From the Alps to Africa: ecology and migration of Northern Wheatears (*Oenanthe oenanthe*) breeding at high elevation, with insights into an intra-tropical migratory system

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PhD Thesis

From the Alps to Africa: ecology and migration of Northern Wheatears (*Oenanthe oenanthe*) breeding at high elevation, with insights into an intra-tropical migratory system

Yann Rime
2024

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A male Northern Wheatear *Oenanthe oenanthe*, and the study site of Val Piora, Central Alps (© Yann Rime)

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Summary

The populations of Afro-Palearctic migratory birds are declining. These species are more sensitive to climate change than short-distance migrants or residents. Because mountain ecosystems are under increased pressure of climate and land-use changes, I investigated one of the few long-distance migrants breeding at high elevations in the Alps, the Northern Wheatear *Oenanthe oenanthe*. The first three chapters of this thesis are focusing on breeding-site ecology in the Swiss Alps and on the avifauna of alpine grasslands. In chapters four and five, I investigated migration of the Northern Wheatear. In the sixth chapter, I broadened the scope by studying a different migration system from the southern hemisphere.

In the first chapter, I identified drivers of nest-site selection and breeding success. Nests were more likely located at lower elevation on gentle, south-exposed slopes. Productive pastures interspersed with rockpiles and bare ground were preferred. As Wheatears are territorial, the surroundings of conspecific nests were avoided for selecting a nest site. Predation was the main driver of breeding failure. Breeding success seemed similar among years with strong inter-annual variation in spring onset, to which laying dates were adjusted.

In the second chapter, the focus shifted to foraging micro-habitat. My colleagues and I observed ringed Northern Wheatears between May and September. Wheatears preferred rocks and short vegetation throughout the presence at the breeding site. The snow front was favoured for foraging only upon arrival from migration, whereas bare ground played an important role while provisioning food for the chicks when the grass layer was high, and after the breeding period. Wheatears preferred the vicinity of burrows of Alpine Marmots *Marmota marmota*, where bare ground was available. The preference for heterogenous habitats on a small scale suggests sensitivity of Northern Wheatears to landscape homogenization due to intensification, or to bush encroachment as a consequence of land abandonment.

In the third chapter, I extended my research beyond the Northern Wheatear. I considered fine-scale and landscape-scale habitat preferences of co-occurring insectivorous species inhabiting alpine grasslands by conducting repeated surveys. The Water Pipit *Anthus spinoletta*, an alpine specialist, had higher densities on gentle, productive slopes, and lower densities in dense shrubs. Wheatears preferred open, south-exposed and gentle slopes with human-made rockpiles. While Wheatears avoided shrubs, the closely related Whinchats *Saxicola rubetra*, a species of conservation concern in Europe, preferred this habitat and had higher densities at lower elevations close to the treeline. Our results underline the importance of high-elevation pastures for the conservation of species that are declining in Europe, as long as low-intensity management maintains patchy habitats.

The following chapters focused on migration, starting with a comparative study in which migration routes and timing of Northern Wheatear populations in the Swiss and Austrian Alps were described. Using light-level geolocators, my co-authors and I compared their migration with a lowland population in Germany. Lowland birds returned earlier compared to birds from the Alps where spring onset is delayed. Wheatears from Switzerland and Austria often directly crossed the Mediterranean Sea, while birds from Germany migrated towards the Iberian Peninsula. All three populations overwintered in the Western Sahel.

In the fifth chapter, I used multi-sensor geolocators to investigate the movements of Northern Wheatears with unprecedented spatial and temporal resolution. Stationary sites were located with enhanced precision compared to light-level geolocation, by correlating the air pressure measured on the birds with global atmospheric pressure data. I identified the role of islands as optional stopover sites while crossing the sea, and I located the main stopover areas between the Mediterranean and the Sahara in the Atlas Mountains. Furthermore, atmospheric pressure data informed on flight altitudes, highlighting longer, faster, and higher flights above the sea and the desert as barrier-crossing behaviour. When the birds returned in May, local altitudinal movements towards the Alpine valley took place in response to unfavourable weather events with snowfall. I also unveiled unexpected diel movements towards roosts a few hundred meters uphill from the breeding territory.

The final chapter extended the new insights on migration to another system in the southern hemisphere, where bird migration is still poorly understood. I applied the analytic framework used for Wheatears to present the full annual cycle of a small-sized intra-African migrant for the first time. Based on multi-sensor logger data, I retrieved stationary sites, flight behaviour and migration timing from five Woodland Kingfishers *Halcyon senegalensis* breeding in South Africa. These birds tracked rainy seasons in both hemispheres, migrating 4000 km north to the same area in South Sudan, where they found habitats similar to those at the breeding site. Migratory flights occurred at night like in Northern Wheatears but were shorter on average. Post-breeding migration was longer than pre-breeding migration. Woodland Kingfishers changed their flight behaviour above the Congo Basin, where I presumed that less suitable stopover habitat resulted in shorter stops as well as in faster, higher, and longer flights. This was a behaviour comparable to that of Wheatears crossing the Mediterranean Sea and the desert. Such findings became only recently possible for small birds by using multi-sensor loggers, which can be used to study intra-tropical and other migratory systems, promising major future advances for global migration research.

To conclude, this thesis establishes a link between the breeding ecology of the Northern Wheatear in the Alps and the other parts of its annual cycle, and further extending to another migratory system. It sheds light on the remarkable challenges faced by Wheatears, flying thousands of kilometres up to 5000 m in the sky, overcoming the heat of the desert and the dangers of the sea, all to reach our harsh mountains still blanketed in snow with freezing temperatures. Once the Wheatears complete their migration, they must then rear their broods amidst the constant threat of predation before preparing for the next journey, resulting in a truly awe-inspiring annual cycle.

General introduction

Migratory birds under threat

Long-distance, trans-Saharan migratory birds are declining in the Western Palearctic (Howard et al., 2020; Sanderson et al., 2006; Vickery et al., 2014, 2023). Afro-Palearctic migratory species are sensitive to environmental changes on the breeding grounds, at non-breeding sites and during migration (Atkinson et al., 2014; Jones & Cresswell, 2010; Ockendon et al., 2014). They are generally more vulnerable to climate change than are short-distance migrants (Both et al., 2010; Vickery et al., 2014). In particular, migration schedules of long-distance migrants are less flexible in response to fast environmental changes than those of species spending the boreal winter north of the Sahara, which can for example lead to a mismatch between the onset of breeding, constrained by arrival time and the optimal conditions for brood provisioning, which are shifting to earlier dates (Both & Visser, 2001; Gordo et al., 2005; Jones & Cresswell, 2010; Saino et al., 2011; Visser et al., 2004). Nevertheless, the relative contributions of the different stages of the annual cycle to population trends are often difficult to disentangle (Morrison et al., 2013; Ockendon et al., 2013). Therefore, obtaining general information on breeding-site ecology and migratory behaviour is a prerequisite to understand the mechanisms underlying population trends.

The importance of breeding ecology in the annual cycle of migratory birds

Migratory species face multiple challenges throughout their annual cycles. Local conditions at stopover and non-breeding sites can influence bird migration phenology (Gordo, 2007; Gordo et al., 2005; Haest et al., 2018; Saino et al., 2007), with effects carrying over to population declines (Both et al., 2010; Gordo et al., 2005; Ockendon et al., 2014). However, climatic conditions and habitat change at the breeding site are often the prime drivers in population trends (Morrison et al., 2013; Ockendon et al., 2013; Saino et al., 2011). To achieve successful reproduction, one of the main components of individual fitness alongside survival, birds must find a spatially suitable breeding site within a territory where sufficient resources are available to sustain themselves and their broods (Lack, 1968). They must also adequately time the onset of breeding to match with seasonal availability of resources (Perrins, 1970).

Modern tracking methods unravel new dimensions in bird migration

While investigating breeding ecology and habitat use at the breeding site can be achieved with field studies, following bird activities throughout their annual cycles remains technically challenging. The development of modern individual tracking methods recently opened new research opportunities to unveil migration behaviour of small songbirds (McKinnon et al., 2013; Nussbaumer et al., 2022). Beyond the importance of building fundamental knowledge on bird migration, advances in biologging allow to gather critical data for bird conservation by identifying population-specific non-breeding sites, migratory connectivity, as well as important stopover areas of migratory birds (Finch et al., 2017; Heim et al., 2020; Jiguet et al., 2019; Scarpignato et al., 2023; Webster et al., 2002). However, individual tracking comes with limitations: tracks of birds that do not achieve successful round-trip migration cannot be retrieved and are thereby not accounted for. Moreover, light-level geolocation accuracy is very limited and latitudinally uninformative around the time of equinox, when many Afro-Palearctic species undergo a north-south oriented migration (Lisovski et al., 2012, 2018). Due to weight limitations (e.g., Naef-Daenzer et al., 2001), GPS technology with high temporal resolution remains out of reach for small birds. Thereby, multi-sensor geolocators also recording atmospheric pressure are currently the best option to locate birds year-round. These devices inform on their flight behaviour and altitudinal movements with a fine temporal resolution (Nussbaumer et al., 2022, 2023; Sjöberg et al., 2018).

Alpine birds facing environmental changes

High-elevation ecosystems are undergoing major climate and land-use changes (Chamberlain et al., 2023; Scridel et al., 2018; Tingley et al., 2009). The effects of climate change are particularly strong at high elevation and high latitude, where seasonality is strong (Beniston, 2003; Brunetti et al., 2009; Gobiet et al., 2014). Hence, the impact on mountain and arctic bird communities and their habitats is higher than in other regions (Chamberlain et al., 2013; Sekercioglu et al., 2008; Virkkala et al., 2008). Lowland agroecosystems, where biodiversity suffers from a massive loss due to the intensification of management practices and an impoverishment in landscape heterogeneity (Benton et al., 2003; Donald et al., 2001), have attracted wide attention by researchers, whereas temperate mountain regions are considered as less impacted by human activities. Mountain ecosystems are often remote and difficult to access, which also explains why fundamental knowledge on the ecology of high-elevation species is scarcer compared to their lowland counterpart (Chamberlain et al., 2012). Nonetheless, recent and increasing changes in land-use occur at high elevation in European mountain ranges. Those are characterized by a polarization between agricultural intensification and land abandonment (Graf et al., 2014; Tasser & Tappeiner, 2002). Such changes in habitat composition affect the avifauna, potentially in interaction with the effects of climate change that remain difficult to disentangle (Chamberlain & Pearce Higgins, 2013; Graf et al., 2014; Laiolo et al., 2004). Thus, general ecological research on high-elevation bird species is needed to identify the relative effects of climate and land-use changes on their populations (Chamberlain et al., 2016). Nevertheless, not all alpine species are expected to respond to changes in a similar way, and specific traits such as migration behaviour might increase their vulnerability to future changes (Flousek et al., 2015; Tingley et al., 2009). Breeding in the Alps with a long-distance migration may impose combined constraints in response to environmental changes, calling for research on long-distance migrant breeding at high elevation.

The Northern Wheatear, Alpine bird and long-distance migrant

Most high-elevation birds in the Alps are sedentary, short-distance or altitudinal migrants. Only two high-Alpine birds migrate south of the Sahara: the Northern Wheatear *Oenanthe oenanthe* and the Rufous-tailed Rock Thrush *Monticola saxatilis* (del Hoyo et al., 2005; Glutz von Blotzheim & Bauer, 1988). All Northern Wheatear populations reach sub-Saharan Africa in the non-breeding season (del Hoyo et al., 2005). The nominal subspecies *O. o. oenanthe* breeds in diverse open habitats within an almost continuous range between Northern Europe and Alaska and overwinters in Western, Central and Eastern Africa, while the subspecies *O. o. leucorhoa* breeds in rocky tundra and grassland of Greenland, Iceland, North-Western Canada and Spitzbergen and migrates to the Senegambian region in Western Africa (Bairlein et al., 2012; Bulte et al., 2014; Corman et al., 2014; Delingat et al., 2008). The subspecies *O. o. libanotica* is found from the Mediterranean and Black Sea regions all the way to central Asia, including lowland steppe habitat and agricultural land (del Hoyo et al., 2005). The North-African Seebohm's Wheatear *Oenanthe seebohmi* overwinters in the Western Sahel and is now often treated as a distinct species (Svensson et al., 1999).

The Northern Wheatear is widespread in lowland northern and central Europe where it is typically breeding in extensive farmland, pastures, vineyards, gravel pits and coastal dune landscapes (Arlt et al., 2008; del Hoyo et al., 2005; Kurlavičius, 1998; Maumary et al., 2007; Tye, 1992). The northernmost populations breed in the tundra, coastal meadows, and pastures (del Hoyo et al., 2005). In Central and Southern Europe, the distribution is mostly restricted to mountains (Issa & Muller, 2015; Keller et al., 2020; Knaus et al., 2018). Population trends in lowland temperate Europe show a recent decline caused by habitat change, mainly due to agricultural intensification (Kämpfer & Fartmann, 2019; Keller et al., 2020; Schneider et al., 2012; van Oosten et al., 2015; Woodhouse et al., 2005).

In Switzerland, Northern Wheatears breed in open habitats above the treeline in the Alps and more locally in the Jura mountains, with an estimated population of 40’000-60’000 breeding pairs (Knaus et al., 2018). They are common in alpine grasslands and pastures interspersed with rocks and boulders, mostly on south-exposed slopes (Glutz von Blotzheim & Bauer, 1988; Knaus et al., 2018; Wartmann, 1985). They typically nest under a rock, in a stonewall or in a rodent burrow. Over the past 20 years, the populations in Switzerland underwent a rapid decline at elevations below 2400 m. a. s. l. and increased above 2400 m. a. s. l. (Hallman et al., 2022; Knaus et al., 2018). The species is not considered threatened in Switzerland (Knaus et al., 2021) where the population trends are stable or positive overall. This contrasts with the negative trends in other parts of Europe (Keller et al., 2020). The species is considered critically endangered in Germany (Gedeon et al., 2015; Kämpfer & Fartmann, 2019), the Netherlands (van Oosten et al., 2015) and is declining in Scandinavia (Byrkjedal & Kålås, 2012; Lehikoinen et al., 2014). This highlights the role of the Alps for the conservation of the species in Europe.

Northern Wheatears must adjust their annual cycle to a long migration and time-limited resources at the breeding site (Arlt & Pärt, 2007; Bastianelli et al., 2017). Rearing two broods is regular in the lowland populations of temperate Western Europe with longer breeding seasons (Conder, 1989; Kudernatsch et al., 2010; van Oosten, 2015), while the Northern populations normally only breed a single time, for example in Sweden (Arlt et al., 2008; del Hoyo et al., 2005). In Alpine populations, first broods are followed by a replacement after a brood failure. With a short breeding season, successful successive broods are exceptional (Sander et al., 2023), but have been documented (Corti & Melcher, 1958; Glutz von Blotzheim

& Bauer, 1988; Wartmann, 1985). The yearly adult survival probability was 0.43 (females) and 0.56 (males) on a British Island (Currie et al., 2000), or 0.42 (females) and 0.50 (males) in Sweden (Low et al., 2010), where survival of males varied between 0.34 and 0.62 depending on the habitat (Arlt et al., 2008). Females had a lower survival and an increased nest predation risk in Sweden (Arlt et al., 2013; Low et al., 2010). First year survival ranged between 0.17 and 0.32 in Sweden (Arlt et al., 2008) or 0.29 to 0.32 in the Netherlands (van Oosten et al., 2015). Wheatears have a relatively short lifespan, and the oldest recorded bird was 9 years and 7 months (Staav, 1998).

Clutch size is comprised between three and eight eggs: southern populations of *O. o. oenanthe* usually lay three to six eggs (Conder, 1989; Wartmann, 1985) and northern populations four to seven eggs (Moreno, 1989). *O. o. leucorhoa* and the Alaskan populations of *O. o. oenanthe* have up to eight eggs (Hussell et al., 2014; Kessel, 1989). Clutch size decreases through the breeding season (Conder, 1989; Currie et al., 2000; Moreno, 1989; Öberg et al., 2014). Reproductive success depends on habitat quality, weather conditions and predation rate (Arlt et al., 2008; Conder, 1989; Moreno, 1989; Schneider et al., 2012). Habitat features such as vegetation height affect both reproductive success and adult survival by influencing parental workload as well as predation risk (Arlt et al., 2008; Arlt & Pärt, 2007; Low et al., 2010; Schneider et al., 2012). Prey accessibility in the direct vicinity of the nest site is essential and enhanced when vegetation is shorter so that the birds can easily see and catch insects on the ground or from a perch (Tye, 1992; van Oosten et al., 2014). Northern Wheatears prefer heterogenous landscapes with perches and breeding sites close to short and sparse vegetation areas where they can forage (Alba et al., 2023; Müller et al., 2023; Sander et al., 2023). Hence, vegetation height in the surrounding of the nest site is of prime importance to define the suitability of a territory (Arlt et al., 2008; Arlt & Pärt, 2007; Low et al., 2010). Adverse environmental conditions while breeding, such as rainfall, negatively impact both reproductive success and adult survival (Öberg et al., 2015). The probability of successful reproduction is lower in second-year males, which arrive later at the breeding site and obtain lower-quality territories than older, experienced males (Pärt, 2001). In a Swedish population, birds breeding later had a lower fitness (Öberg et al., 2014). Breeding late in the season does not affect adult survival in the subsequent year (Öberg et al., 2014) but the survival of late-hatched chicks is reduced during the post-fledging, migration, and wintering periods (van Oosten et al., 2017).

The forgotten migratory systems: from Afro-Palearctic migration to intra-African migration

The focus of this thesis was the Northern Wheatear. Since bird migration is a diverse phenomenon worldwide, we extended the scope with another, poorly known migration system. Recent individual tracking advances focused on birds breeding in Europe and North America (e.g., Briedis et al., 2020; McKinnon et al., 2013). On-site studies on non-breeding, migratory birds in the Afrotropic are generally oriented towards afro-palearctic migrants (Gremion et al., 2022; Leisler, 1992; Lindström et al., 1993; Marcacci et al., 2023). In contrast, bird migration within tropical regions remains poorly studied (Chesser, 1994; Dingle, 2008; Huber et al., 2005; Jahn et al., 2020). This constitutes a substantial gap in our understanding of bird migration. Conservation challenges call for more research on intra-tropical movements: this is especially urgent on the African continent, subject to large-scale changes in habitat and seasonal weather patterns (Biasutti, 2019; Dunning et al., 2018; Maitima et al., 2009). Intra-African migratory systems are complex and diverse but poorly known. Based on the scarce existing knowledge, intra-African migration is often defined as seasonal movements within the Afro-tropical biogeographic realm, ranging from nomadism tracking temporary resources to typical migration featuring seasonally distinct breeding and non-breeding sites (Cresswell et al., 2008; Dingle, 2008; Hockey, 2000; Ivande & Cresswell, 2016). Intra-African migration often occurs over short distances (Garcia-Heras et al., 2019; Iwajomo et al., 2018), but also involves long-distance, trans-equatorial migratory flights (Jensen et al., 2006; Nussbaumer et al., 2022). Such systems also include birds migrating from the Northern part of the continent across the equator such as the Abdim's Stork *Ciconia abdimii* (Jensen et al., 2006) or Austral migrants leaving southern Africa to the Sahel region, like the Pennant-winged Nightjars *Caprimulgus vexillarus* (Del Hoyo et al., 1999). The movement ecology of large Afrotropical birds has been increasingly investigated during the past decades, including nomadic and resident species, typically raptors (Diekmann et al., 2004; Garcia-Heras et al., 2019; Zvidzai et al., 2020), as well as other species that are large enough to carry a GPS device (Iwajomo et al., 2018; Jensen et al., 2006; Lenz et al., 2011, 2015). Nevertheless, a critical gap of knowledge remains for smaller migrants covering large distances throughout their entirely African annual cycle. In this context, state-of-the-art multi-sensor geolocators allow to explore new dimensions in the movement behaviour of birds in these diverse and poorly understood migratory systems.

The Woodland Kingfisher: a long-distance migrant in an Afrotropical system

Woodland Kingfishers *Halcyon senegalensis* from Southern Africa can perform the same migration distance as Northern Wheatears from the Alps (Meier et al., 2022; Rime et al., 2023; Sander et al., 2021). They also use distinct breeding and non-breeding sites (Nussbaumer et al., 2022; Tarboton & Tarboton, 2014). While Afro-Palearctic migrants such as the Northern Wheatear reach the Sahel region in the dry season (Sander et al., 2021; Schmaljohann et al., 2016), most austral trans-equatorial migrants reach their non-breeding site in the rainy season. Furthermore, the Woodland Kingfisher's migration does not face major apparent migratory barriers compared to Northern Wheatears that cross the Mediterranean Sea and the Sahara Desert (Meier et al., 2022; Rime et al., 2023). Woodland Kingfishers are a common, non-threatened species in Sub-Saharan Africa. They use a wide range of open wooded habitats, from Savannah to forest clearings and gardens, with a preference for riverine woodland. Three subspecies are described: *H. s. cyanoleuca* from Southern Africa and *H. s. senegalensis* from the Sahel and Western Africa are migratory in large parts of their range. *H. s. fuscopileus* from central to western African equatorial forests is essentially described as sedentary (del Hoyo, J., Elliott, A., & Sargatal, 2001; Fry et al., 1988).

Scope of the thesis

In the context of habitat and climate change impacting migratory birds and their habitats (Bairlein, 2016; Vickery et al., 2014, 2023), it is necessary to understand the ecology of birds during their full annual cycle to envision the mechanisms underlying past, current, and future changes in populations. General information on breeding ecology, migration routes, flight behaviour, stop-over strategies and non-breeding site ecology is still lacking in many migratory species. I, and my collaborators, investigated two main aspects of the annual cycle in birds, breeding and migration.

For the first part on breeding-site ecology, this thesis focuses on a population of the Northern Wheatear in the Alps (Glutz von Blotzheim & Bauer, 1988; Knaus et al., 2018). As a crucial part of the annual cycle, breeding ecology was investigated by monitoring nests, assessing breeding success and mapping the surrounding habitat of the nests. The goal was to determine which environmental predictors influence nest-site selection and breeding success. To identify environmental factors predicting habitat use throughout the presence on the breeding grounds, the lack of information on small-scale foraging preferences in the Alps was addressed with an observational study during the pre-breeding, breeding and post-breeding periods. Since Northern Wheatears share their habitat with a broader community of Alpine grassland birds, mostly insectivorous species, a survey of all species present in the study area was conducted to disentangle species-specific habitat requirements. Habitat heterogeneity enhances biodiversity in lowland farmland (Benton et al., 2003). I expected similar importance of habitat heterogeneity in Alpine grassland, with species-specific habitat preferences (Jähnig et al., 2020; Mermillon et al., 2021).

