et al. 2017c). From GPS data, we calculated daily travel speed, defined as the distance travelled between consecutive

observed locations in 24h interval periods (km/day). Second, we calculated flight altitude above ground level by subtracting the elevation of the landscape from the recorded altitude. The altitude of the landscape was derived from the CleanTOPO 30 arc second global bathymetric and terrestrial elevation dataset (Becker et al. 2009).

Grouping data according to biome

To analyse differences in migration tactics in response to biomes, a global classification of natural communities in a particular region based on dominant or major vegetation types and climate (Ricketts 1999, Olson et al. 2001), we extracted information from the Terrestrial Ecosystems of the World dataset version 2.0 (Dataset published by World Wildlife Fund) for each position estimate and GPS observation. GPS observations were assigned to biomes using the point sampling tool in QGIS version 3.10.10 (QGIS-Development-Team 2021). To account for the spatial inaccuracy of geolocator position estimates (Lisovski et al. 2020), we determined the most abundant biome in the 97.5% credible interval around each position estimate using the zonal statistics tool in QGIS.

The width of the 97.5% credible interval around geolocation position estimates on active migration days was on average 21.23 ± 9.01 degrees in latitude and 9.30 ± 2.14 degrees in longitude. While these credible intervals are large, the most abundant biome represented on average 61.73 ± 15.34 % of the surface area. In the East Atlantic flyway, the following biomes were the most abundant in the credible intervals around the different position estimates: “Temperate Broadleaf and Mixed Forests”, “Mediterranean Forest, Woodland and Scrub”, “Desert and Xeric Shrubland”, “(Sub)Tropical Grassland, Savannah and Shrub” and “(Sub)Tropical Moist Broadleaf Forest”. In the East Asia/East African flyway these were: “Temperate Grassland, Savannah and Shrub”, “Montane Grassland and Savannah”, “Desert and Xeric Shrubland” and “(Sub)Tropical Grassland, Savannah and Shrub”. Two position estimates from the East Asia/East African Flyway, one categorized as “Boreal Forest” and one as “(Sub)Tropical Moist Broadleaf Forest” were excluded from further analyses since these were the only recorded position estimates in these biomes. In further analyses we distinguished between two categories of biomes, namely ecological barriers, and hospitable biomes (*sensu* (Vansteelant et al. 2021)). The ecological barriers include the "Desert and Xeric scrub" and the "Mediterranean Forest, Woodland and Scrub" biome as well as the "Tropical Moist Broadleaf Forest" biome which is presumed to be a soft ecological barrier for migrating Nightjars (Evens et al. 2017c). Other biomes consist of semi-open habitats and are presumed hospitable biomes.