To complete the annual cycle, this thesis also investigates migration ecology, primarily focusing on the Alpine population of the Northern Wheatear. Using light-level geolocation (Lisovski et al., 2020), migration routes of birds from the Swiss Alps were compared with two nearby central European populations, in the Austrian Alps and in lowland Germany, to unveil migratory connectivity and differential routes or timing in these populations. Multi-sensor loggers recording atmospheric pressure (Nussbaumer et al., 2022, 2023) were subsequently used for the first time in Northern Wheatears. The resulting data allowed to unveil migration routes, stop overs, flight behaviour, local movements, and non-breeding site ecology.

This thesis is complemented by a study on another long-distance migratory system in Africa, the Woodland Kingfisher's, applying similar methods using atmospheric pressure data. It is only recently that technical advances allowed to track small songbird-sized birds with light-weight loggers, opening new research opportunities (e.g. Hill, 1994; McKinnon et al., 2013; Nussbaumer et al., 2022). For both species, and for many more migratory systems in the future, the introduction of various sensor functions, such as pressor sensors and accelerometers, open new research possibilities. Using data from an international collaboration, I aimed to describe migration behaviour of this intra-African migrant in a similar way to the studies on Northern Wheatears, to review the literature on intra-African migration and to compare the migration of the Woodland Kingfisher with other intra-African migrants and migratory systems.

Thesis outline

Chapter 1. Drivers of nest site selection and breeding success in an Alpine ground-nesting songbird

Rime, Y., Korner, P., Helm, B., Müller, T., Amrhein, V., Liechti, F., Meier, C. M. (*in prep.*). Drivers of nest site selection and breeding success in an Alpine ground-nesting songbird
Revisions under review in *Journal of Ornithology*

During four breeding seasons, I and my collaborators monitored nest sites of the Northern Wheatear *Oenanthe oenanthe* at our study site of Val Piora in the central Swiss Alps. In a first step, I investigated how topography, vegetation structure and productivity influenced the selection of a nest site using conditional logistic regression. I then analysed the relationships between these environmental factors and breeding success. Further, I aimed at describing how breeding phenology varied within and between years and whether breeding success changed between first broods and replacement broods. I also investigated the level of tolerance of the species with respect to inter-annual variation of meteorological conditions. Since the preferred habitat is still widely available in the Alps and given the negative population trends in Western Europe, I discussed the role of the Alpine range as a refuge for the Northern Wheatear.

Chapter 2. Finding food in a changing world: Small-scale foraging habitat preferences of an insectivorous passerine in the Alps

Müller, T. M., Meier, C. M., Knaus, F., Korner, P., Helm, B., Amrhein, V., & Rime, Y. (2023). Finding food in a changing world: Small-scale foraging habitat preferences of an insectivorous passerine in the Alps. Ecology and Evolution, 13(5), e10084. DOI : 10.1002/ece3.10084

Together with my colleagues, I supervised the master student Thomas Müller in investigating the foraging habitat preferences of Northern Wheatears throughout their presence at a breeding site in the central Alps. We repeatedly observed 121 adult and juvenile ringed individuals between May and September. We applied Bayesian logistic regression models to investigate which habitat characteristics influenced foraging habitat selection on a fine spatial scale. We also investigated how habitat use varied temporally, as shifts in habitat preferences might have crucial implications in the context of changes in vegetation phenology and management practices. We then discussed whether the preferences for a habitat that is under pressure from land-use and climate change suggest that this Alpine bird species may be sensitive to habitat loss.

Chapter 3. Breeding habitat preferences and niche partitioning of declining insectivorous songbirds in Alpine grasslands

Rime, Y., Korner, P., Helm, B., Amrhein, V., Meier, C. M. (*in prep*.). Breeding habitat preferences and niche partitioning of declining insectivorous songbirds in Alpine grasslands.

While species-specific studies in chapters one and two informed on fine-scale habitat requirements of the Northern Wheatear at the breeding site, I considered here the entire bird community, including other species of conservation concern. Using repeated surveys within our study area, the study was designed to describe niche partitioning and species-specific habitat preferences in birds, especially insectivorous migratory species sharing the same Alpine grassland habitat matrix. On a small spatial scale, I identified different, but overlapping niches in the closely related Northern Wheatear, Whinchat *Saxicola rubetra* and Black Redstart *Phoenicurus ochruros*. The Water Pipit *Anthus spinoletta* did not show any preference at this scale. I then modelled the influence of topography, vegetation productivity and habitat composition on the density of the most common species within the study area, here at the scale of the landscape. These analyses aimed at characterizing habitat preferences in Alpine grassland species and how these preferences vary between species. This was a priority for Whinchats, which are declining migrants primarily specialized in hay meadows, but showed unexpectedly high densities in the low-intensity pastures of our study area. Habitat preferences of this species above the treeline were contrasted with preferences of other insectivorous inhabitants of Alpine grasslands such as Northern Wheatears and Water Pipits, the most common birds in our study area. These results highlight that preserving habitat heterogeneity in high-elevation pastures is necessary to ensure their role as a refuge for insectivorous species that are declining in lowland Europe.

Chapter 4. Locally adapted migration strategies? Comparing routes and timing of Northern Wheatears from Alpine and lowland European populations

Meier, C. M., Rime, Y., Lisovski, S., Buchmann, M., & Liechti, F. (2022). Locally adapted migration strategies? Comparing routes and timing of northern wheatears from alpine and lowland European populations. Journal of Avian Biology, e02932. DOI: 10.1111/jav.02932

This collaborative study compared the migration patterns of two Alpine populations with those from the lowland breeding population in Germany. C. Meier and I analysed the migration routes and timing of Northern Wheatears using light level geolocators tracks collected before this thesis started. F. Liechti and C. Meier collected data on the migration of the Northern Wheatears in the Swiss Alps and M. Buchmann, a German collaborator, equipped individuals in South-Western Germany and in the Austrian Alps. We aimed at identifying potentially differential migration timing and routes between populations under different seasonal constraints. Spatially, we wanted to disentangle if different crossing strategies of the Mediterranean Sea existed and if they were based on the origin of a bird. Temporally, we investigated if a difference in timing existed between lowland and high-elevation birds of central Europe. To show the relationships between migration timing and migration distance, and to investigate whether migration distance was the relevant driver of migration phenology, we compared the timing of the three studied central-European populations mentioned above to the migratory schedule of other populations.

Chapter 5. Multi-sensor geolocators unveil global and local movements in an Alpine-breeding long-distance migrant

Rime, Y., Nussbaumer, R., Briedis, M., Sander, M. M., Chamberlain, D., Amrhein, V., Helm, B., Liechti, F., & Meier, C. M. (2023). Multi-sensor geolocators unveil global and local movements in an Alpine-breeding long-distance migrant. Movement Ecology, 11(1), 1–13. DOI: 10.1186/s40462-023-00381-6

In this chapter, I used data from multi-sensor geolocators recording light intensity and atmospheric pressure to describe migration strategies of the Northern Wheatear with unprecedented spatial and temporal resolutions. By correlating the pressure measured on the birds with global atmospheric pressure data, migration routes, stopovers and non-breeding sites were identified. Furthermore, I described flight behaviour and compared barrier-crossing flights with other migratory flights and studied the movement behaviour throughout the annual cycle. The role of islands as stopover while crossing the sea was investigated and the main stopover areas between the barrier-crossing flights of the Mediterranean and the Sahara Desert were located. I studied if non-breeding movements occurred within the Sahel and if non-breeding locations suggested migratory connectivity. Flight behaviour was described both in autumn and spring, including precise migration schedules and a description of altitudinal behaviour in-flight. In addition, atmospheric pressure data allowed to discover the details of local altitudinal movements at the breeding site and how these movements varied during the presence in the Alps.

Chapter 6. Long-distance movements driven by rainy seasons across the equator in an intra-African migratory bird

Rime, Y., Osinubi, S. T., Liechti, F., Helm, B., Nussbaumer, R. (*in prep.*). Long-distance intra-African migratory birds tracking rainy seasons in two hemispheres.

For the first time, I and my colleagues applied similar methods as those used for Wheatears to present the full annual cycle of a small-sized intra-African migrant based on multi-sensor logger data from five Woodland Kingfishers. The data were collected by S. Osinubi in South Africa. Atmospheric pressure data allowed to retrieve stationary sites, flight behaviour and migration timing. I studied whether these birds would follow their seasonal ecological niche and if they would migrate across the Equator to do so, and how their migratory strategies compared to other migratory systems under different environmental constraints. I investigated non-breeding site connectivity, an unprecedented information in a long-distance austral migrant land bird. Furthermore, the role of the Congo Basin rainforest as a potential barrier compared to favourable Savanna habitats was examined, as well as the adjustments of migration strategy in relation to the underlying habitat. I further discussed how migration routes of Woodland Kingfishers from Southern Africa overlapped with two conspecific subspecies, of which one had similar ecological requirements and opposite breeding seasons.

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Chapter 1

Drivers of nest site selection and breeding success in an Alpine ground-nesting songbird

Nest habitat and nest with eggs of Northern Wheatear *Oenanthe oenanthe* in Val Piora (© Yann Rime)

Drivers of nest site selection and breeding success in an Alpine ground-nesting songbird

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Abstract

Birds breeding in high-Alpine habitats must select a suitable breeding site and achieve successful reproduction within a restricted time. During four breeding seasons, we monitored nest sites of the Northern Wheatear, a high-Alpine long-distance migrant. We investigated how ecological factors predicted the selection of a site for nesting within the home range, using conditional logistic regression. Birds preferred south-exposed productive pastures on gentle slopes, interspersed with non-vegetated ground and human-made rockpiles. The direct vicinity of conspecific nests was avoided, as were shrubby or north-exposed areas. We investigated if habitat also influenced breeding success. We analysed the impact of environmental factors on breeding success, which was primarily driven by predation. The probability of the brood fledging successfully decreased on north-exposed slopes or on areas with low coverage of non-vegetated ground. The vicinity of conspecific nests did not have a clear effect. Further, we describe how breeding success varied within and between years. Within years, replacement broods had a higher breeding success. The apparent absence of variation in breeding success between years and a delay of the breeding period in the year with late spring onset suggest a high level of tolerance with respect to inter-annual variation of meteorological conditions. Since the preferred habitat is still widely available in the Alps and given the negative population trends in Western Europe, the Alpine range might serve as a refuge for the Northern Wheatear, as long as low-intensity management and heterogenous habitats are maintained.

Keywords: *Oenanthe oenanthe*, Alpine grassland, conditional logistic regression, nest site selection, breeding success, replacement brood

Introduction

Organisms in seasonal habitats face multiple challenges when breeding within a restricted period with favourable conditions (Lack, 1968; Martin & Wiebe, 2004; Perrins, 1970). In temperate mountain habitats, the availability of suitable habitat and the abundance of food resources change over the breeding season and may vary between years (Martin, 2001). In a broader timeframe, Alpine habitats are under pressure from climate change and land-use modifications, leading to changes in seasonality and habitat structure and eventually to population declines (Chamberlain et al., 2013; La Sorte & Jetz, 2010; Lehikoinen et al., 2014; Scridel et al., 2018).

Breeding ecology is central to understand the underlying mechanisms of population trends. The selection of a suitable nesting site affects breeding success and is usually driven by environmental factors (Hinde, 1956; Martin, 1993). The factors related to the selection of a nest site are often similar to, but not necessarily the same as those influencing breeding success *per se* (Arlt & Pärt, 2007; Gilroy et al., 2011). The selection of breeding habitats often depends on the availability of suitable nest locations, but also on the suitability of the surrounding habitat, especially for foraging and feeding the nestlings (Barras et al., 2020; Brambilla et al., 2017; Resano-Mayor et al., 2019). While access to food resources is key to breeding success, other factors such as predation risk may influence the choice of a breeding site (Low et al., 2010; Martin, 1993; Schneider et al., 2012). Moreover, for bird species that rely on the same territory during their presence in the breeding region, the suitability of the habitat is also important during the pre- and post-breeding periods (Arlt & Pärt, 2008; Müller et al., 2023).

Topographic characteristics such as elevation, slope, and aspect often influence the micro-habitat and the microclimate of a nest and hence can influence incubation behaviour and breeding success in high-Alpine bird species (Camfield & Martin, 2009; MacDonald et al., 2016; Niffenegger, Dirren, et al., 2023). Habitat structures in the surroundings of the nest, including perches and shelter for the fledglings, can also explain nest site selection. Vegetation development, which generally follows snowmelt in Alpine environments, drives the abundance of food resources, but also their accessibility (Barras et al., 2020; Brambilla et al., 2017; Müller et al., 2023; Resano-Mayor et al., 2019). For ground-foraging birds, shrub and fast-growing grass reduce access to food. On the other hand, short swards and bare ground improve accessibility (Müller et al., 2023; Schaub et al., 2010; Tagmann-Ioset et al., 2012). Social factors, such as intra-specific competition, as well as predation, often influence nest site selection and breeding success (Lack, 1968; Martin, 1993).

We investigated the influence of environmental predictors on nest site selection and breeding success in an Alpine population of the Northern Wheatear. While the populations of this long-distance migrant have undergone a strong decline in Europe (Keller et al., 2020; López-Ramírez et al., 2024; van Oosten et al., 2015), the Swiss Alps are still a stronghold with positive trends overall (Knaus et al., 2018). This calls for a better understanding of the habitat selection and breeding success of this bird in changing Alpine ecosystems. In this territorial species, adults usually use the same area throughout their presence in the breeding region (Müller et al., 2023; Rime et al., 2023). The availability of nest sites is a limiting factor at lowland breeding grounds (Brooke, 1979; Kämpfer & Fartmann, 2019; van Oosten et al., 2014) but seems not as limiting in the Alps, where the species nests under stones, in burrows, rockpiles, or walls (Glutz von Blotzheim & Bauer, 1988; Knaus et al., 2018; Maumary et al., 2007; Wartmann, 1985). If nest sites themselves are sufficiently available, habitat around the cavities is expected to predict the selection of a nest site and to influence breeding success.

We surveyed nests in a high-Alpine valley during four breeding seasons to investigate the influence of surrounding habitat on the selection of nest sites and the breeding success of Northern Wheatears. We expected nests to be south-exposed and preferably located close to suitable foraging habitats, i.e. relatively productive pastures interspersed with rocks and high prevalence of bare ground (Müller et al., 2023; Sander et al., 2023). We predicted the habitat to influence breeding success, which is likely to be mediated by other factors such as predation. We further discuss how breeding success varied within and between years and how breeding phenology was related to inter-annual meteorological variation.

Methods

Study area and study species

Our study area was situated in Val Piora, Swiss Alps (46°33’N, 8°42’E, Figure 1). It encompassed 6 km^2 of alpine grassland interspersed with rocks, screes, rockpiles and low shrub, ranging from 1850 and 2450 m a.s.l. Most of the relatively productive parts of the area are grazed by milk cows under a low-intensity rotational management in July and August. The area is generally covered by snow between November and April. It harbours > 100 pairs of Northern Wheatears, i.e. >15 pairs / km^2, a typical population density in Alpine habitats (Knaus et al., 2018). Wheatears are present between May and September (most of the breeding birds arrive at the end of April or early May) and overwinter in the Sahel (Meier et al., 2022; Müller et al., 2023; Rime et al., 2023; Schmaljohann et al., 2016). Incubation lasts 14 days, and chicks remain in the cavity for 14 days before fledging (Conder, 1989; Glutz von Blotzheim & Bauer, 1988). Successive, successful broods regularly occur in lowland populations, generally in less than half of the breeding pairs (Buchmann et al., 2009; Conder, 1989; Öberg et al., 2014; van Oosten et al., 2017). In the Alps, Wheatears only have one brood, but in case of failure they generally attempt to renest (Müller et al., 2023; Sander et al., 2023; Wartmann, 1985). In our study area, observations and unpublished camera trap images suggested that typical predators were mustelids such as Stoat *Mustela erminea*, Weasel *Mustela nivalis* and Badger *Meles meles*. Fox *Vulpes vulpes* also predated nests, as well as Alpine Marmot *Marmota marmota*. This primarily herbivorous rodent seemed to predate nests opportunistically (Y.R., personal observations).

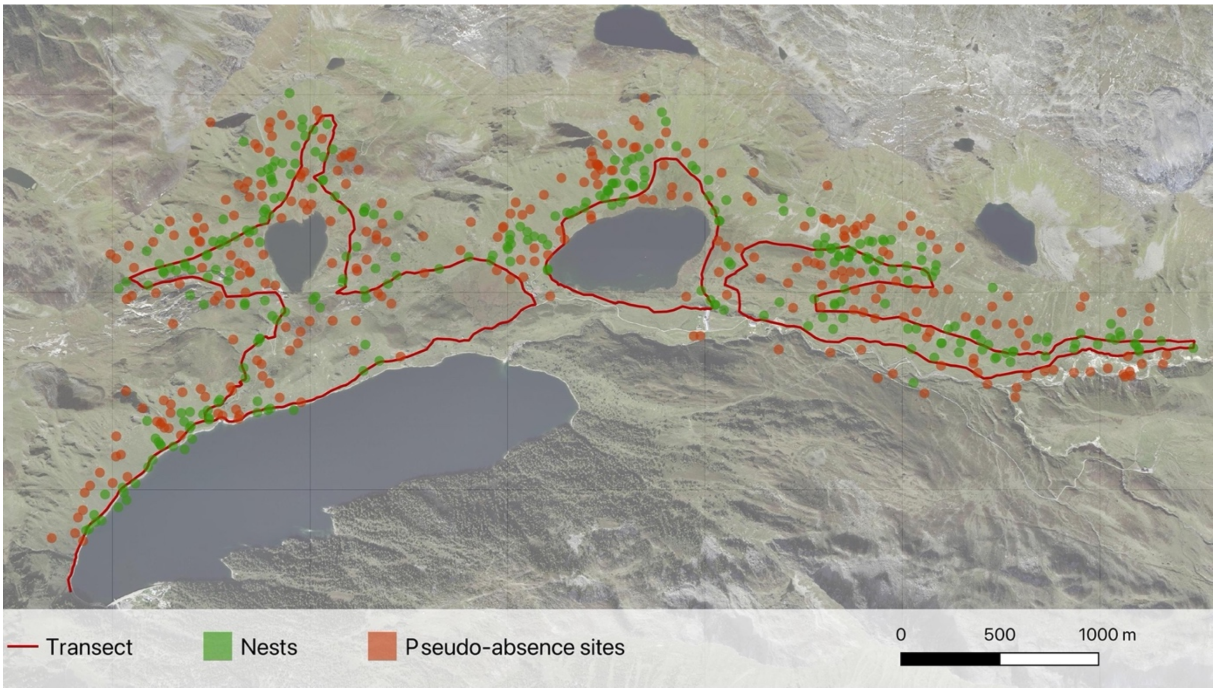

Figure 1. Map of the study area with the transect (red solid line), nest sites (green dots), and pseudo-absence sites (red dots).

Study design

We monitored nests during four breeding seasons between 2019 and 2022. Breeding success was assessed in 2020, 2021 and 2022. From mid-May to the end of July, we weekly surveyed the entire study area following constant transects (Figure 1). Nests were searched during the building phase, by following incubating females during their foraging excursions until they returned to the nest, or while both parents were feeding chicks. The coordinates of the nest were recorded in tablets using Qfield (QGIS Development Team, 2020). The nest content was monitored using an endoscope (Meier et al., 2022; Müller et al., 2023; Rime et al., 2023). Each nest was revisited weekly until fledging. At each visit, we assessed whether the nest was intact or failed. The start of incubation was calculated based on the age of the chicks. Age was estimated using reference pictures of chicks from known age with a precision of ± 1 day (as described in Öberg et al., 2014). Assessing productivity with a precise count of fledglings was difficult. Predation generally resulted in complete brood loss: hence, we considered a brood successful if at least one chick fledged. In case of predation, clear signs were generally visible, such as nest dug out, a damaged nest cup, presence of eggshells, feathers, or blood. Broods with unknown fate were included in the nest site selection analyses but excluded from analyses on breeding success. To describe breeding phenology, we summed the clutches laid by five-days periods in each breeding season. We distinguished between first broods and late broods, i.e. certain replacement broods, based on the gap between them using threshold dates in each year (9 June for 2020, 19 June for 2021 and 9 June for 2022; see Figure 4 in the results section for the annual phenology). Data on precipitation, temperature, and hours of sun exposure were obtained for each month of the breeding season from a nearby automated meteorological station at the same elevation (Robiei, 46°26'N, 8°30'E, 1898 m. a.s.l, distance to the study site = 16 km, data in the supplementary material, table S1).

Habitat variables

For each nest, we extracted remotely sensed habitat variables within a 25-m radius (Table 1). This radius was selected based on previous territory mapping (Müller et al., 2023). To compare the selected sites with the available habitat in the territory, we randomly generated one pseudo-absence location per nest site at a distance of 50 m to 200 m, where we extracted the same variables as we did for the nest sites (Table 1). Actual nest locations in any year of the study were excluded from the potential area for pseudo-absence sites. Given the high density of nests, we used only one pseudo-absence location per nest site.

Average values of the topographic variables (elevation, slope, and aspect) within the 25-m radius were extracted from the digital elevation model SwissAlti3D (Swisstopo, 2018) with a resolution of 0.5 m. Aspect was transformed into northness (cos(aspect)) and eastness (sin(aspect)). We calculated an NDVI (Normalized Difference Vegetation Index) raster from Sentinel 2 satellite imagery (ESA, 2015), with a spatial resolution of 10 m in Google Earth Engine (Gorelick et al., 2017). We applied a cloud filter (<50% cloud cover) and selected, for each year, the closest image to mid-May (beginning of snowmelt period and territory settlement) and mid-June (end of the snowmelt period and peak of the breeding period, Müller et al., 2023; Rime et al., 2023). Mean values within the 25-m radius were extracted in R using the *extract* function from the *terra* package (Hijmans et al., 2022). The proportion of non-vegetated ground, i.e., bare ground and stones, was calculated using a supervised image classification algorithm from the SCE plug-in in QGIS (QGIS Development Team, 2020) based on the 2022 "SwissImage" aerial pictures with 10-cm resolution (Swisstopo, 2022). Due to limitations of the algorithm in distinguishing between spectral signatures of the different types of vegetations (woody vegetation, grass, and trees), shrubs (*Rhododendron ferrugineum* and

Juniperus communis) were mapped manually in QGIS (QGIS Development Team, 2020) from the "SwissImage" pictures with a 10-cm resolution. We also did so for artificial rockpiles in the study area. We calculated the three-dimensional distance to the nearest nest of a conspecific in the same year for each actual nest site and pseudo-absence site. To do so, we used the Pythagorean theorem based on the horizontal distance and the vertical elevational difference from the SwissAlti3D DEM (Swisstopo, 2018).

Data

We surveyed 292 nests and retained 281 for the analyses: 55 in 2019, 93 in 2020, 68 in 2021 and 65 in 2022. Eight nests were discarded because they were located on the shore of a temporarily empty lake, which is not representative of a natural habitat in the Alps, and three had insufficient data. Out of 281 nests, we could assess the breeding success for 191 (6/55 in 2019, 68/93 in 2020, 58/68 in 2021, 59/65 in 2022). Only the 185 nests from 2020, 2021 and 2022 were used for modelling the probability of nest success.

Statistical analyses

All analyses were conducted in R, version 4.2.0 (R Core Team, 2023). Models were fitted in a Bayesian framework (Gelman et al., 1995; McElreath, 2018). We performed two analyses: First, we used a paired design comparing nest sites with pseudo-absence locations to model nest site selection. Second, we investigated the environmental drivers influencing breeding success, comparing successful with failed broods. We selected predictors (Table 1) based on *a priori* assumed biological importance (Korner-Nievergelt et al., 2015). The same predictors were included as fixed effects in both analyses. Dates of start of incubation were included only for breeding success.

All predictors were standardized (mean = 0, SD = 1). Non-linear effects were accounted for by including the first and second orthogonal polynomials of all variables using the *poly* function in the *stats* package (R Core Team, 2023). Model selection was only done for non-linear effects, by comparing the WAIC value with and without the quadratic polynomials of each predictor (Korner-Nievergelt et al., 2015). We retained the models with the lower WAIC and eventually excluded non-linear terms in the final models based on this selection. There was no strong collinearity among explanatory variables (all Spearman's correlation coefficients $|r_s| < 0.5$).

Nest site selection was modelled with nest sites (1) and the randomly generated pseudo-absence (0) as a binary response variable. To account for non-independence of the observations of a year, year was included as a random factor. We applied a conditional logistic regression using the function *stan_clogit* in the *rstanarm* package (Goodrich et al., 2020). We used uninformative priors (Berger, 2006; Kass & Wasserman, 1996). Presence and pseudo-absence pairs were defined as strata in the conditional logistic regression, which links the presence and pseudo-absence locations in the model. To interpret the effect of each variable on the nest site selection probability, we plotted predictions from the model relative to a reference, defined as the mean value of each predictor, assuming a 50% presence probability for the reference point. Such an arbitrary value is needed to produce effect plots since the conditional logistic regression does not estimate an intercept.

We modelled the breeding success in relation to environmental factors following Bolker (2019). We built a generalized linear model with a binomial distribution, using a modified logit-link function accounting for exposure time (the number of days a nest was active between two visits). Specifically, the model aimed to account for nests that failed before being found. We modelled the probability of a nest to be intact, i.e. without predation or abandonment, using the function *glm* from the *stats* package in R (R Core Team, 2023). The status of the nest at each visit (alive or failed) was used as a response, and the observation year was included as a fixed effect factor of three levels in the model (excluding the 6 nests from 2019 due to the limited effort in nest monitoring in this year). We present plots showing the effect of each predictor on the probability of nesting success, with the other predictors set to their means. For all estimates and effect plots, we present 95% uncertainty intervals using the 2.5% and 97.5% quantile from the posterior distribution (Korner-Nievergelt et al., 2015).

Table 1. Predictors used to model the nest site selection (presence compared to pseudo-absence) and the breeding success probability, with the category of a variable, the name of the variable, the data source, the description of the variable, the unit, the specification of data transformation, and the mean and range of variables for 1) the actual nest sites, 2) the pseudo-absence sites, and 3) the data subset used to model breeding success.

Category	Variable	Data source	Description	Unit	Data transformation	Nest-sites (n = 281) mean; range	Pseudo-absences (n = 281) mean; range	Breeding success (n = 191) mean, range
Topographic variables	Elevation	SwissAlti3D DEM	Mean elevation above sea level in 25-m radius	m	*z*	2033; 1849 to 2278	2059; 1854 to 2447	2031; 1849 to 2227
	Slope	SwissAlti3D DEM	Mean inclination of the slope in 25-m radius	%	*z*	23; 0.5 to 63.5	27.6; 4 to 61,2	21.6; 0.5 to 56.6
	Northness	SwissAlti3D DEM	cos(aspect)*pi/180 from the mean aspect value in a 25-m radius		*z*	"-0.73; -1 to 0.84"	"-0.62; -1 to 0.89"	"-0.73; -1 to 0.84"
	Eastness	SwissAlti3D DEM	sin(aspect)*pi/180 from the mean aspect value in a 25-m radius		*z*	0.09; -1 to 1	0.05; -1 to 1	0.08; -1 to 1
Remotely-sensed variables	NDVI May	Sentinel-2 satellite image	Normalized difference vegetation index for mid-May in the corresponding year	Index	*z*	0.27; -0.07 to 0.73	0.29; -0.07 to 0.8	0.29; -0.05 to 0.72
	NDVI June	Sentinel-2 satellite image	Normalized difference vegetation index for mid-June in the corresponding year	Index	*z*	0.63; 0.11 to 0.86	0.62; 0.12 to 0.87	0.62;-0.1 to 0.86
	Non-vegetated ground	Supervised image classification SwissImage 10 cm	Non-vegetated mineral ground (bare soil, stones and rock)	%	*z*	6.9; 0 to 40.7	4.4; 0 to 40.8	7; 0 to 40.7
	Scrub	Swissimage 10 cm and on-site mapping	Area of scrub	m^2	*z*	162; 0 to 1933	372; 0 to 1961	165; 0 to 1933
Man-made landscape elements	Rockpiles	Swissimage 10 cm and on-site mapping	Number of rockpiles in a 25-m radius		*z*	2.7; 0 to 25	0.3; 0 to 11	3.2; 0 to 25
Conspecific interaction	Distance3D	SwissAlti3D DEM	Three-dimensional (pythagorean distance from horizontal and vertical distances) to the nearest nest in the same year	m	*z*	118; 13 to 502	130; 53 to 294	110; 13 to 351
Phenology	Estimated start of incubation	Nest monitoring	Estimated day of the start of the incubation	Day of the year	*z*	-	-	155; 134 to 191

Results

Our models suggest that nest site is selected depending on a set of environmental factors (Table 2, Figure 2). Nests were built preferably at lower elevations (within the elevational gradient at our study site) and on gentle rather than steep slopes, suggesting a preference for gentle slopes over steep slopes. Northness had a negative effect, indicating an avoidance for north-exposed slopes, while eastness had no effect. Artificial rockpiles had a strong positive effect on nest site selection. Shrub did not have any clear effect, whereas a larger proportion of non-vegetated ground increased the probability of a location to be used for nesting. The NDVI in May did not show a clear effect, but the NDVI in June had a positive effect. Finally, we observed a preference for locations away from other nests in the same year, with a positive effect of the three-dimensional distance to the nearest nest.

Table 2. Summary output of the nest-site selection model and the breeding success model (Bayesian mixed-effect model). The probability of presence of a nest site was modelled comparing actual nest sites and randomly selected pseudo-absence sites using a mixed conditional logistic regression, with presence vs absence pair as strata argument and observation year as random effect. The probability of success was modelled using a Bayesian mixed-effect model using a logistic regression with a logit-link function, including observation year as a random effect. The other variables were included as fixed effects in each model, with the start of incubation being used as predictor only in the breeding success model. For each model, estimates where the 95% credible intervals do not contain 0 are highlighted in bold.

	Nest-site selection					**Breeding success**		
Variables	**Estimate**	**Mean**	**SD**	**2.5%**	**97.5%**	**Estimate**	**2.5%**	**97.5%**
Elevation	**-1.747**	**-1.8**	**0.4**	**-2.621**	**-0.922**	0.290	-0.117	0.708
Slope	-0394	-0.4	0.2	-0.856	0.053	-0.268	-0.657	0.128
Northness	**-0.526**	**-0.5**	**0.2**	**-0.940**	**-0.145**	**-0.344**	**-0.622**	**-0.065**
Eastness	0.187	0.2	0.2	-0.202	0.591	-0.017	-0.321	0.299
Rockpiles	**1.473**	**1.5**	**0.3**	**0.920**	**2.178**	**-0.414**	**-0.667**	**-0.155**
Shrub	-0.162	-0.2	0.2	-0.475	0.130	0.067	-0.246	0.377
Non-vegetated ground	**0.752**	**0.8**	**0.2**	**0.451**	**1.087**	0.436	-0.028	0.893
NDVI May	-0.012	0.0	0.3	-0.624	0.550	0.055	-0.549	0.672
NDVI June	**0.945**	**0.9**	**0.2**	**0.472**	**1.444**	-0.055	-0.599	0.475
Distance3D	**0.372**	**0.4**	**0.2**	**0.064**	**0.707**	0.245	-0.105	0.597
Start of incubation	-	-	-	-	-	0.133	-0.239	0.483
Year 2021	-	-	-	-	-	-0.488	-1.897	0.874
Year 2022	-	-	-	-	-	-0.455	-1.515	0.610

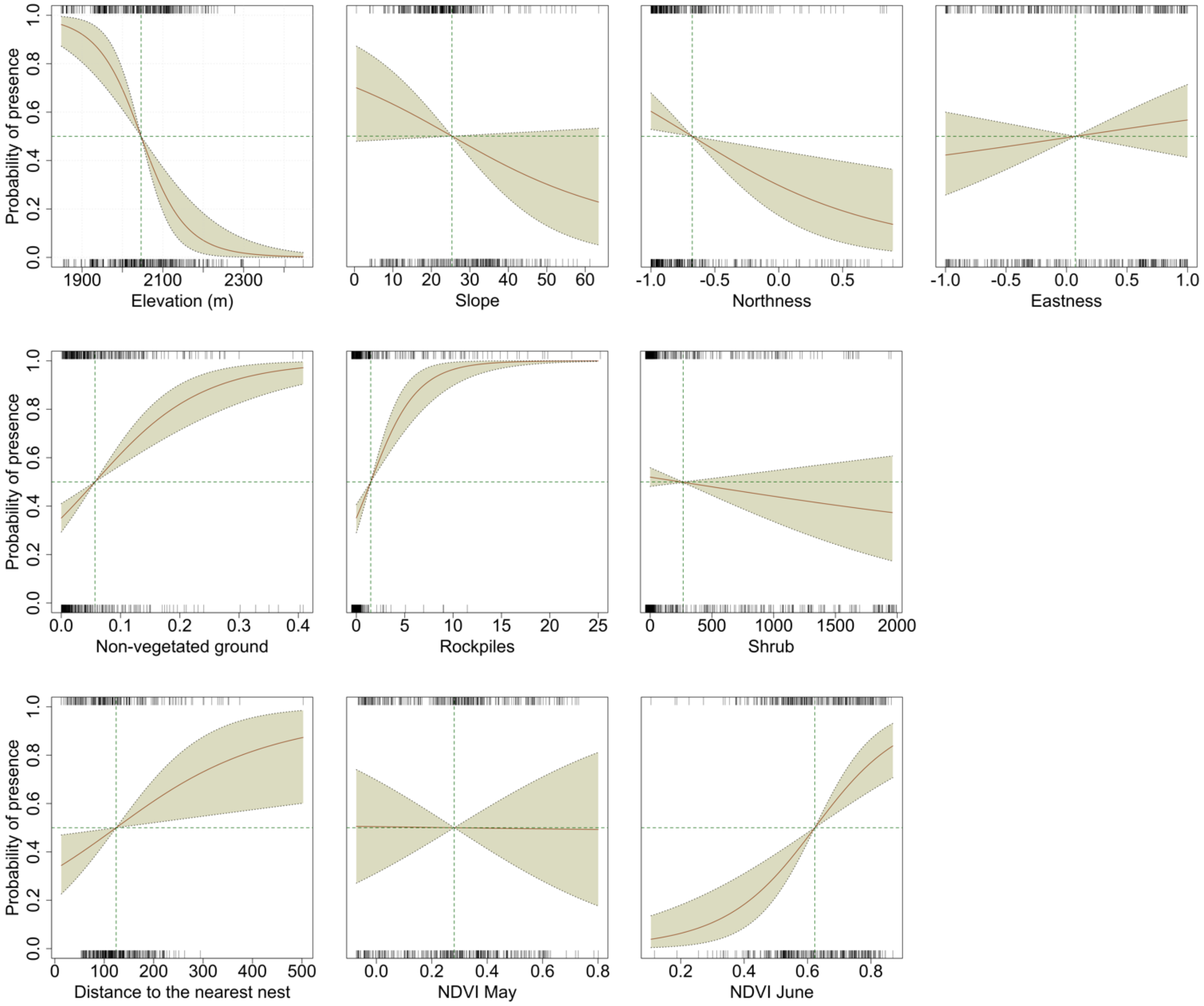

Figure 2. Predictions from the conditional logistic regression showing the relative probability of presence of a nest site compared to a reference point, which is defined as the probability of presence for the mean observed value of the plotted predictor. Other predictors were set to their mean. The coloured areas are 95% credible intervals, and the ticks show the row data (upper side = presence, lower side = pseudo-absence).

The overall observed breeding success of 191 nests was 0.62. Failure was almost always due to predation; this cause was attributed for all but five cases out of 73 failures (other causes were brood abandonment or unknown cause). Yearly observed breeding success was similar across years: 0.60 in 2020 (n= 68), 0.66 in 2021 (n=58) and 0.64 in 2022 (n=59). The modelled breeding success, which accounts for exposure time of the nests, estimated the reproductive success at 0.61 [0.33 ; 0.80] for 2020, 0.45 [0.18 ; 0.70] for 2021 and 0.47 [0.26 ; 0.64] for 2022, with no statistically clear difference between years (Table 2, Figure 3). Data from the six nests from 2019 were excluded from the model.

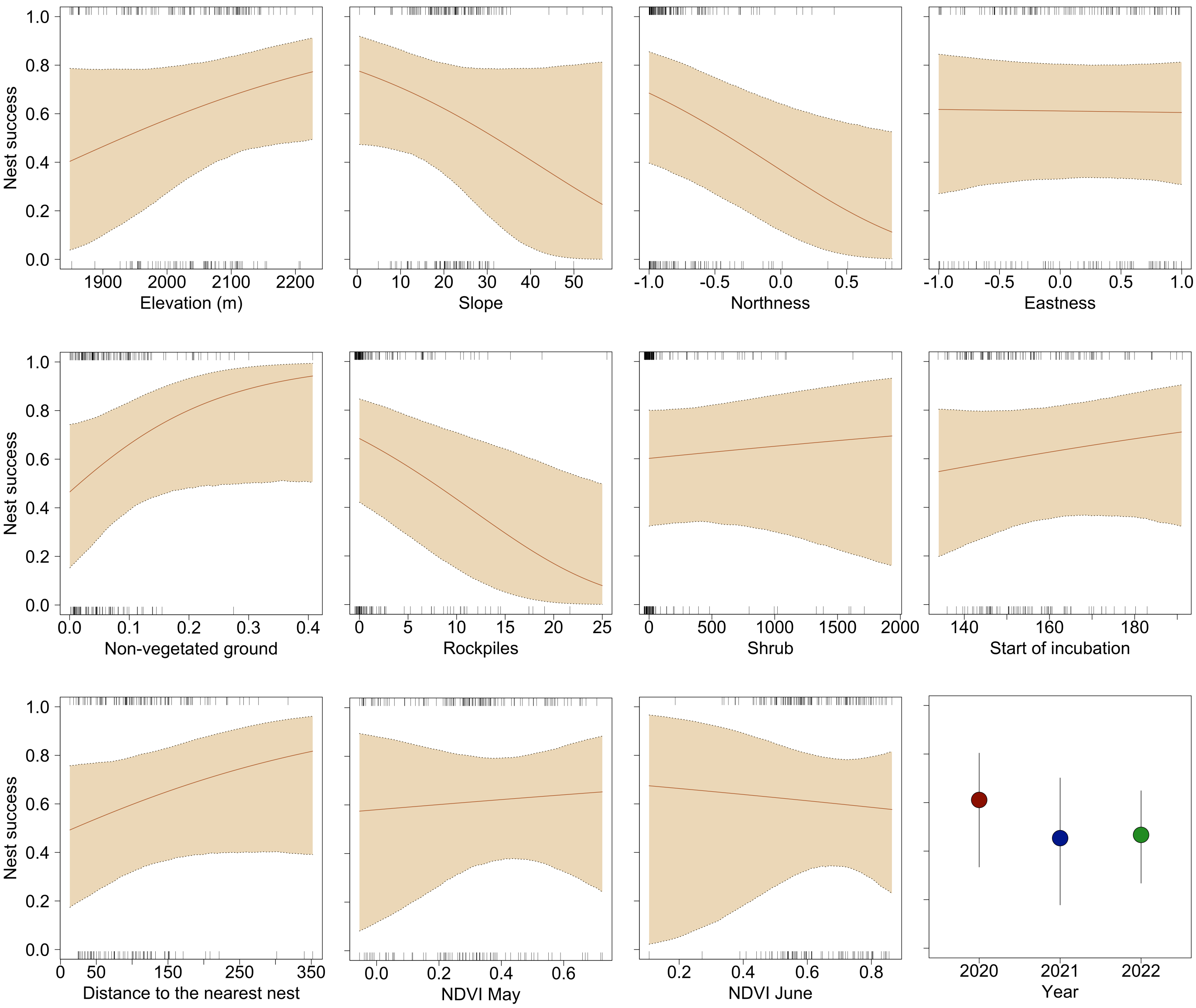

Figure 3. Predictions from the logistic regression showing the average effect (solid line) of each predictor on breeding success (0 = failed broods, 1 = successful broods), when other predictors were set to their mean. The coloured areas are 95% credible intervals, and the ticks show the row data.

The logistic regression showed effects of some environmental predictors on breeding success, with fewer variables involved compared to nest site selection (Table 2, Figure 3). Elevation seemed to have a positive effect on the probability of breeding success, while slope showed a negative effect but had large uncertainty. Northness had a clear negative effect, while eastness did apparently not influence the probability of a successful brood. Broods were less likely to be successful at sites with more rockpiles. Shrub showed no clear effect on breeding success. No clear effect was detected for NDVI in May, nor in June. Non-vegetated ground had a positive effect on breeding success. The distance to the nearest conspecific nest and the estimated date of start of incubation was positively correlated with the breeding success, but their estimates had high uncertainty.

Breeding success showed no clear weather-related differences (2021 was rainier, colder and with later snowmelt, while 2020 and 2022 were drier, warmer and with exceptionally early snowmelt; Figure 4). We monitored 153 first broods (observed success = 0.61) and 32 replacement or late broods (observed success = 0.75). The mean start of incubation of the first broods was 29 May. In 2020 (early, warm and dry spring), the mean start of incubation of first broods was 28 May, in 2021 (late, cold and wet spring) 5 June, and in 2022 (early, warm and dry spring) 25 May (Figure 4 and supplementary material, Table S1). The earliest incubation started on 14 May (2020), 24 May (2021) and 16 May (2022). The incubation of the latest brood started on 10 July. A mean ± sd clutch size of 4.97 ± 0.7 eggs (range 3 to 6 eggs) could be assessed for 74 nests. First broods had 5.03 ± 0.66 eggs, and replacement broods had 4.33 ± 0.82 eggs. Due to a larger uncertainty in the ageing of the chicks and the corresponding estimation of hatch date, 2019 data were excluded from the yearly comparison of breeding phenology.

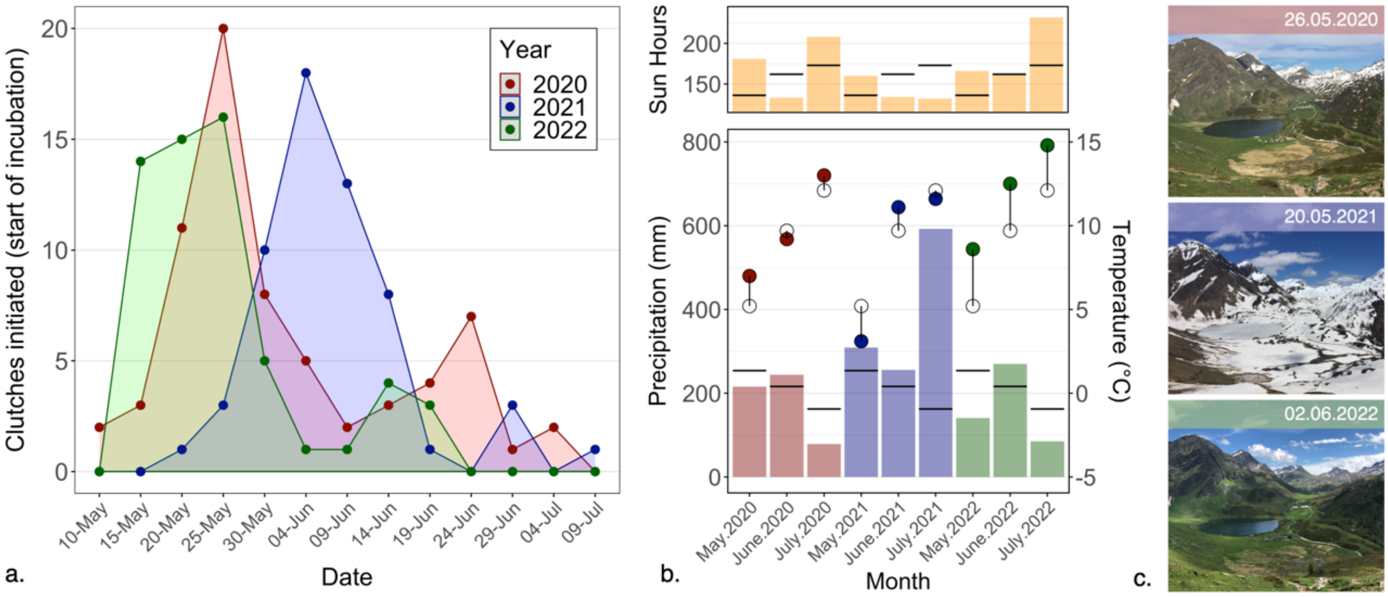

Figure 4.

a. Distribution of clutches laid per five-day period in 2020 (red), 2021 (blue), and 2022 (green), showing a clear difference between 2021 (late snowmelt year with cold and rainy meteorological conditions during the breeding season) compared to 2020 and 2022 (early snowmelt years with warm and dry meteorological conditions during the breeding season).

b. Hours of sun per month (in orange, the black bar shows the average 1991-2020), sum of precipitation per month (coloured bars for each month of the breeding season, the black bar shows the average 1991-2020), and mean monthly temperature (filled dots) compared to the average 1991-2020 (empty dots).

c. The study area in three contrasting years with large variations in spring onset and snowmelt.

Discussion

The selection of a nest site in Northern Wheatears from an Alpine population was consistently influenced by topography, vegetation productivity and habitat composition, especially by the direct proximity of suitable foraging habitat. The probability of successful breeding was mainly driven by predation, with indirect effects of topography and habitat composition. A comparison between three breeding seasons suggested a delay in laying dates with late spring onset and cold, rainy weather. However, breeding success seemed overall similar in 2020, 2021 and 2022, indicating a high tolerance to inter-annual variation of meteorological conditions in Alpine habitats.

In Alpine ecosystems, fine-scale habitat characteristics often explain a species' distribution (Jähnig et al., 2020; Müller et al., 2023). While the restricted availability of nest cavities can be limiting for Northern Wheatears in parts of their range (Conder, 1989; D. Currie et al., 2000; Kämpfer & Fartmann, 2019), nest-cavities are abundant in heterogenous, well-structured alpine grasslands such as those in our study area (Sander et al., 2023; Wartmann, 1985). Hence, rather than the availability of cavities, the surrounding habitat played a major role in the selection of a nest site. Other Alpine species such as the White-winged Snowfinch *Montifringilla nivalis* also select a nest based on the surrounding habitat quality, but often move longer distances between the nest and the foraging sites (e.g. Niffenegger et al., 2023). In our study on Northern Wheatears, most of the parameters influencing nest-site selection were related to the suitability of the vicinity of the nest (25 m) for foraging. Foraging preferences were described in another study at the same site (Müller et al., 2023). Wheatears use stones as perches, from which they access ground-dwelling invertebrates in short flights (Sander et al., 2023; Wartmann, 1985). Access to these food items is enhanced by low vegetation and bare ground, within areas of relatively high productivity in low-intensity farmed pastures. The preference for gentle south-exposed slopes (Glutz von Blotzheim & Bauer, 1988; Knaus et al., 2018; Wartmann, 1985) is probably due to the presence of herbaceous vegetation, where food abundance is higher compared to cliffs, debris, or shrub (Müller et al., 2023). Even though we did not detect collinearity between elevation and slope, the avoidance of areas at higher elevation is probably related to the topography of our study area, where sites at higher elevation are steeper and less productive. Our results are restricted to the habitat in direct vicinity of the nest site and do not account for the habitat used at larger distances or in the pre- and post-breeding period (Alba et al., 2023; Müller et al., 2023; Rime et al., 2023).

The probability of a site being selected for nesting increased with the amount of human-made rockpiles in the surroundings, highlighting the importance of these typical elements of Alpine pastures under low-intensity traditional management. These rockpiles often hosted nest cavities in our study area, but also offered a place to hide for fledgelings. Moreover, they were located in productive pastures that are favoured for foraging (Müller et al., 2023). As for other insectivorous birds, access to ground-dwelling arthropods (Rime et al., 2020; Schaub et al., 2010; Tagmann-Ioset et al., 2012) is most likely explaining the preference for sites with more non-vegetated ground on nest site selection (Müller et al., 2023). For the same reason, shrub was usually avoided for foraging (Müller et al., 2023) but was not clearly avoided for nesting.

Nest-sites were more likely located in areas where the vegetation was productive relatively to the surrounding landscapes during food provisioning, with a positive correlation between selected sites and NDVI in June, i.e. after snowmelt. However, NDVI only informs on the vegetation greenness around the nest site and not on the fine-scale vegetation structure (Müller et al., 2023; Sander et al., 2023). No clear effect was detected for the measure of vegetation greenness in May, when birds arrived from migration and snow was melting (Rime et al., 2023; Sander et al., 2021). According to our observations, vegetation development was faster on steeper slopes that are first free of snow but that were avoided for nesting. The absence of effect of NDVI in May suggests that birds did not select their territory based on the state of the vegetation upon arrival but used other cues, potentially gathered in the previous year (Pärt et al., 2011).

In addition to these habitat-related predictors, conspecifics played a role in the selection of a nest-site. A distance of more than 124 m to the nearest nest was preferred, which is probably explained by a high breeding density of this territorial species and the result of a trade-off between breeding in favourable habitat while keeping a sufficient distance to minimize energy expenditure in defending the surroundings of the nest against competitors (Arlt & Pärt, 2007; Brooke, 1979; Conder, 1989).

As in other parts of the Alps (Sander et al., 2023; Wartmann, 1985), the probability of a nest to be successful was mainly driven by predation, one of the main factors influencing reproductive success (Martin, 1995; Martin & Briskie, 2009). The influence of habitat quality on breeding success hence needs to be interpreted mainly indirectly, i.e. through the influence of topography, habitat composition or vegetation productivity on the risk of predation.

Topography influenced the breeding success: we found a strong negative correlation, indicating lower breeding success with north-exposed aspect. Predation risk is usually higher at lower temperatures, when provisioning rates must be increased (Low et al., 2008; Moreno, 1989; Öberg et al., 2015; Schneider et al., 2012). Habitat composition also influenced breeding success. Non-vegetated ground, favoured for selecting a nest site, had a positive effect on breeding success. Predation risk was found to increase in low-quality foraging habitats in a Swedish lowland population (Pärt, 2001). Previous studies on lowland and high-elevation populations of the Northern Wheatear showed enhanced access to ground-dwelling prey in short vegetation and patches of bare ground: birds breeding in better habitats might need less frequent but more effective provisioning visits to the brood, thus reducing predation risk (Arlt et al., 2008; Arlt & Pärt, 2007; Low et al., 2010; Müller et al., 2023; Sander et al., 2023).

The distance to conspecific nests seemed positively correlated with breeding success, but the uncertainty of the model was high. Breeding further away from conspecific may reduce the negative effects of intra-specific competition in this territorial species (Alba et al., 2023; Conder, 1989; D. Currie et al., 2000; D. R. Currie et al., 1998). Social factors might also explain why rockpiles in the surroundings, which were favoured for selecting a nest site, negatively affected breeding success. Higher breeding densities in this *a priori* optimal habitat might lead to more competition (Maurer, 1984) and to an increased risk of predation from predators specialized in preying on birds, as they might target areas with high densities of nests (Andersson & Wiklund, 1978; Larivière & Messier, 1998; Taylor, 1976). The overall advantages of breeding in areas with rockpiles, such as a high-quality foraging habitat (Müller et al., 2023), nest cavity availability, perches (Alba et al., 2023), and refuge for fledgelings, are probably more relevant when selecting a nest site than a potentially increased predation risk.

Although the effect in our model was weak, the observed breeding success seemed higher in replacement broods compared to first broods. This confirms similar findings in the Italian Alps (Sander et al., 2021, 2023). Due to a short breeding season, second broods are rare at high elevation (Müller et al., 2023; Wartmann, 1985) and mostly consisted of replacement broods after predation in our study. A better success late in the season contrasts with lowland populations, where late breeding is associated with a decrease in fitness (Öberg et al., 2014). Nevertheless, Sander et al., 2023 found a reduced weight of chicks in late breeders, which might therefore face other disadvantages such as delayed moult with carry-over effects on survival (Buchmann et al., 2009; Magrath, 1991; Sander et al., 2023; Streby et al., 2014; Tinbergen & Boerlijst, 1990).

With a time-limited availability of food resources to feed the chicks (Chamberlain et al., 2023; Martin & Wiebe, 2004), many bird species are facing a mismatch between breeding timing and the optimal availability of food resources (Both & Visser, 2001; Jones & Cresswell, 2010; Saino et al., 2011; Visser et al., 2004). Such mismatch was found for Alpine bird species (e.g., Schano et al., 2021; Wann et al., 2019) and was described as a potential cause for variation in breeding success of Northern Wheatears (Sander et al., 2021). We did not measure food availability or food provisioning here, but we found no evidence of changes in breeding success in years with varying spring onset and different meteorological conditions. The onset of the breeding season occurred later in spring 2021, which was marked by late snowmelt and rainy, cold weather conditions. This contrasted to 2020 and 2022, years with early snowmelt and warm weather, indicating that Wheatears can adjust lay dates to annual phenology. Overall, breeding success seemed similar between these years, suggesting a limited sensitivity of this species to inter-annual variations in spring onset and weather conditions. Furthermore, the probability of success seemed higher in late broods. This would not be expected if the birds were not able to time the onset of breeding to the availability of food resources (Jones & Cresswell, 2010; Saino et al., 2011; Wann et al., 2019). Hence, habitat quality in general might be more relevant for Northern Wheatears than the seasonality of food resources. Nonetheless, the relationships between inter-annual cyclic fluctuations of predators and their alternative prey may also influence the annual breeding success, with potentially more complex interactions with weather conditions (Ibáñez-Álamo et al., 2015; Maag et al., 2024). However, our short-term study does not suggest changes of breeding success between years.

In the context of a decline of the Northern Wheatear in Europe (Gedeon et al., 2015; Keller et al., 2020), the positive situation in the Alps (Knaus et al., 2018) indicates that mountain ranges are currently crucial for the conservation of the species at a continental scale. Our results highlight a preference for South-exposed, relatively productive grasslands with high heterogeneity on a small spatial scale, a habitat still widely available in the Alps. As the species underwent recent upwards distribution range shifts (Hallman et al., 2022; Knaus et al., 2018; López-Ramírez et al., 2024), habitats in pastures directly above the treeline such as our study site might no longer be suitable in the future. Nonetheless, at present, thanks to the tolerance of the Northern Wheatear for changing weather conditions among years, a warmer climate might improve the breeding conditions for the species in the Alps, as long as habitat quality is maintained. A loss of habitat suitability at lower elevations, especially through bush and shrub encroachment (Braunisch et al., 2016; Laiolo et al., 2004), might be buffered by conserving traditional pastoral activities and promoting heterogenous habitats. The situation in the well-preserved high-elevation valley where this study took place is not entirely representative of other locations in the Alps, particularly to those subject to land abandonment or, conversely, to agricultural intensification.

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Supplementary material

Table S1. Data on precipitation, temperature, and hours of sun exposure were obtained for each month of the breeding season from a nearby automated meteorological station at the same elevation (Robiei, Ticino, Switzerland, 46°26’N, 8°30’E, 1898 m. a.s.l.). These data were compared with the norm 1991-2020.

Precip	Precip_norm	Ecart_P_norm	Ecart_tot_precip	Temp	Temp_norm	Ecart_T_norm	Ecart_temp	Sun	Sun_norm	Ecart_sun	Month	Year
143,5	253,8	-110,3	-81	3,2	5,2	-2	1,6	180	136	44	May	2019
289	216,2	72,8	-81	11,5	9,7	1,8	1,6	189	162	27	June	2019
119	162,5	-43,5	-81	13,9	12,1	1,8	1,6	190	173	17	July	2019
215,7	253,8	-38,1	-93,7	7	5,2	1,8	2,2	181	136	45	May	2020
244	216,2	27,8	-93,7	9,2	9,7	-0,5	2,2	133	162	-29	June	2020
79,1	162,5	-83,4	-93,7	13	12,1	0,9	2,2	208	173	35	July	2020
308,9	253,8	55,1	524,7	3,1	5,2	-2,1	-1,2	160	136	24	May	2021
255,5	216,2	39,3	524,7	11,1	9,7	1,4	-1,2	134	162	-28	June	2021
592,8	162,5	430,3	524,7	11,6	12,1	-0,5	-1,2	132	173	-41	July	2021
140,9	253,8	-112,9	-136,5	8,6	5,2	3,4	8,9	166	136	30	May	2022
269,7	216,2	53,5	-136,5	12,5	9,7	2,8	8,9	161	162	-1	June	2022
85,4	162,5	-77,1	-136,5	14,8	12,1	2,7	8,9	232	173	59	July	2022

Chapter 2

Finding food in a changing world: Small-scale foraging habitat preferences of an insectivorous passerine in the Alps

Fine-scale habitat and female Northern Wheatear *Oenanthe oenanthe* provisioning food for the brood (© Yann Rime)

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RESEARCH ARTICLE

Finding food in a changing world: Small-scale foraging habitat preferences of an insectivorous passerine in the Alps

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Abstract

Organisms living in high-elevation habitats are usually habitat specialists who occupy a narrow ecological niche. To envision the response of alpine species to a changing environment, it is fundamental to understand their habitat preferences on multiple spatial and temporal scales. However, information on small-scale habitat use is still widely lacking. We investigated the foraging habitat preferences of the migratory northern wheatear *Oenanthe oenanthe* during the entire presence at a breeding site in the central Alps. We repeatedly observed 121 adult and juvenile individuals. We applied Bayesian logistic regression models to investigate which habitat characteristics influenced foraging habitat selection on a fine spatial scale, and how habitat use varied temporally. Throughout their presence on the breeding grounds, northern wheatears showed a consistent preference for a mosaic of stones and bare ground patches with slow-growing, short vegetation. The proximity of marmot burrows was preferred, whereas dense and low woody vegetation was avoided. After arrival at the breeding site, short vegetation, preferably close to the snow, was favored. The preference for open habitat patches that provide access to prey underlines the critical role of small-scale habitat heterogeneity for northern wheatears. The strong and consistent preference for a habitat that is under pressure from land-use and climate change suggests that this alpine bird species may be sensitive to habitat loss, leading to a potential range contraction. We highlight the need to conserve habitat diversity on a small spatial scale to ensure the long-term availability of suitable habitat for northern wheatears in the Alps.

KEYWORDS

alpine birds, elevation, ground cover, habitat heterogeneity, insectivorous

TAXONOMY CLASSIFICATION

Behavioural ecology, Biodiversity ecology, Community ecology, Ecosystem ecology, Global change ecology, Landscape ecology, Life history ecology, Phenology, Spatial ecology

1 | INTRODUCTION

The ecological niche of a species is defined on multiple spatial and temporal scales (Mahon et al., 2016). Hence, to understand or preserve a species, it is necessary to identify its relevant habitat preferences from large-scale distributions to small-scale habitat features. The availability of suitable foraging habitat plays a special role in the niche configuration and is crucial for survival and successful reproduction. More specifically, food availability, comprised of food abundance and accessibility, is a major driver of foraging habitat selection that is influenced by habitat features on a fine scale (Arlettaz, 1999; Barras et al., 2020; Cody, 1985; Dussault et al., 2005). Food abundance and accessibility, however, are often promoted by different habitat characteristics and are temporally variable (Atkinson et al., 2004; Dussault et al., 2005; Fuller et al., 2007). Particularly, species with narrow requirements, so-called specialists, are expected to be relatively sensitive to changes in food availability (McPeek, 1996). Typically, alpine species are often adapted to a short vegetation period, and they are restricted to a higher elevational range that is characterized by habitat heterogeneity on a finer scale, compared to lowland habitats (Cortés & Wheeler, 2018). For insectivorous alpine birds, prey abundance is driven by a stronger seasonality at high elevation (Pilar et al., 2020; Resano-Mayor et al., 2019). Arthropod abundance, diversity, and species richness peak in early summer and then decrease to relatively low levels until autumn (Pilar et al., 2020). Consequently, the time window is limited for prey availability to match food demand for brood provisioning, for expensive maintenance such as molt, and for juvenile post-fledging establishment (Arlt & Pärt, 2008; Resano-Mayor et al., 2019; Tulp & Schekkerman, 2008).

Alpine regions are more vulnerable to climate change than low-elevation areas (Brunetti et al., 2009). They experience adverse effects of rising temperatures, altered precipitation patterns, as well as advanced snowmelt and vegetation development that lead to an upward shift of the treeline (Gehrig-Fasel et al., 2007; Gobiet et al., 2014; Keller et al., 2005; Theurillat & Guisan, 2001). Moreover, land-use changes influence vegetation development in alpine areas through two opposed processes (Kulakowski et al., 2011): Low-intensity agricultural activities such as livestock grazing are being abandoned, leading to bush encroachment and ultimately to forest encroachment (Baur et al., 2006), while areas that are still managed tend to undergo agricultural intensification (Fischer et al., 2008). Land-use and climate change have fundamental effects on the majority of organisms across trophic levels, through either the loss of suitable habitat or shifting vegetation phenology (Ferrarini et al., 2017; Hughes, 2000; Inouye, 2020; Keller et al., 2005). For migratory birds in particular, advanced vegetation phenology can lead to a potential phenological mismatch (Jones & Cresswell, 2010; Saino et al., 2011; Visser et al., 2004), because it reduces prey accessibility for ground-foraging species as a result of increased vegetation height and of advances in the peak in arthropod abundance (Renner & Zohner, 2018; Tulp & Schekkerman, 2008).

As a long-distance migratory songbird, the northern wheatear (*Oenanthe oenanthe*) is affected by changing habitat characteristics and shifting vegetation and prey phenology on multiple spatial and temporal scales (Jähnig et al., 2020; Sander et al., 2021, 2022). The species has a circumpolar distribution and overwinters in sub-Saharan Africa (Bairlein et al., 2012; Dunn et al., 2020; Meier et al., 2022; Rime et al., 2023). In Northern European lowland breeding sites, where seasonality is less strong compared to alpine habitats, northern wheatears favor open fields with short vegetation (Arlt et al., 2008; Arlt & Pärt, 2007; Paquet et al., 2019) and seem to be more limited by prey accessibility than by prey abundance (van Oosten et al., 2014). Unlike lowland breeding ranges, in Switzerland, the species is limited to high elevations above the tree line (Knaus et al., 2018). While in most parts of Europe, northern wheatear populations are declining, the Swiss Alpine population is stable overall while experiencing an upward shift in the elevational distribution (Hallman et al., 2022; Keller et al., 2020; Knaus et al., 2018). The population trend of the Alpine northern wheatear population points toward an increasingly important role of alpine habitats for the conservation of this species in central Europe (Knaus et al., 2018). This Alpine population faces spatial and temporal landscape dynamics that are different from those in the European lowland (Brunetti et al., 2009; Pilar et al., 2020). To examine the sensitivity of the species to current and future habitat changes and shifting vegetation phenology in the Alps, it is important to understand how the species interacts with the highly seasonal and variable habitat that the alpine ecosystem provides on a fine spatial and temporal scale.

Here, we conducted an observational study on uniquely identifiable individuals to determine the preferred foraging habitat of northern wheatears in their Alpine breeding range throughout their stay. We focused on the microhabitat at foraging locations and compared it with the available habitat at random locations within the territory. We investigated the role of vegetation height and ground cover composition in providing accessibility to prey. Foraging preferences may change throughout the annual cycle. Therefore, we considered the birds' entire presence at the breeding site, including during the pre-breeding and postbreeding periods. This also covers key processes such as molt and premigratory fuel deposition, as well as the high-risk phase of post-fledging establishment of juveniles. To determine the role of prey accessibility on Alpine breeding grounds, we examined the importance of small-scale heterogeneity in providing suitable foraging habitat. Furthermore, we explored the role of grazing cattle and alpine marmots (*Marmota marmota*) in shaping habitat heterogeneity on a small scale.

2 | METHODS

2.1 | Study area

Our study area is located in Val Piora in the central Swiss Alps (46°33′N 8°42′E, Figure 1). It covers 6 km^2 of mostly south-exposed slopes above the tree line, ranging from 1850 to 2200 m.a.s.l. and hosting more than 100 breeding pairs of northern wheatears. The habitat is characterized by heterogenous open

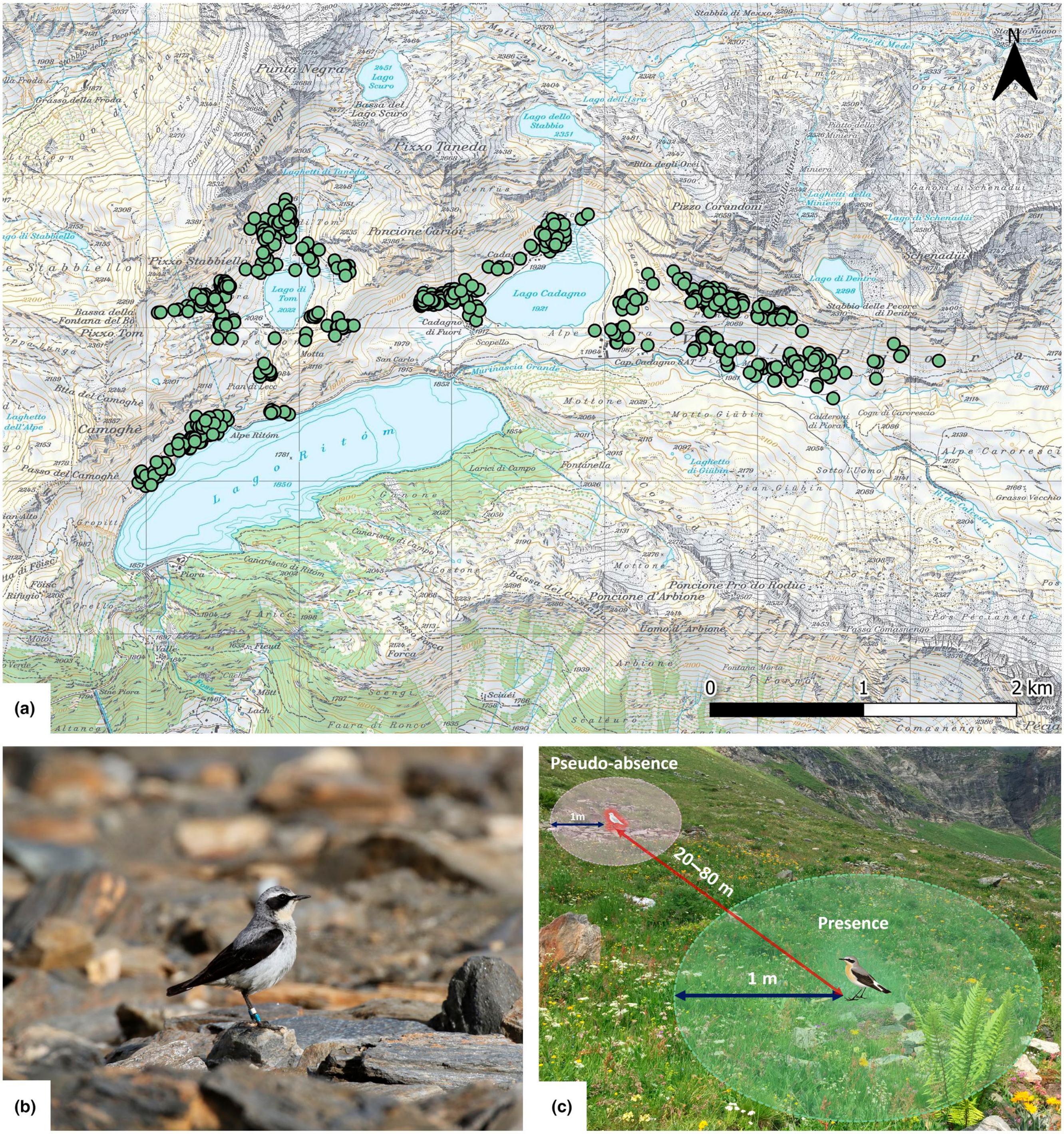

FIGURE 1 The map (a) shows the position of all foraging points (green dots) recorded in the study area in Val Piora. Foraging habitat data were recorded for color-ringed northern wheatears (b) on a 1-m radius around foraging (presence) and pseudo-absence locations (c). Pseudo-absence locations were located randomly within 20–80 m and at a random angle (relative to true North) of each foraging location. background map: ©swisstopo, photos: ©Y. Rime.

grassland interspersed with rocks, boulders, debris fields, and remains of man-made rockpiles and stonewalls. Between July and September, the pastures are grazed in a rotational manner and the cattle are frequently moved, constituting a low-intensity grazing regime. The area is usually covered by snow between November and May.

2.2 | Study design

In the frame of a project on migration and ecology of northern wheatears, individuals have been ringed in the study area since 2010 (Meier et al., 2022; Rime et al., 2023; Schmaljohann et al., 2016). Each bird was ringed with a unique combination of one metal ring and three plastic color rings (Figure 1). Adults were caught using baited spring traps and cage-traps that were placed at the nest entrance. Where they could be reached, chicks were ringed at their nest once they were 7 days old.

We observed ringed individuals between May 12 and September 03, 2021, covering the arrival, incubation, feeding (period of food provisioning for chicks), and postbreeding stages. Northern wheatears arrive on their Alpine breeding grounds between the end of April and mid-May and depart for fall migration around mid-September (Glutz Von Blotzheim & Bauer, 2001; Meier et al., 2022; Rime et al., 2023; Sander et al., 2021). During this period, ringed birds were followed weekly from the distance, using binoculars and a scope, until the first foraging attempt of each observation. We recorded the exact location of the foraging event on a photograph taken through the scope. After the bird had left the foraging location, we immediately mapped the microhabitat on site and recorded the exact coordinates and information on the individual (color ring combination, sex, age, and nest ID) in QField (QGIS Development Team, 2020). To compare the foraging (presence) locations with locations that have not been chosen by the bird, we mapped the microhabitat at a nearby location within a randomly selected distance of 20–80 m to the foraging location at a random angle (0°–360°) for each foraging event (Figure 1, Barbet-Massin et al., 2012; Johnson, 1980). This distance range was selected to ensure that pseudo-absence locations were located within the territory of the observed bird (Glutz Von Blotzheim & Bauer, 2001). Adult birds usually remained within their territory throughout their entire stay in the study area, including for foraging activities (Rime et al., 2023). To make sure that each presence-pseudo-absence pair is independent, we moved on to the next territory after having recorded all ringed individuals sighted within their territory.

We recorded the following set of habitat variables (Table 1 and Table S1) on a 1-m radius around foraging (presence) and pseudo-absence locations (Figure 1): ground cover estimates (percentage of live vegetation, dead vegetation, woody vegetation, bare ground, stones [granulometry >4 mm], and snow) and vegetation height. We calculated the vegetation height using the mean of three representative measurements within the 1-m radius. Additionally, we estimated the distance to the closest marmot burrow and recorded cattle grazing activity, immediate cattle presence, and presence of cow dung within the 1-m radius. For each foraging and pseudo-absence location, we also computed the distance to the nest if it was found, and the normalized difference vegetation index (NDVI) and its rate of change between months. The distance to the nest was calculated based on the SwissALTI3D digital elevation model (swisstopo, 2018) in QGIS (QGIS Development Team, 2020). NDVI raster images for the study area were generated on Google Earth Engine (Gorelick et al., 2017) based on Sentinel-2 satellite images with a spatial resolution of 10 m (ESA, 2015). After applying a cloud filter (<50% cloud area), the image with the clearest conditions for each month (April–September 2021) was manually selected, and the NDVI values were extracted in R (R Core Team, 2021) using the *extract* function from the package *raster* (Hijmans, 2021). To detect local shifts in greenness, the rate of NDVI change was computed as the difference between the NDVI values extracted from the images of the previous and the following month of the foraging event at each foraging and pseudo-absence location. To allow for a comparison between different habitat scales, we additionally recorded the same set of variables on a 2-m radius around the foraging and pseudo-absence locations.

As the birds' needs are expected to change during their presence at the study site, we assigned three stages to each of the foraging events on a per-breeding pair basis. The arrival and incubation stage lasts until the chicks hatch after an incubation period of 13–15 days (Moreno, 1989a). This is followed by a feeding period that includes feeding chicks 13–15 days in the nest and feeding fledglings for 10 days out of the nest until they become largely independent (Glutz Von Blotzheim & Bauer, 2001; Moreno, 1984). The postbreeding period includes the remaining time until both adults and juveniles depart for fall migration (Arlt & Pärt, 2008). During this period, young wheatears must establish themselves, and both the adults and immatures undergo complete molt and deposit fuel for their long-distance migratory journey (Arlt & Pärt, 2008; Glutz Von Blotzheim & Bauer, 2001).

In total, we recorded 620 foraging locations and an equal number of pseudo-absence locations ($n_{\text{tot}} = 1240$) during the period of presence of northern wheatears in the study area (Figure 1). We followed 121 ringed individuals (53 adult males, 47 adult females, and 21 juveniles). Sixty-nine adults were returning individuals ringed in previous years, while 31 adults and 21 juveniles were newly ringed during the study period. We collected data for 193 foraging locations during the arrival and incubation stage, 193 during the feeding stage, and 182 during the postbreeding stage, of which 38 were from juveniles.

2.3 | Statistical analysis

We modeled the foraging habitat selection by comparing the recorded variables between foraging (presence) and pseudo-absence locations using logistic regression models (logit-link function) with presence/absence as a binary outcome variable. In all models, the ground cover estimates, vegetation height, distance to marmot burrow, NDVI, and its rate of change were included as fixed effects. To account for individual preferences and repeated observations of the same individual, we included the bird ID (color ring combination) and the point ID (unique number for each presence/pseudo-absence pair) as random effects (Korner-Nievergelt et al., 2015; Laird & Ware, 1982). All statistical analyses were conducted in R (R Core Team, 2021). Models were fitted in a Bayesian framework (Gelman et al., 2013; McElreath, 2016), using the *brm* function from the *brms* package (Bürkner, 2017). For each model, we ran four chains, each with 2000 iterations of which the first 1000 were discarded as the burn-in period (McElreath, 2016). A prior sensitivity analysis (Figure S1) suggested that the model results were sufficiently robust to changing prior specification (Depaoli & van de Schoot, 2017; Link et al., 2002; Nicenboim et al., 2021). Hence, we chose uninformative priors for our models (Berger, 2006; Kass & Wasserman, 1996;

TABLE 1 Predictors used to model the foraging probability (presence vs. pseudo-absence).

Category				Analysis				
				General model ($n = 542$)	Arrival and incubation ($n = 193$)	Feeding ($n = 190$)	Postbreeding ($n = 182$)	
Fixed effects	**Variables**	**Description**	**Unit**	**Mean (range) (2.5%; 97.5%)**	**Mean (range) (2.5%; 97.5%)**	**Mean (range) (2.5%; 97.5%)**	**Mean (range) (2.5%; 97.5%)**	**Transformation**
Ground cover	Dead vegetation	Brown vegetation grown in the previous year	%	10 (0–100) (0; 64.9)	25.9 (0–100) (0; 80)	5.3 (0–85) (0; 38.6)	3.6 (0–40) (0; 29.6)	Poly[a], z[b]
	Woody vegetation	Shrubs and other plants with a woody stem	%	6.2 (0–100) (0; 70)	3.9 (0–93) (0; 40.8)	5.5 (0–100) (0; 67.6)	6.7 (0–100) (0; 76.5)	Poly[a], z[b]
	Bare ground	Bare ground with no vegetation cover	%	17.3 (0–100) (0; 64.9)	20.9 (0–90) (0; 65)	17.7 (0–100) (0; 70)	12.7 (0–85) (0; 45.9)	Poly[a], z[b]
	Stones	Stones and rocks (granulometry >4 mm)	%	12.1 (0–100) (0; 65)	9.6 (0–100) (0; 56.1)	10.2 (0–73) (0; 50)	14.3 (0–100) (0; 70)	Poly[a], z[b]
	Snow cover	Area covered by snow	%	Not included	15.5 (0:100) (0; 100)	Not included	Not included	Poly[a], z[b]
	Vegetation height	Mean height of three representative measurements	cm	13.24 (0–94) (1; 36)	5.45 (0–55) (0; 18)	14.91 (0–94) (3; 36)	15.58 (0–55) (3; 38)	z[b]
Ecosystem engineers	Distance to marmot burrow	Distance to the closest marmot burrow (if within 100 m)	m	7.93 (0–130) (0; 27)	8.75 (0–60) (0.63; 32.75)	8.88 (0–130) (0.48; 33.05)	6.86 (0–76) (1; 22.85)	z[b]
Vegetation Index	NDVI	Normalized difference vegetation index	Index	0.65 (0–0.92) (0.1; 0.87)	0.38 (0–0.88) (0; 0.81)	0.68 (0–0.92) (0.15; 0.88)	0.72 (0.28–0.9) (0.52; 0.87)	Poly[a], z[b]
	Rate of NDVI change	Change in vegetation greenness	Index change rate	0.18 (−0.36 to 0.83) (−0.22; 0.69)	0.4 (−0.05 to 0.86) (0; 0.74)	0.2 (−0.32 to 0.82) (−0.08; 0.73)	−0.02 (−0.36 to 0.58) (−0.27; 0.3)	Poly[a], z[b]
Random effects				**No. of levels**	**No. of levels**	**No. of levels**	**No. of levels**	
Point info	Point ID	Unique identifier for each point pair		542	193	190	182	
Bird info	Bird ID	Color ring combination		119	57	72	95	

Note: Snow cover was only included in the arrival and incubation model. For each model and variable, the mean per 1-m radius plot, range, 2.5% quantile, and 97.5% quantile are given, and the applied data transformation is provided. Point ID and bird ID were included as random effects for which the number of levels is given for each model.

[a] The first two orthogonal polynomials were included.

[b] Centered to 0 and scaled to 1 SD.

Zhou et al., 2014). For the intercept and the group-level variances (bird ID and foraging ID), we chose default student-t priors ($\beta \sim Student(3, 0, 2.5)$) and determined a normal prior distribution for the population-level effects ($\beta \sim Normal(0, 100)$).

Prior to modeling, numeric variables were z-transformed (mean = 0, SD = 1). As we expected nonlinear relationships, we included the first two orthogonal polynomials of the ground cover variables and the vegetation index variables in the models using the *poly* function. We checked for collinearity between covariates by calculating the Spearman's correlation coefficient and did not detect strong collinearity among explanatory variables (all $|r_s| < .7$).

Observations in the field suggested potential differences in foraging habitat preferences between adult and juvenile birds. To detect differential preferences of northern wheatears that are related to their age class (adult, juvenile) or sex (female, male), we applied principal component analysis (PCA) using the variables summarized in Table 1. PCA were generated with the *ggbiplot* R package (Vu, 2011) but did not reveal relevant differences between age classes or sexes (Figure S2). As a result, age and sex class were not included in the models.

To detect stage-dependent differences in foraging habitat preferences during the study period, we analyzed each of the three stages in a separate model, in addition to a general model including the data from the entire study period. To compare foraging habitat preferences across different scales, we also fitted each of the four models with the data collected on the 2-m radius around the foraging and pseudo-absence locations.

Due to the strong seasonality in the study area, snow can only be expected at the beginning of the season. As a result, we only used snow cover in the arrival and incubation model. Furthermore, snow cover may lead to biased relative estimates for the other ground covers. Therefore, all locations containing snow ($n = 156$) were removed from the general model. Whenever foraging locations had to be removed, the corresponding pseudo-absence location was discarded as well. Because ground cover variables always added up to 100%, they could not all be included in the models. Therefore, the main ground cover component, live vegetation, was not used in the models. Visual data exploration did not suggest differences in the topographic variables between foraging and pseudo-absence locations, which can be explained by the small distance between them (Figure S3). Therefore, topographic variables were not included in statistical models. Similarly, grazing variables were discarded, as they always fell into the same category due to the small distance between foraging and corresponding pseudo-absence locations. We did not apply any further model selection steps, and no interactions were considered.

We verified model convergence based on Gelman–Rubin convergence diagnostics and visually confirmed convergence using "trace" plots (MCMC plots; Depaoli & van de Schoot, 2017; Rizzo, 2008). We checked for autocorrelation within the MCMC chains using the *mcmc_plot* function from the *bayesplot* package (Gabry & Mahr, 2021). Additionally, we checked for spatial autocorrelation using bubble plots and semivariograms from the *gstat* package (Gräler et al., 2016). In addition, we calculated the area under the curve (AUC) and visually evaluated the goodness of fit (Figure S4) by comparing the fitted values with the data (Korner-Nievergelt et al., 2015). For each model, we calculated the conditional and marginal Nakagawa's R^2 (Nakagawa et al., 2017; Nakagawa & Schielzeth, 2013) using the *performance* package (Lüdecke et al., 2021).

To quantify the effect of each predictor on the foraging probability (probability of presence), we present effect plots for each predictor (Korner-Nievergelt et al., 2015). To do so, for each draw from the posterior distribution, we calculated the regression line over the range of the variable that is shown in the effect plot. From these regression lines, we used the median as a point estimate regression line and the 2.5% and 97.5% quantiles as 95% credible interval (CrI; Korner-Nievergelt et al., 2015). When showing the effect of a ground cover variable across its range, the remaining area was divided among the other ground cover variables (including live vegetation) proportional to their mean proportions across all locations (and snow cover was set to zero). This was done due to the unit-sum constraint of ground cover variables. Data, code, and supplementary material used in this study are available under the DOI: 10.5281 at https://doi.org/10.5281/zenodo.7805040 (Müller et al., 2023).

3 | RESULTS

Our models revealed a positive effect of short vegetation and bare ground on the foraging probability (presence vs. pseudo-absence) of northern wheatears after the snow has melted, while the habitat characteristics changed as the season advanced. The most common ground cover type at foraging and pseudo-absence locations was live vegetation with a mean ± SD of 54.3% ± 30.0%, followed by bare ground (17.3% ± 17.0%), stones (12.1% ± 17.8%), dead vegetation (10.0% ± 17.3%), and woody vegetation (6.2% ± 16.9; Table 1). Snow was only present during the arrival and incubation period (15.5% ± 33.6%; Table 1). Characteristic seasonal developments were observed with decreasing snow, bare ground, and dead vegetation covers, while live vegetation increased as the season advanced (Figure S5).

The birds' foraging and pseudo-absence locations had a similar average vegetation cover in May and June. However, pseudo-absence locations rose to a higher level of live vegetation before stabilizing at the beginning of June. After that, mean cover of live vegetation remained higher at pseudo-absence locations compared to foraging locations until the end of the study period. Nevertheless, the general seasonal patterns followed the same trend in foraging and pseudo-absence locations (Figure S5). Overall, vegetation height at foraging and pseudo-absence points had a mean ± SD of 13.24 cm ± 9.46 cm and increased throughout the study period. In accordance with the changing ground cover composition and vegetation development, the mean NDVI value was 0.65 ± 0.19 and increased throughout the season. The mean rate of NDVI change was 0.18 ± 0.24, indicating an increase in vegetation greenness from May to July until it started to decline in August (Figure S5).

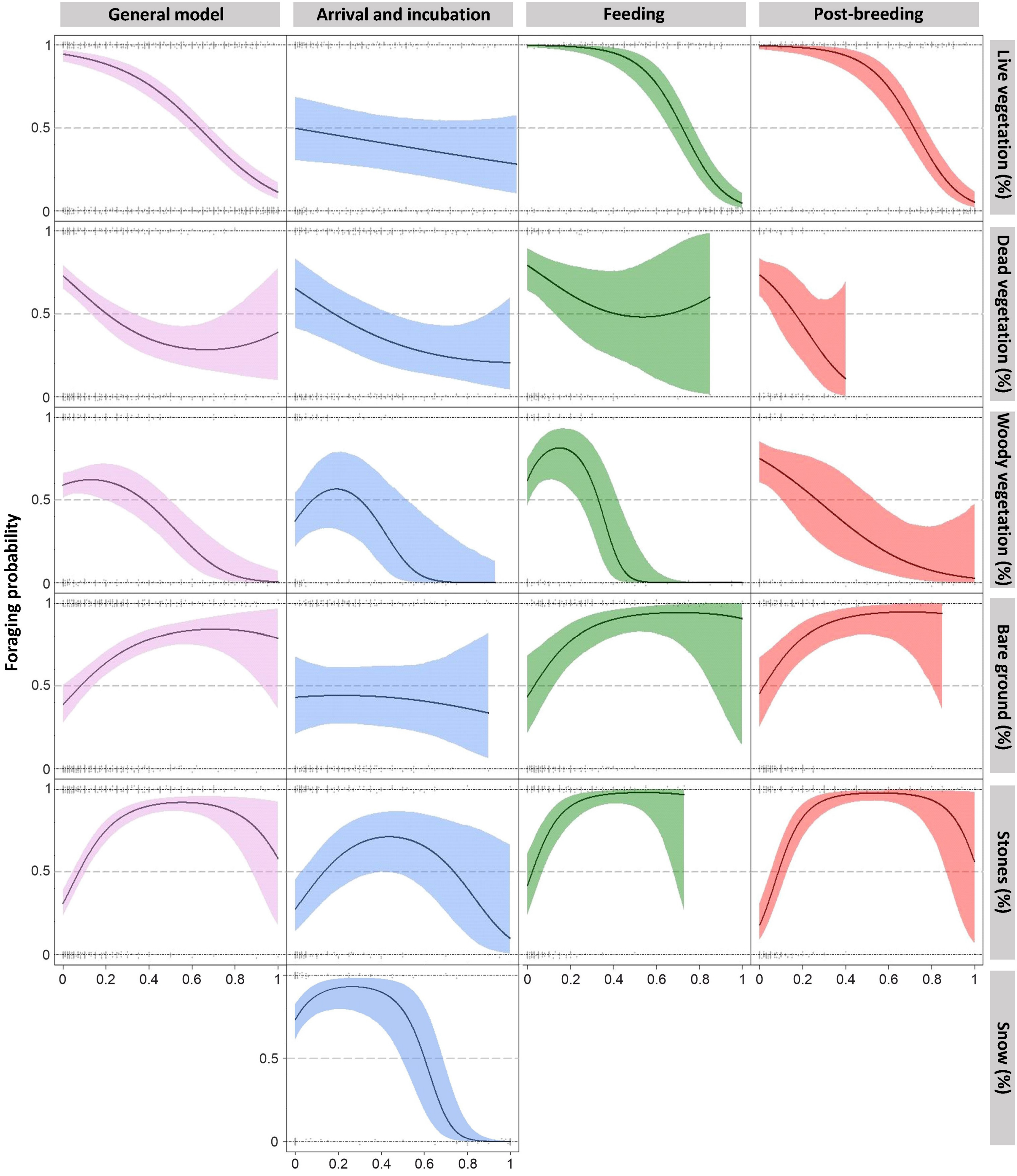

FIGURE 2 Predictions from logistic regression models showing the average effect (solid line) of each ground cover variable (labeled on the righthand side of the plots) on the foraging probability (presence vs. pseudoabsence) for the general model (whole study period; first column) and each period separately (other columns) within 1 m of the foraging (presence = 1) and pseudo-absence (0) locations. "Live vegetation" was not used as a predictor in the model but it is a derived parameter from the other ground cover parameters and is given here because all ground covers add up to 100%. The colored areas represent the 95% Bayesian credible intervals and the gray dots show the raw data.

TABLE 2 Summary of the output of the general (all-season) model, arrival and incubation, feeding (food provisioning for chicks), and postbreeding model using the 1-m data.

	General model			Arrival and incubation			Feeding			Postbreeding		
		CrI			CrI			CrI			CrI	
Variables	**Estimate**	**2.5%**	**97.5%**	**Estimate**	**2.5%**	**97.5%**	**Estimate**	**2.5%**	**97.5%**	**Estimate**	**2.5%**	**97.5%**
Bird ID (Intercept)	**0.13**	**0.01**	**0.35**	**0.19**	**0.01**	**0.54**	**0.35**	**0.02**	**0.94**	**0.22**	**0.01**	**0.64**
Point ID (Intercept)	0.09	0.00	0.25	**0.14**	**0.01**	**0.41**	**0.22**	**0.01**	**0.64**	**0.21**	**0.01**	**0.62**
Dead vegetation	−0.04	−0.24	0.15	−0.25	−0.64	0.13	0.14	−0.20	0.46	−0.24	−0.62	0.10
Dead vegetation^2	**0.21**	**0.06**	**0.37**	0.14	−0.15	0.43	0.16	−0.16	0.45	−0.05	−0.39	0.27
Woody vegetation	−0.20	−0.50	0.07	−0.54	−1.41	0.09	**−2.74**	**−5.43**	**−0.70**	−0.11	−0.54	0.28
Woody vegetation^2	**−0.33**	**−0.61**	**−0.09**	**−0.67**	**−1.46**	**−0.10**	**−1.96**	**−3.61**	**−0.62**	−0.01	−0.42	0.36
Bare ground	**0.81**	**0.62**	**1.01**	0.09	−0.27	0.44	**1.26**	**0.82**	**1.78**	**1.03**	**0.63**	**1.50**
Bare ground^2	−0.18	−0.36	0.00	−0.05	−0.36	0.27	−0.27	−0.67	0.20	−0.22	−0.56	0.18
Stones	**1.15**	**0.96**	**1.37**	**0.41**	**0.10**	**0.73**	**1.58**	**1.10**	**2.18**	**1.80**	**1.31**	**2.35**
Stones^2	**−0.49**	**−0.67**	**−0.29**	**−0.45**	**−0.73**	**−0.17**	−0.37	−0.79	0.13	**−0.95**	**−1.34**	**−0.52**
Snow				**−2.92**	**−4.54**	**−1.72**						
Snow^2				**−1.18**	**−1.84**	**−0.66**						
Vegetation height	**−1.04**	**−1.29**	**−0.80**	**−1.10**	**−1.58**	**−0.65**	**−1.59**	**−2.18**	**−1.05**	**−1.21**	**−1.69**	**−0.78**
Distance to marmot burrow	**−0.42**	**−0.64**	**−0.21**	**−0.37**	**−0.71**	**−0.05**	−0.44	−0.92	0.01	**−0.68**	**−1.18**	**−0.20**
NDVI	**0.49**	**0.29**	**0.70**	0.08	−0.31	0.47	**0.71**	**0.31**	**1.16**	**0.50**	**0.07**	**0.96**
NDVI^2	0.01	−0.16	0.18	0.03	−0.30	0.36	0.26	−0.11	0.68	0.02	−0.34	0.36
Rate of NDVI change	**−0.29**	**−0.49**	**−0.10**	−0.18	−0.49	0.13	**−0.62**	**−1.10**	**−0.18**	**−0.40**	**−0.82**	**−0.01**
Rate of NDVI change^2	0.03	−0.14	0.19	−0.18	−0.51	0.14	−0.30	−0.72	0.09	0.27	−0.13	0.66

Note: Foraging versus pseudo-absence points were modeled using a logistic regression with logit-link function. Bird ID and point ID are random effects, while all other variables are fixed effects. Given are the estimate and lower (2.5%) and upper (97.5%) limits of the 95% credible interval. Estimates where the 95% credible interval does not contain zero are highlighted in bold.

Based on AUC values as well as marginal and conditional R^2, the all-season model (AUC 0.87, R^2 marginal .59, R^2 conditional .6), the arrival and incubation model (AUC 0.83, R^2 marginal .78, R^2 conditional .78), the feeding model (food provisioning for chicks, AUC 0.92, R^2 marginal .88, R^2 conditional .89), and the postbreeding model (AUC 0.92, R^2 marginal .74, R^2 conditional .74), all performed well. The difference between the marginal and the conditional R^2 was consistently small, indicating a small effect of the random factors (i.e., individual and local preferences).

Vegetation height had a strong negative linear effect on the foraging probability (Figure 2), with the effect being strongest while feeding (Table 2). During this period, the mean vegetation height at foraging points was 10.3 cm (±7.3 cm) and 16.2 cm (±10.4 cm) at pseudo-absence points. Bare ground was positively related to the foraging probability, especially during the feeding period (Table 2, Figure 2). However, no effect of bare ground was found for the arrival and incubation stage when short vegetation and melting snow patches prevailed. Stone cover had a positive effect: during the feeding period, only the linear effect was well supported by the data, whereas in all other models, a maximum probability of foraging was observed at an intermediate (20%–70%) stone cover (Table 2, Figure 2). Locations with low stone cover (<15%) were less likely to be chosen for foraging (Figure 2). In the general model, woody vegetation showed a maximum at a low woody vegetation cover (Figure 2). Especially while feeding, woody vegetation had a negative effect on the foraging probability (Table 2). Locations with more than 40% woody vegetation were never used as foraging locations in the feeding period (Figure 2). In the postbreeding period, woody vegetation only had a weak negative effect (Table 2). Dead vegetation did not play an important role during any of the periods and only showed a weak negative trend in the general as well as the arrival and incubation models (Table 2, Figure 2). During the arrival and incubation period, snow cover showed a strong quadratic effect, indicating a high foraging probability at low to intermediate snow cover levels (Table 2, Figure 2). Locations with more than 60% snow were avoided (Figure 2). Foraging attempts were never observed directly on snow, even when it still covered a large part of the study area.

Increasing distance to the closest marmot burrow had a negative effect throughout the study period (Table 2, Figure 3), indicating a preference for foraging locations close to burrows (Figure 3). This effect was strongest at the postbreeding stage (Table 2). Except for the arrival and incubation stage, NDVI had a positive linear effect in each model, being strongest during the feeding period (Table 2, Figure 3). Even though vegetation was greening and growing fast during arrival and incubation (Figure S5), the rate of NDVI change had no strong effect on the foraging probability at that stage (Table 2), but it had a negative effect in the other models (Table 2, Figure 3). In the postbreeding stage, the rate of NDVI change had a slightly negative linear effect (Table 2, Figure 3).

We ran all models based on a 2-m-radius with very similar results (Table S2, Figure S6): Although some effects were stronger on the smaller scale, the general patterns were the same (Table 2, Table S2, Figure S6).

4 | DISCUSSION

Our study highlights the importance of small-scale characteristics in the foraging preferences of a long-distance migrant breeding in high-alpine habitats. Accessibility to the ground and habitat heterogeneity determined, on a very fine scale, whether a location was chosen for foraging. Habitat structure and ground cover composition changed as the season advanced, but northern wheatears generally showed similar habitat preferences throughout their presence in the study area. Interestingly, the habitat preferences were consistent between females and males as well as between adults and juveniles. We found a specific preference for open patches, interspersed with stones within vegetated areas, where prey abundance is expected to be higher (Morris, 2000). This underpins that a diverse habitat is necessary to sustain food availability for northern wheatears throughout their stay on the Alpine breeding grounds. Preferred foraging habitat in the study area was composed of multiple types of ground cover. Especially the presence of bare ground patches seemed important, which allow birds to detect and access prey more easily than in the surrounding vegetation (Schaub et al., 2010; Vickery & Arlettaz, 2012). In particular, bare ground plays a crucial role during food provisioning for chicks, when food demand is enhanced and vegetation is growing fast (Moreno, 1989b). Rocks and boulders may have played a similar role, as they served as perching positions, allowing the birds to detect prey more easily. Particularly in the postbreeding period, stones may also have hosted an increased amount of prey, as we have repeatedly observed birds picking ants and other prey items from boulders or directly from anthills located in rocky areas; this was not the case earlier in the season.

Nonetheless, our NDVI results indicate that vegetation productivity is an important component of the foraging microhabitat. This result must be interpreted in the context of larger-scale effects. The minimal spatial resolution of sentinel-2 satellite data is 10 m, which means that the available information summarizes a larger area than the sampling locations, informing on the productivity in the habitat matrix around the foraging location. Even though patches with bare ground and stones were preferred on a small scale, they lay within the territories in the study area where heterogeneous and productive grassland is the dominating habitat type. On the one hand, this result implies that northern wheatears selected productive areas for foraging that offer high arthropod abundance and diversity (Morris, 2000), which increases with vegetation height (Atkinson et al., 2004). On the other hand, high vegetation decreases visibility and access to the ground (Atkinson et al., 2004; Vickery & Arlettaz, 2012) and reduces the probability of a foraging attempt being successful (Dennis et al., 2008). As a ground-foraging insectivore, the northern wheatear requires visibility of and access to the ground for foraging (Arlt & Pärt, 2007; van Oosten et al., 2014). The preference for short vegetation on a fine scale suggests that prey accessibility is more limiting for successful foraging than prey abundance. This result is consistent with findings from study sites in the lowland of Northern Europe. In the Netherlands, where prey abundance remains stable throughout the breeding season,

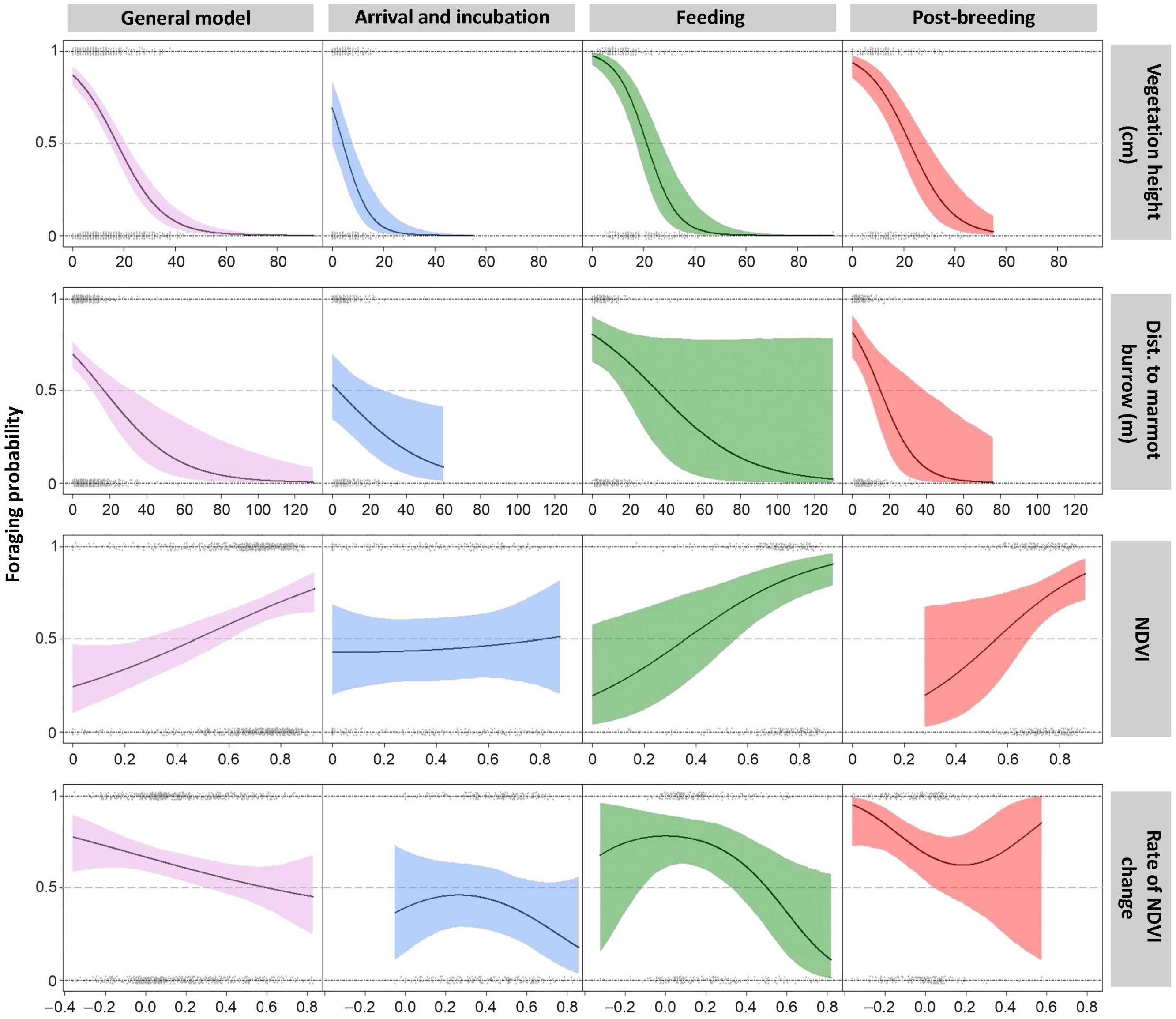

FIGURE 3 Model predictions from logistic regression models showing the average effect (solid line) of vegetation height, distance to marmot burrow, NDVI, and the rate of NDVI change (labeled on the righthand side of the plots) on the foraging probability (presence vs. pseudo-absence) for the general model (whole study period; first column) and each period separately (other columns) within 1 m of the foraging (presence = 1) and pseudo-absence (0) locations. The colored areas represent the 95% Bayesian credible intervals and the gray dots show the raw data.

northern wheatears are more limited by prey accessibility than by prey abundance, as they preferentially forage in short grass (van Oosten et al., 2014). Similarly, northern wheatear populations had improved growth rates in short-vegetation habitats compared to tall field layers in Swedish farmland (Arlt et al., 2008), where the presence of short vegetation is a major driver of population growth (Arlt et al., 2008; Paquet et al., 2019) and an important clue for habitat selection (Arlt & Pärt, 2007). The preference for short vegetation has been consistently described for lowland bird communities (Atkinson et al., 2004; Rime et al., 2020; Vickery & Arlettaz, 2012) as well as for other insectivorous alpine birds (Barras et al., 2020; Brambilla et al., 2017; Resano-Mayor et al., 2019).

Even though woody vegetation reduces ground accessibility and was usually avoided, it played a specific role later in the season when it provided berries as an additional food source, explaining the observed weaker avoidance of this habitat type in the post-breeding season. We then observed northern wheatears foraging on *Vaccinium myrtillus* and *Daphne mezereum* berries. Coloring of the feces confirmed the consumption of berries (García-Rodríguez et al., 2022). Many insectivorous birds become frugivorous when their main food source becomes scarce (Bairlein, 2003; Fry, 1992). Berries are important sources of nutrients that may enhance molt and are crucial for migration (Bairlein, 2003; Eeva et al., 2018). Berries are therefore actively chosen, while including berries in an insectivorous diet most likely also reduces foraging energy expenditure and further supports fattening for migration (Lindström, 2003). Nevertheless, northern wheatears still preferred open habitat in the postbreeding period, suggesting a sufficient abundance of arthropods (Beck et al., 2010; Pilar et al., 2020; Resano-Mayor et al., 2019).

The preference for highly accessible patches within more productive areas has been described for a variety of ground-foraging insectivorous farmland birds (Atkinson et al., 2004; Martinez et al., 2010; Schaub et al., 2010; Tagmann-Ioset et al., 2012; Vickery et al., 1999; Vickery & Arlettaz, 2012; Weisshaupt et al., 2011) as well as for alpine specialists (Barras et al., 2020; Brambilla et al., 2017; Resano-Mayor et al., 2019). Food abundance for insectivores is higher in heterogeneous habitat (Cole et al., 2010), and fine-scale habitat diversity provides accessible patches within species-rich landscapes that support high food abundance (Atkinson et al., 2004; Vickery & Arlettaz, 2012). Furthermore, habitat heterogeneity maintains food availability temporally by allowing diverse vegetation phenology to coexist and supply sufficient food throughout the season (Benton et al., 2003; Hovick et al., 2015; Vickery & Arlettaz, 2012). This is important because the habitat characteristics in the study area were strongly influenced by seasonal changes, while the species' foraging habitat preferences remained similar. The availability of suitable foraging habitat mainly depended on the progress of spring greening-up. In 2021, the area experienced a late and cold spring. When the birds arrived in the breeding region in May, most of their territories were still covered by snow. During the melting period, the edges of snow fields played an important role, providing accessible habitat with high prey abundance (Barras et al., 2020; Brambilla et al., 2017; Leingärtner et al., 2014; Resano-Mayor et al., 2019). Once vegetation growth increased and ground accessibility declined, habitat heterogeneity and the availability of open habitat patches became crucial in providing suitable foraging habitat. Similar results were found at a larger scale in Swedish farmland habitats, where fields with low vegetation became increasingly important for northern wheatears and positively influenced reproductive success later in the season (Arlt & Pärt, 2007). Sander et al. (2022) showed that nest survival of northern wheatears benefitted from a higher vegetation at another site in the Alps with a broader elevational gradient. This could be explained by a sparser and generally lower vegetation in more mineral-based high-elevation habitats. This is in line with the preference for more productive grasslands with an intermediate ground cover of stones and rock in our study area. At our study site, most northern wheatears remained in their territories throughout their presence (Rime et al., 2023). Other ground-dwelling insectivorous birds seem to be less capable of finding suitable habitat in their breeding territories as the season advances. For example, white-winged snowfinches (*Montifringilla nivalis*) rely on Tipulidae larvae at the retreating snow front (Brambilla et al., 2017; Resano-Mayor et al., 2019), a food resource used by adult northern wheatears only in the pre-breeding period, while ring ouzels (*Turdus torquatus alpestris*) rely mainly on earthworms and perform diel and seasonal altitudinal movements to track suitable foraging habitat as spring advances (Barras et al., 2020, 2021). Similarly, water pipits (*Anthus spinoletta*) perform within-season movements to avoid dense and high grassland as vegetation growth progresses (Ceresa et al., 2020).

Due to this strong dependence of northern wheatears on the small-scale habitat mosaic that maintains suitable foraging habitat, the species is likely sensitive to climate and land-use change (Scridel et al., 2018; Theurillat & Guisan, 2001). In most parts of Europe, northern wheatear populations are declining, while the Alpine populations are stable overall (Gideon et al., 2014; Hallman et al., 2022; Issa & Muller, 2015; Keller et al., 2020; Knaus et al., 2018). Northern wheatears might be less vulnerable to climate change than other high-elevation specialists as long as micro-habitat heterogeneity is maintained. The rock ptarmigan (*Lagopus muta*) and the white-winged snowfinch (*Montifringilla nivalis*) for instance show a decrease in all but the uppermost part of their distributional range where populations remain stable (Issa & Muller, 2015; Keller et al., 2020; Knaus et al., 2018). The population trends suggest that these species are limited in their ability to find suitable habitat, even at higher altitudes.

For northern wheatears, an upward shift in elevation has been observed in Switzerland, with the increase above 2400 m being higher than the loss at lower elevation, resulting in a stable or increasing general population trend (Hallman et al., 2022; Knaus et al., 2018). However, such an ongoing shift could lead to range contraction in the future (Dirnböck et al., 2003; Jähnig et al., 2020). Furthermore, winters in the Alps tend to become shorter, and spring greening-up is expected to advance earlier (Asam et al., 2018; Chamberlain & Pearce-Higgins, 2013; Gobiet et al., 2014). The resulting rise of the tree line, the increasing bush encroachment, and higher vegetation density are threatening the availability of accessible foraging habitat also for the northern wheatear (Ceresa et al., 2021; Jähnig et al., 2020). Land-use change enhances population threats even further (Kulakowski et al., 2011): Agricultural intensification leads to landscape homogenization (Benton et al., 2003) and to higher nutrient levels, accelerating vegetation development and altering species composition (Dirnböck et al., 2003; Fischer et al., 2008). Even more apparent in alpine regions, pastoral abandonment leads to an increased vegetation height and eventually to shrub and forest encroachment (Gehrig-Fasel et al., 2007; Kulakowski et al., 2011; Laiolo et al., 2004). On the other hand, low-intensity grazing of cattle positively influences ground-foraging birds (Atkinson et al., 2004; Laiolo et al., 2004; Vickery et al., 1999) and maintains suitable foraging habitat for the northern wheatear (Maron & Lill, 2005). It is important to note that the positive effects of grazing on grassland bird communities are associated with low-intensity grazing, as applied in our study area, whereas high-intensity grazing can negatively affect them (Brambilla et al., 2020; Garcia-Pausas et al., 2017). Even though we were not able to quantify the effects of grazing with our method focusing on small-scale habitat parameters, low-intensity grazing is an important driver of landscape dynamics (Laiolo et al., 2004; Yoshihara et al., 2010). In areas that were grazed, vegetation height was lower and more heterogenous, and the growing dynamic was disrupted. With the onset of grazing in the study area, mean vegetation height stopped increasing and leveled off. Additionally, northern wheatears showed a preference for patches with stable vegetation dynamics that ensure long-term habitat heterogeneity (Hovick et al., 2015; Vickery & Arlettaz, 2012). Furthermore, the foraging habitat of northern wheatears was probably positively influenced by alpine marmots, as northern wheatears where often foraging close to their burrows. Despite field observations suggesting marmots as potential nest predators, benefits of association with marmots seem to persist. Marmots maintain structural heterogeneity and accessible habitat by creating patches of bare ground, keeping the vegetation short, and potentially improving arthropod abundance and species richness (Ballová et al., 2019; Buyandelger et al., 2021; Buyandelger & Otgonbayar, 2022; Davidson et al., 2012).

Even though resource availability and habitat characteristics change temporally within a season, the foraging habitat preferences of northern wheatears remained similar at the study site. Northern wheatears depend on the availability of suitable foraging habitat within the same territory for the entire presence at the breeding site, even after the chicks are fully independent. Within an ecosystem that is characterized by spatiotemporal dynamics that are different to those in lowland habitats, Alpine northern wheatears inhabit an ecological niche that features a mosaic of accessible patches within vegetated areas that provide high prey abundance. Due to pressures from climate and land-use change on alpine ecosystems, this habitat is fragile and northern wheatears may be sensitive to habitat loss and range contraction. Our study emphasizes the importance of the Alpine breeding area for northern wheatears. It underlines the necessity to maintain and preserve the spatiotemporal availability of structural diversity and small-scale habitat heterogeneity that is critical in providing suitable foraging habitat for northern wheatears in the Alps in the long term.

AUTHOR CONTRIBUTIONS

Christoph M. Meier: Conceptualization (supporting); formal analysis (supporting); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (equal). **Florian Knaus:** Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (equal). **Pius Korner:** Data curation (supporting); formal analysis (equal); methodology (supporting); software (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal). **Barbara Helm:** Funding acquisition (equal); project administration (supporting); resources (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (equal). **Valentin Amrhein:** Supervision (supporting); validation (supporting); writing – review and editing (equal). **Yann Rime:** Conceptualization (lead); data curation (supporting); formal analysis (equal); funding acquisition (lead); investigation (supporting); methodology (lead); project administration (lead); resources (equal); software (equal); supervision (lead); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal). **Thomas M. Müller:** Conceptualization (supporting); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); project administration (equal); software (equal); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and codes used in this study are deposited on Zenodo under the DOI: 10.5281 at https://doi.org/10.5281/zenodo.7805040 (Müller et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Supplementary Material

Table S1: Variables recorded or calculated for each point but not included in the multivariate statistical models.

Category	Variable	Description	Unit
Point information	Coordinates	X and Y coordinates of the point location	X, Y
Bird Information	Age	Age class (juvenile, adult)	
	Sex	Adult sex (female, male)	
	Stage	Breeding stage (arrival, incubation, feeding, post-breeding)	
Nest	Nest ID	Unique identifier for the individual's nest	
	Distance to Nest	3D-distance from point to nest	m
Ground cover	Live vegetation	Green vegetation grown this year	%
Snow	Distance to snow	Distance to closest snow patch (if within 100 m)	m
Ecosystem Engineers	Cows	Cows present within 5m radius (Yes/No)	2 categories
	Grazing	Meadows ungrazed, currently grazed, previously grazed this year or grazed in the previous years	4 categories
	Cow dung	Presence of cow dung within the radius	2 categories
Topography	Elevation	Altitude	m. a. s. l.
	Slope	Slope inclination (steepness)	%
	Aspect	Orientation	°
Berries	Number of berries	Estimated number of berries within the radius	Number of berries

Table S2: Summary of the output of the **general** (all-season) model, **arrival and incubation**, **feeding** and **post-breeding** model using the **2-m** data. Foraging vs. pseudo-absence points were modelled using a logistic regression with logit-link-function. Bird ID and point ID are random effects, while all other variables are fixed effects. Given are the estimate and lower (2.5%) and upper (97.5%) limits of the 95% Credible Interval. Estimates where the 95% Credible Interval does not contain zero are highlighted in bold.

	General model			Arrival and incubation			Feeding			Post-breeding		
		CrI			CrI			CrI			CrI	
Variable	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%
bird ID (Intercept)	0.11	0.00	0.32	**0.16**	**0.01**	**0.46**	**0.24**	**0.01**	**0.69**	**0.19**	**0.01**	**0.55**
point ID (Intercept)	0.08	0.00	0.23	0.13	0.00	0.37	**0.18**	**0.01**	**0.51**	**0.20**	**0.01**	**0.57**
dead vegetation	-0.14	-0.35	0.05	-0.30	-0.67	0.07	0.05	-0.28	0.36	**-0.51**	**-0.90**	**-0.14**
dead vegetation^2	0.08	-0.11	0.25	-0.09	-0.40	0.20	0.12	-0.20	0.41	-0.13	-0.57	0.26
woody vegetation	0.06	-0.14	0.25	-0.08	-0.45	0.24	-0.30	-1.05	0.28	0.03	-0.33	0.36
woody vegetation^2	-0.20	-0.41	-0.00	-0.21	-0.54	0.08	-0.55	-1.30	0.03	-0.08	-0.43	0.25
bare ground	0.71	0.52	0.90	0.01	-0.31	0.35	**1.18**	**0.76**	**1.64**	**0.75**	**0.41**	**1.13**
bare ground^2	-0.16	-0.32	0.02	-0.05	-0.34	0.24	-0.13	-0.51	0.35	-0.26	-0.56	0.07
stones	**1.07**	**0.87**	**1.30**	**0.30**	**0.03**	**0.58**	**1.26**	**0.90**	**1.68**	**1.62**	**1.18**	**2.12**
stones^2	**-0.35**	**-0.53**	**-0.17**	**-0.35**	**-0.60**	**-0.09**	-0.33	-0.68	0.06	**-0.61**	**-1.00**	**-0.16**
snow				**-2.04**	**-3.06**	**-1.18**						
snow^2				**-0.89**	**-1.45**	**-0.43**						
vegetation height	**-1.02**	**-1.26**	**-0.79**	**-1.00**	**-1.41**	**-0.58**	**-1.36**	**-1.84**	**-0.92**	**-1.23**	**-1.67**	**-0.80**
distance to marmot burrow	**-0.44**	**-0.68**	**-0.22**	**-0.34**	**-0.64**	**-0.04**	**-0.48**	**-0.93**	**-0.05**	**-0.67**	**-1.15**	**-0.22**
NDVI	**0.39**	**0.19**	**0.60**	-0.01	-0.37	0.37	**0.56**	**0.18**	**0.93**	**0.57**	**0.12**	**0.99**
NDVI^2	0.06	-0.11	0.23	0.06	-0.26	0.38	**0.34**	**0.01**	**0.69**	0.09	-0.26	0.42
rate of NDVI change	**-0.32**	**-0.51**	**-0.13**	-0.24	-0.54	0.04	**-0.66**	**-1.06**	**-0.27**	**-0.41**	**-0.81**	**-0.02**
rate of NDVI change^2	-0.05	-0.22	0.11	-0.17	-0.46	0.13	-0.20	-0.55	0.14	0.25	-0.15	0.64

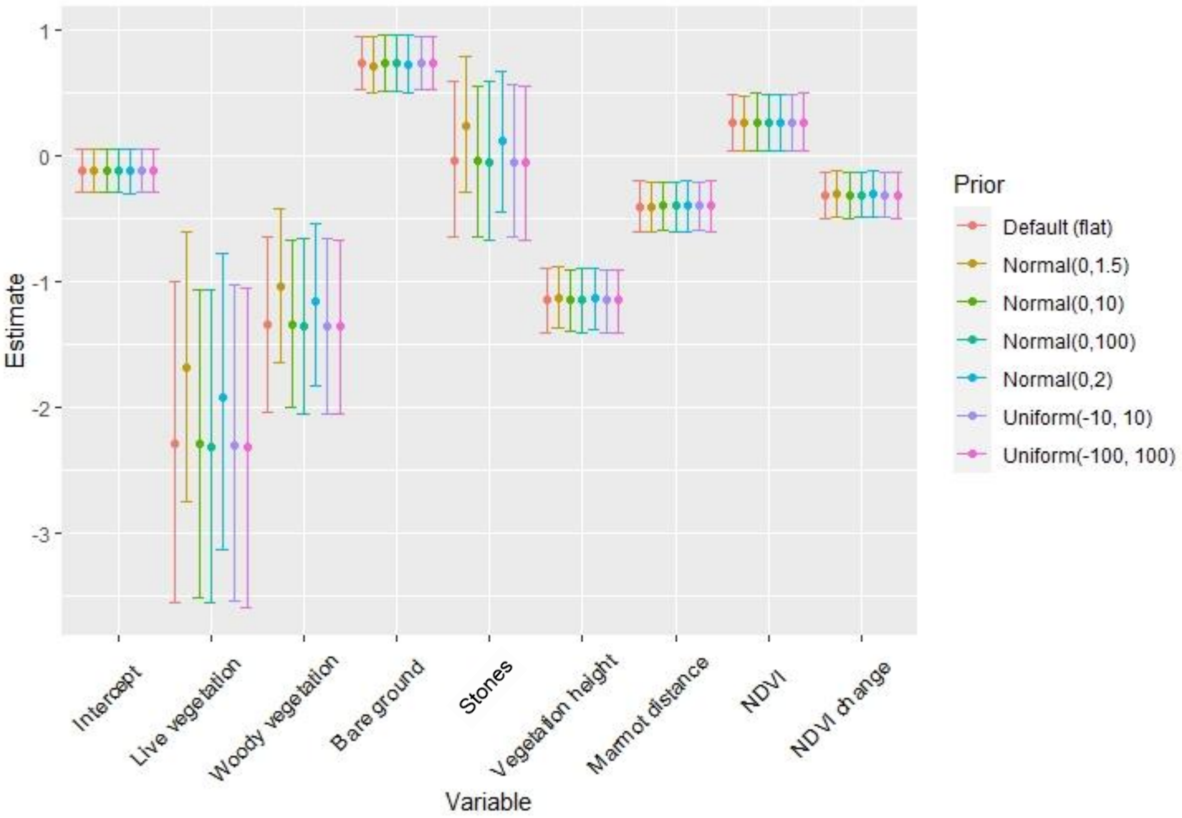


Fig. S1: Sensitivity analysis plot showing the estimates and 95%-credible intervals (CrI) for different prior distributions for the population-level effects of a preliminary model. The two very informative priors N(0,1.5) and N(0,2) influence the results quite strongly while the uninformative priors lead to very similar results. As a conclusion, we chose flat priors (N(0,100)).

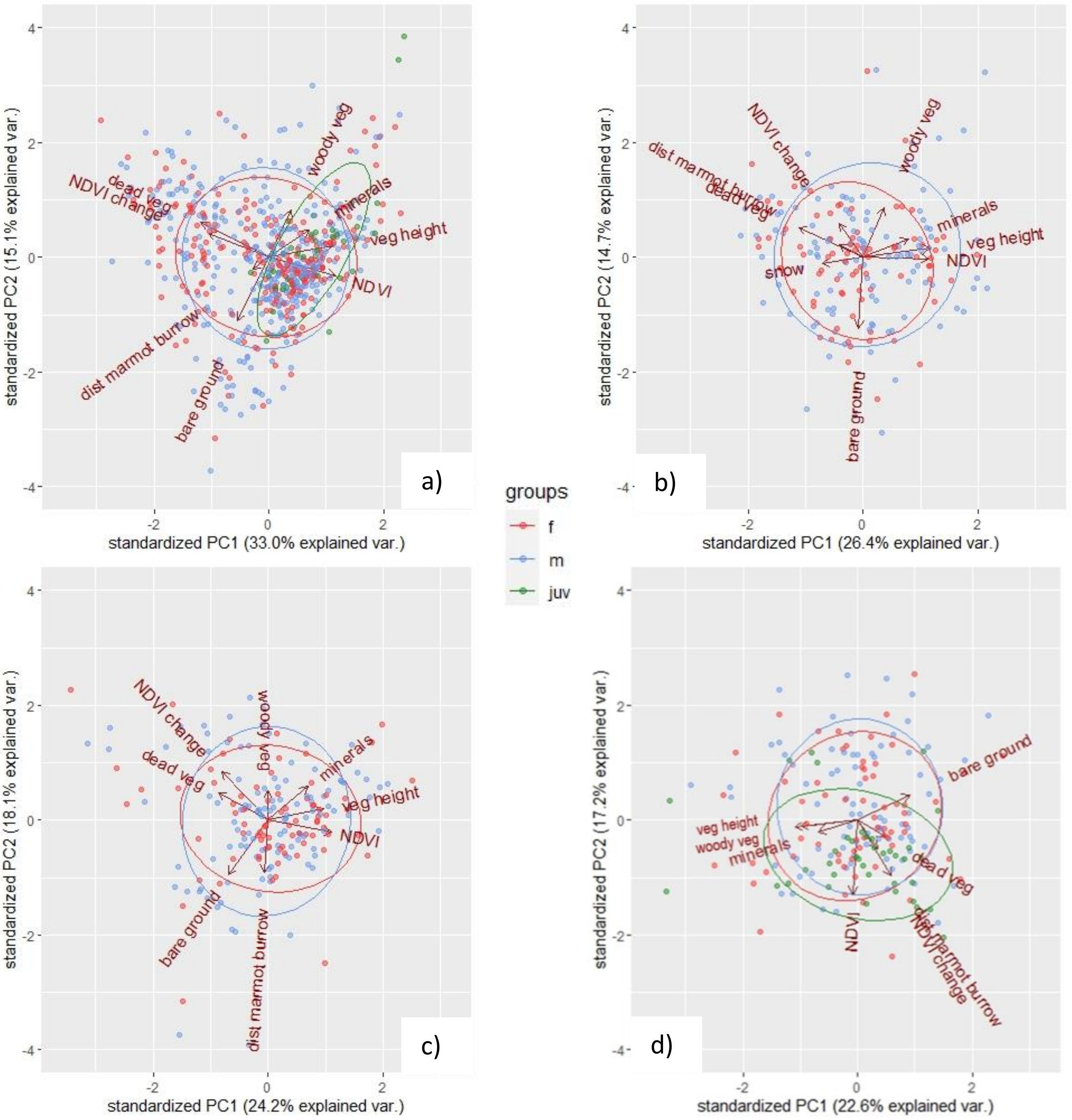


Fig. S2: Principal Component Analysis showing the first 2 principal components (PC1 & PC2) with foraging data (presence points only) of the entire study period (general model) (a), arrival and incubation (b), feeding (c) and post-breeding periods (d) and the variables used in the respective models. Colours distinguish points of females (red), males (blue) and juveniles (green), and the coloured circles group the respective categories together. Juveniles were only present in the post-breeding period and therefore do not occur in the arrival & incubation and the feeding PCA. The variation within the model stage that is explained by each of the principal components is given on the x (PC1) and y (PC2) axis.

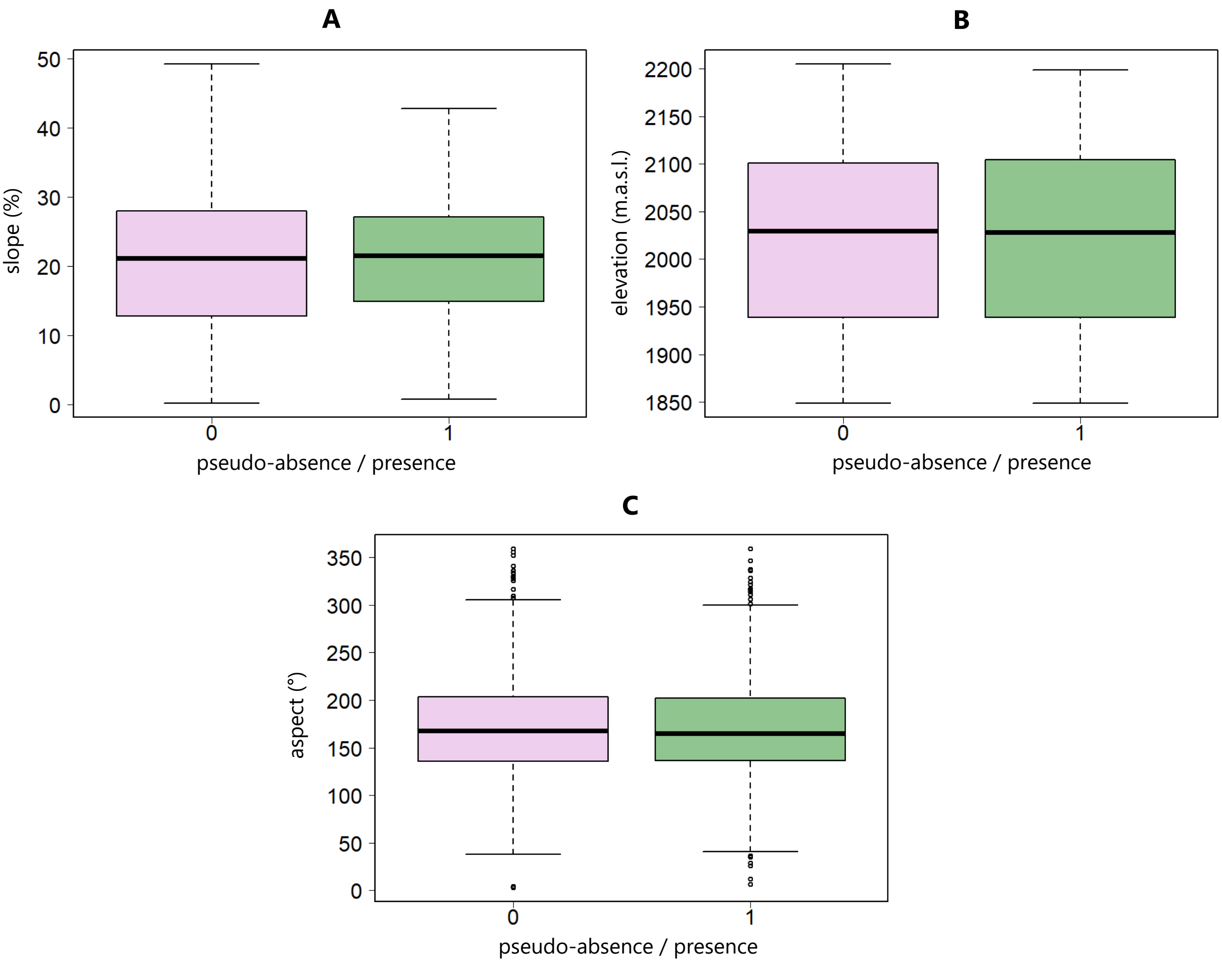


Fig. S3: Boxplots showing the distribution of the topgographic variables for presence (1) and pseudo-absence (0) points from the entire study season. Plot A shows the slope (%), B shows the elevation (m.a.s.l.) and C shows the aspect (°). The bold black line indicates the median and the boxes show the interquartile ranges. The dotted line covers the range of datapoints. Univariate mixed models (using Bird ID and Point ID as random factors) for topographic variables were additionally run. They revealed no strong effects of the slope (Estimate: 0.06, 95%-CrI: -0.06 to 0.18), elevation (Estimate: 0.01; 95%-CrI: -0.11 to 0.13), and aspect (Estimate: -0.02; 95%-CrI: -0.14 to 0.1) on the foraging probability.

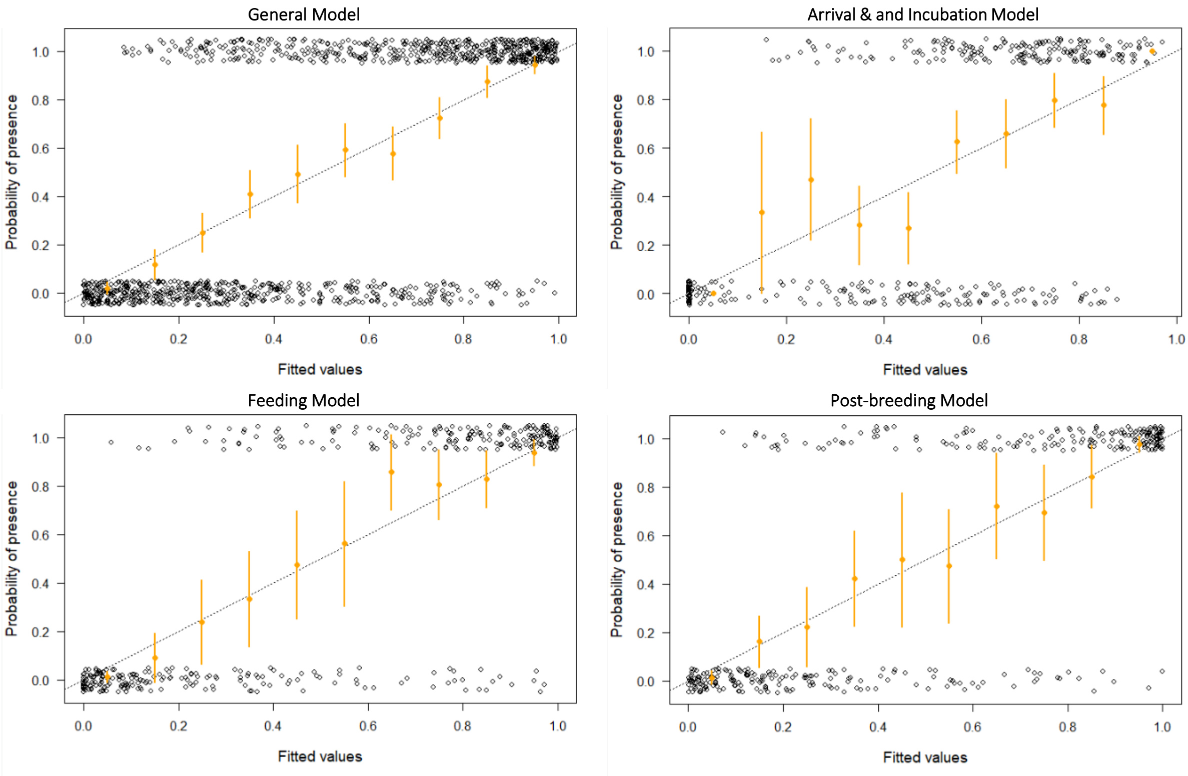


Fig. S4: Goodness of fit plots showing how well the fitted values match the data in each model. The open circles show observed foraging (presence=1) and pseudo-absence (absence=0) points. Orange dots indicate the mean (and 95% confidence intervals as orange lines) of observations on an interval of 0.1. Perfect coincidence between observed and fitted values is indicated by the dotted line.

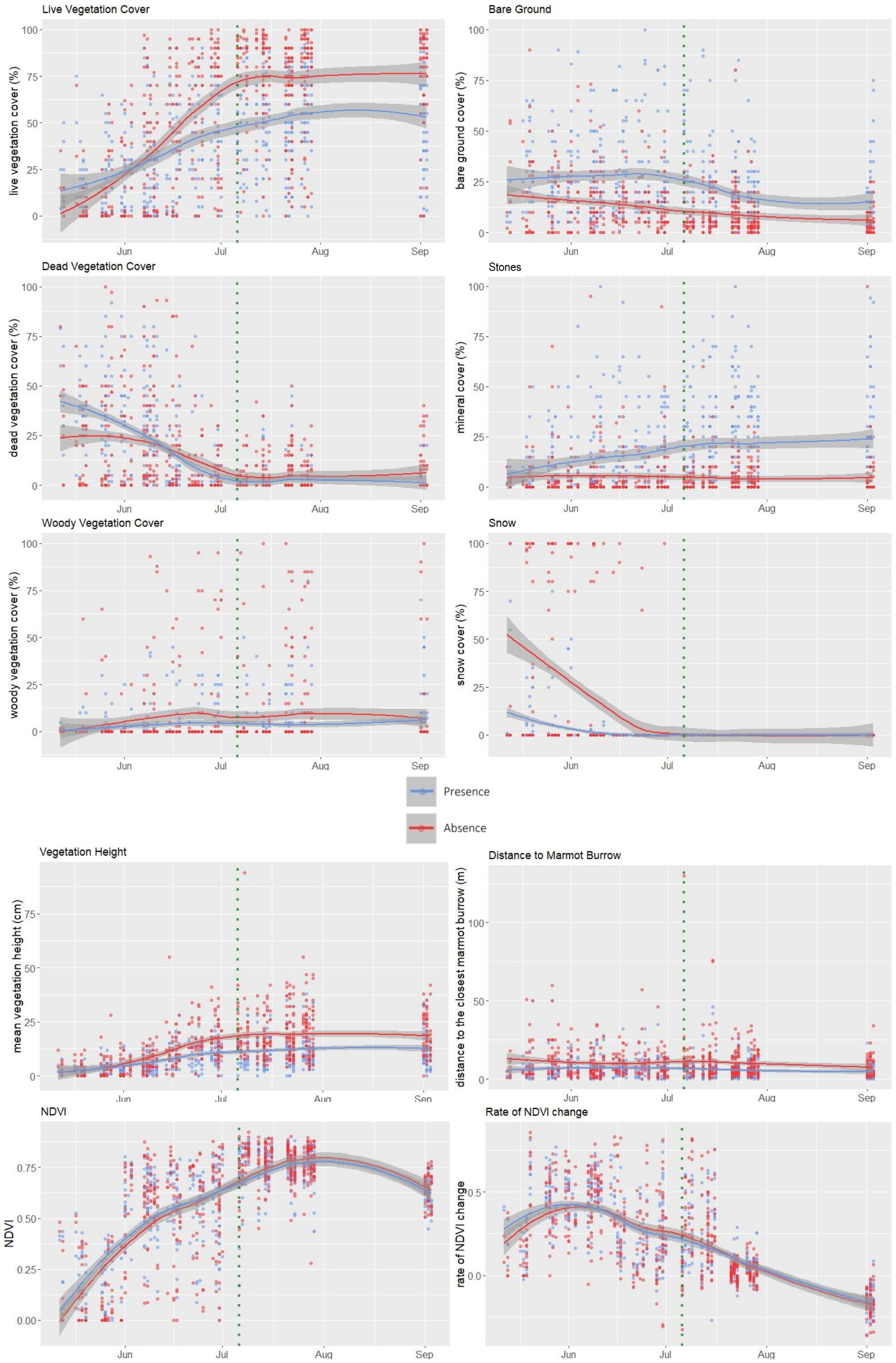


Fig. S5: Seasonal development of each variable on the 1-m radius. The coloured points represent the foraging (blue) and pseudo-absence points (red). The solid lines show the mean development at foraging (blue) and pseudo-absence points (red) with the standard deviation (grey area). The green dotted line indicates the onset of grazing in the study area.

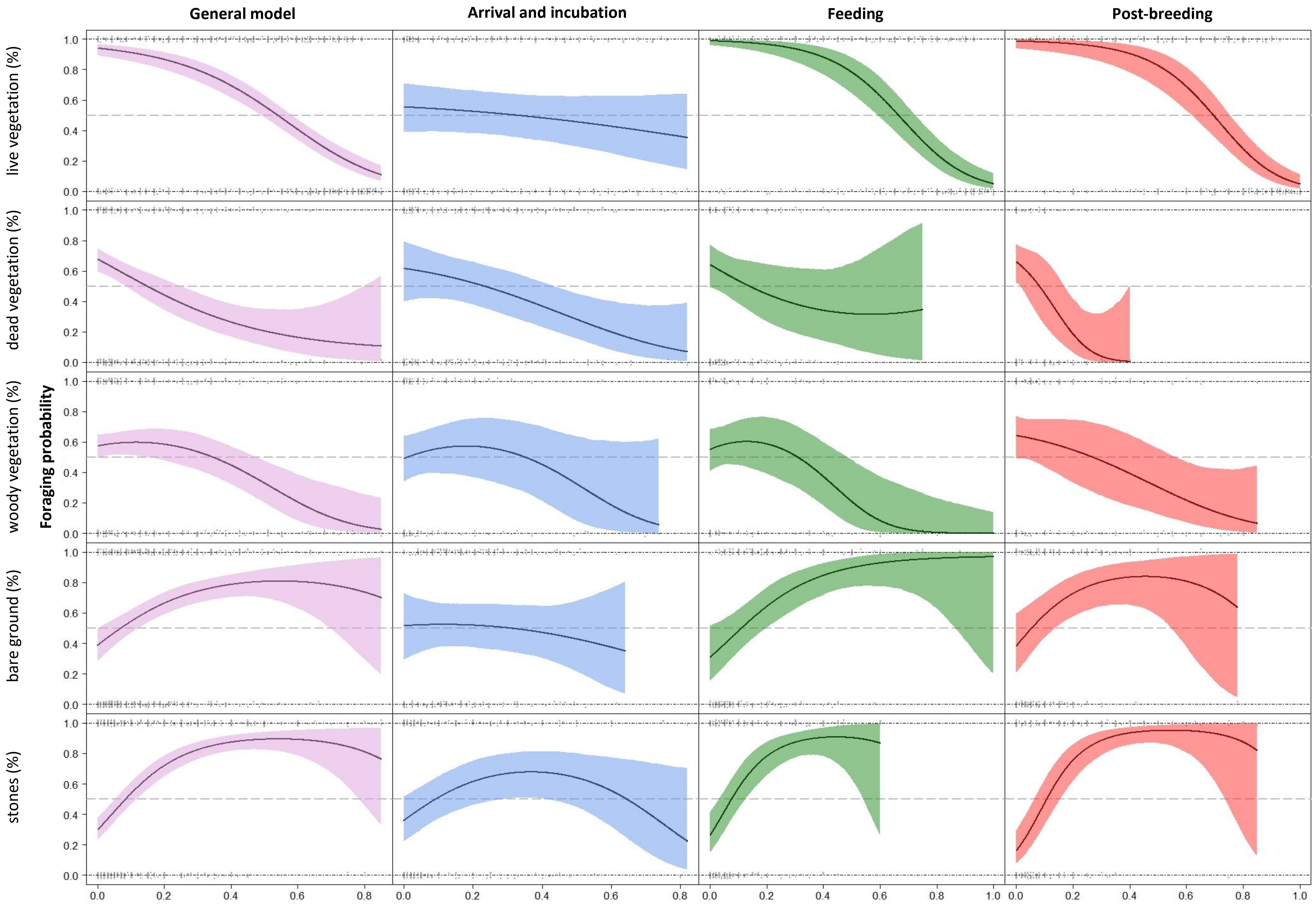
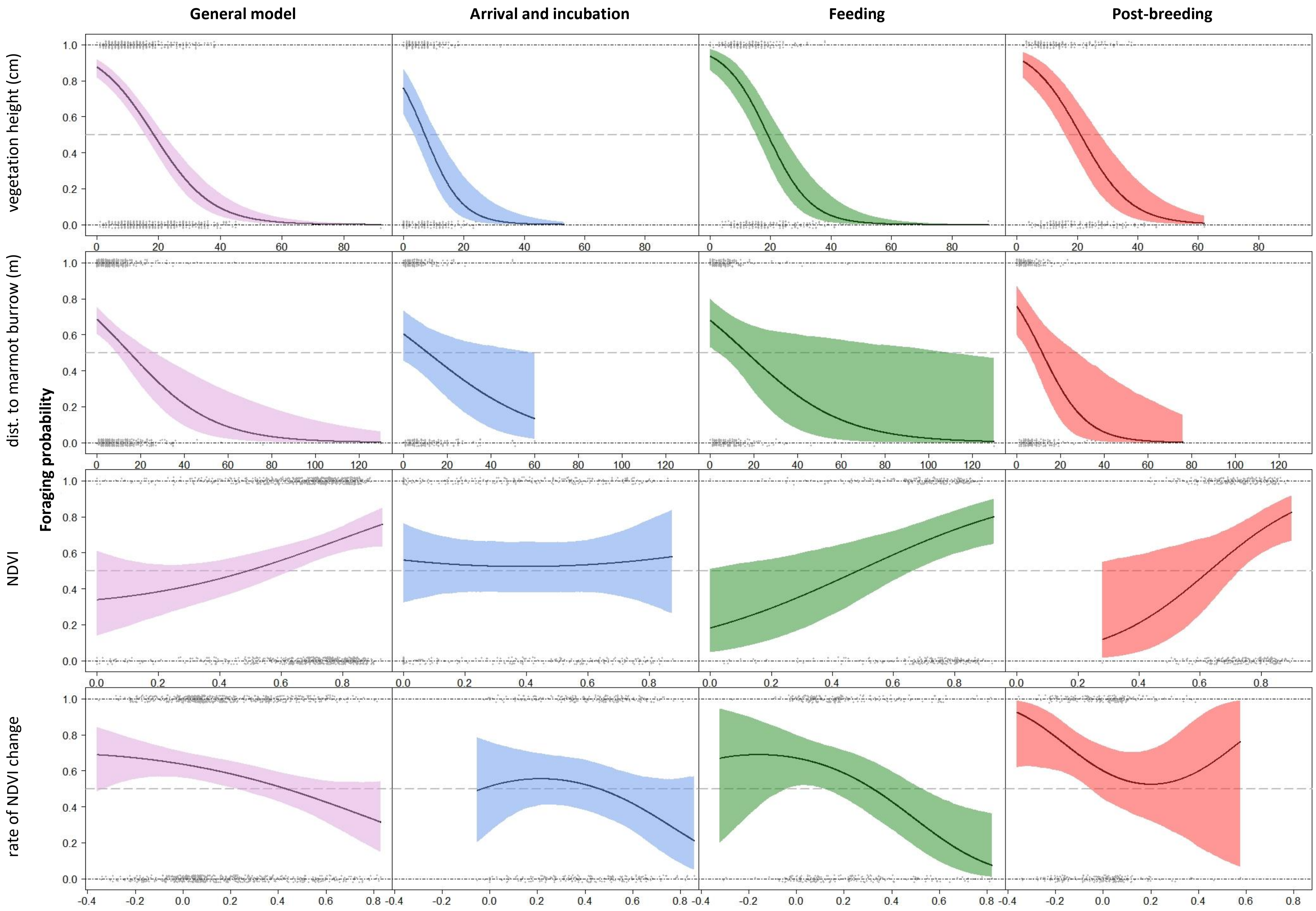


Fig. S6: Model predictions from logistic regression models showing the average effect (solid line) of each variable on the foraging probability (presence vs. pseudo-absence) for the general model (whole study period; 1st column) and each period separately (2nd-4th column) using the 2-m data. “Live vegetation” was not used as a predictor in the model but it is a derived parameter from the other ground cover parameters and given because all ground covers add up to 1. The coloured areas represent the 95% Bayesian Credible Intervals and the grey dots show the raw data. The plot is continued on the next page.


General model
Arrival and incubation
Feeding
Post-breeding
Foraging probability
vegetation height (cm)
dist. to marmot burrow (m)
NDVI
rate of NDVI change
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
120
-0.4
-0.2

Chapter 3

Breeding habitat preferences and niche partitioning of declining insectivorous songbirds in Alpine grasslands

Alpine grassland habitat in Val Piora and male Whinchat *Saxicola rubetra* (© Yann Rime)

Breeding habitat preferences and niche partitioning of declining insectivorous songbirds in Alpine grasslands

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Abstract

Alpine grasslands are increasingly facing pressures of climate and land use changes. Warmer temperatures and pastoral abandonment lead to treeline shift and to bush encroachment. Conversely, agricultural intensification causes eutrophication and landscape homogenization. However, Alpine grasslands host important populations of Alpine specialists subject to range contraction, such as Water Pipits. Moreover, insectivorous, ground-breeding migratory species, such as Northern Wheatears and Whinchats, still have stronghold populations in high-elevation habitats. These species undergo Europe-wide declines, and the Alps are key for their conservation. While lowland farmland suffered more acute biodiversity losses and received wider research attention, fewer studies characterized community composition and species-specific habitat preferences in changing Alpine grasslands, often focusing on single species. Here, we conducted repeated surveys during the breeding season in a high-elevation Alpine valley. We carried out a principal component analysis highlighting fine-scale niche partitioning in the four most common species, which are all insectivorous migrants. We then analysed landscape-scale habitat preferences of the six most common species, using their abundance as a response variable explained by predictors related to topography, vegetation productivity, and habitat composition. Water Pipits, Northern Wheatears and Whinchats were most abundant and had higher densities on gentle, productive slopes that are the prime target of pastoralism in mountain regions, but are often subject to intensification. Shrub cover had positive effects on the density of Whinchats and Dunnocks but was avoided by Water Pipits. These species-specific preferences call for maintaining landscape heterogeneity and low-intensity management, to preserve the role of Alpine grasslands as a refuge for declining insectivorous species.

Keywords: Alpine grassland, *Anthus spinoletta, Oenanthe oenanthe, Saxicola rubetra, Prunella modularis*

Introduction

Alpine ecosystems are under threat of climate and land-use changes, leading to modifications in habitat composition and seasonality (Chamberlain et al., 2023). Open, Alpine grasslands above the treeline are generally under low-intensity management and received little research attention compared to lowland farmland, where agricultural intensification had stronger negative consequences on biodiversity (Donald et al., 2001), especially through a loss of habitat heterogeneity (Benton et al., 2003; Fahrig et al., 2011; Rime et al., 2020). However, changes also occur at high elevations: climate change can lead to earlier onset of vegetation growth, bush encroachment, and upwards shift of the treeline in Alpine grassland (Cudlín et al., 2017; Gehrig-Fasel et al., 2007; Leonelli et al., 2011). At the same time, land-use changes often lead either to intensification in areas that are easy to reach and manage, or to land abandonment in more remote mountain regions (Chemini & Rizzoli, 2003; Cudlín et al., 2017; Tasser et al., 2005). Climate and land-use changes impact mountain bird communities (Lehikoinen et al., 2014; Maggini et al., 2014; Scridel et al., 2018), but their relative influences remain difficult to disentangle (Alba et al., 2022; Barras et al., 2021; Chamberlain & Pearce Higgins, 2013; Laiolo et al., 2004). Climate and habitat changes in mountain regions mostly have negative effects, such as range-contraction of cold-adapted species (Brambilla et al., 2018; Hallman et al., 2022; La Sorte & Jetz, 2010; Sekercioglu et al., 2008). Nevertheless, in their current form, Alpine grassland can play a key role for the conservation of bird species that are declining in lowland agricultural areas, such as ground-breeding and insectivorous species (Alba et al., 2022; Knaus et al., 2018).

Birds breeding in these highly seasonal habitats benefit from a high abundance in insect food during brief periods (Martin & Wiebe, 2004). Alpine-specialized insectivorous birds of conservation concern are very common in this habitat, such as the Water Pipit *Anthus spinoletta*: this species is the most abundant bird of Alpine grassland but undergoes upwards range shift (Bollmann & Reyer, 2001; Hallman et al., 2022; Knaus et al., 2018). The populations of the insectivorous Northern Wheatear *Oenanthe oenanthe* and Whinchat *Saxicola rubetra*, both ground-breeding migrants, decreased widely in lowland Europe, while the Alps still host major strongholds for both species (Keller et al., 2020; Knaus et al., 2018). For Northern Wheatears, an upward shift occurs in the Alps, with populations at lower elevations decreasing, and populations above 2400m a.s.l. increasing. Given the extent of available habitat at high elevation, this currently results in a general augmentation of the population. Such a positive trend contrasts with the overall negative trends in lowland Europe (Hallman et al., 2022; Keller et al., 2020; Knaus et al., 2018).

In Northern Wheatears, preferences for heterogenous habitats with bare ground and short vegetation are well documented concerning choice of nest sites and micro-habitats used for foraging in Alpine grasslands (Alba et al., 2023; T. M. Müller et al., 2023; Sander et al., 2023). Whinchats, which are closely related to Northern Wheatears, primarily breed in hay meadows, where increasing fertilization allows earlier and more frequent mowing, often resulting in brood destruction (Border et al., 2017; Britschgi et al., 2006; Fay et al., 2020). Upland habitats host strongholds of Whinchat populations in other European regions such as the United Kingdom (Stanbury et al., 2022), but the decrease of this species seems to affect all populations, including those of the Alps (Knaus et al., 2018). However, while the ecology of the species in hay meadows is well understood (Britschgi et al., 2006; Fay et al., 2020; M. Müller et al., 2005), the status of the species and its habitat preferences in Alpine pastures are poorly known. Therefore, characterizing habitat preferences of Whinchats above the treeline in the Alps is of prime importance to the conservation of the species.

Non-threatened insectivorous species that are not specialized on high elevations co-occur in Alpine grasslands, such as Black Redstarts *Phoenicurus ochruros* and Dunnocks *Prunella modularis.* Black Redstarts prefer the vicinity of rocks, cliffs, and buildings, while Dunnocks are more related to forest edges, shrubby areas, and heathlands (Glutz von Blotzheim & Bauer, 1988; Jähnig et al., 2018; Knaus et al., 2018). In addition to these insectivorous species, some seed-eating birds such as Common Linnets *Linaria cannabina* are also common in Alpine grasslands; this Fringillidae species, declining in the lowlands, undergoes a strong increase at higher elevations (Knaus et al., 2018).

In addition to climate and land use changes, Alpine grasslands are increasingly used for infrastructure development like ski-runs (Brambilla et al., 2016; Caprio et al., 2011; Rolando et al., 2007), and more recently for renewable energy such as photovoltaic panel farms (Díaz & van Vliet, 2018; Grilli et al., 2017). However, only few studies characterized community composition and species-specific habitat preferences in changing Alpine grasslands above the treeline, often focusing on single species (e.g., Alba et al., 2023; Jähnig et al., 2020; Loe et al., 2007; Mermillon et al., 2021; T. M. Müller et al., 2023; Rolando et al., 2006; Sander et al., 2023).

Here, we conducted an observational study covering an entire high-elevation Alpine valley dominated by open grassland habitat. We aimed at identifying the composition of the songbird community, and determining which habitat were most relevant for insectivorous species. To understand how birds sharing an insectivorous diet share the same habitat, we disentangled species-specific fine-scale habitat preferences in the most common species, of which three were closely related Muscicapidae of similar size (Northern Wheatear, Whinchat, Black Redstart). As we expected landscape-scale habitat preferences to be species-specific, we then modelled the effects of topography, temporal vegetation productivity and habitat composition on the density of the most common species at a landscape-scale.

Methods

Study area

Our study area was situated in Val Piora, Swiss Alps (46°33’N, 8°42’E, Figure 1). It encompassed 6 km^2 of Alpine grassland interspersed with rocks, screes, rockpiles, walls and shrub, ranging between 1850 and 2450 m a.s.l.. Most of the accessible parts are grazed by milk cows under a low-intensity rotational management in July and August. The area is usually covered by snow between November and April (T. M. Müller et al., 2023; Rime et al., 2023).

Study design

In 2021, three survey rounds were conducted following line-transects covering the entire study area (Bibby et al., 2000, Figure 1). The study area was divided into three sectors, each covered by a transect surveyed on a different day. Surveys took place between 30 minutes before and six hours after sunrise in good weather conditions, i.e., without rain or snowfall, fog, or strong wind. Surveys were carried out on 1 June, 16 June, and 6 July (West part), on 4 June, 17 June, and 9 July (central part), and on 2 June, 15 June, and 14 July (East part). We delineated the study area based on a 250 m-distance buffer around the transects.

We first mapped all birds in the study area and delineated a 25-m radius around each individual observation, used to determine fine-scale habitat preferences. To study landscape-scale preferences, the area was divided into 93 square plots of 250 m x 250 m following the Swisstopo map grid, i.e. into plots (grid cells) of 6.25 hectares. The areas located further than 250 m from the transects were not considered, and thus plot size was reduced in cases where some area of a plot was further than 250 m from the transect (Figure 1). 12 plots covering less than 1.5 hectares were discarded from the analyses. Thus, study plots ranged in size from 1.5 to 6.25 hectares. Based on the results from each survey, we 1) summed the total count of individuals per plot per survey (used as a response variable in the statistical analyses) and 2) determined the total number of territories for each species within the study area using minimum convex polygons, clustering observations close to each other in the three successive visits to define a territory (Bibby et al., 2000; Knaus et al., 2018).

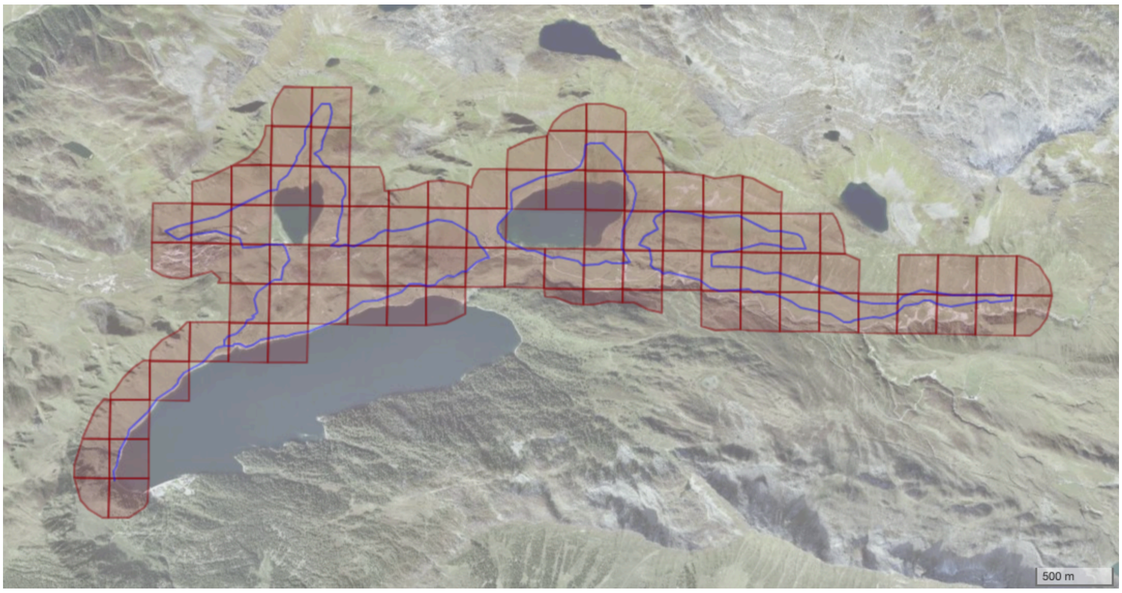

Figure 1: Map of the study area, with the plots (in red) and the transect (blue line).

Habitat variables

To analyse habitat preferences, we established a set of habitat variables related to topography, vegetation productivity (using Normalized Difference Vegetation Index, hereafter NDVI, as a proxy) and habitat composition (Table 1). We selected predictors (Table 1) based on a priori assumed biological reasoning (Korner-Nievergelt et al., 2015), covering potential key habitat features for alpine grassland bird communities. Average values of the topographic variables (elevation, slope, and aspect) within the plots were extracted from the digital elevation model SwissAlti3D (Swisstopo, 2018) with a resolution of 0.5 m. Aspect was transformed into northness (cos(aspect), 0° from north = 1, 180° from north = -1). To estimate productivity, we calculated an NDVI raster from Sentinel 2 satellite imagery (ESA, 2015) with a spatial resolution of 10 m in Google Earth Engine (Gorelick et al., 2017). We applied a cloud filter (<50% cloud cover) and selected the closest image to mid-May (beginning of snowmelt and territory settlement phase in the most common species) and mid-June (post-snowmelt, time of the surveys, breeding period of the most common species). For habitat composition, the proportion of non-vegetated ground, i.e., bare ground and stones, was calculated using a supervised image classification algorithm from the SCE plug-in in QGIS (QGIS Development Team, 2020) based on the 2022 "SwissImage" aerial pictures with 10-cm resolution (Swisstopo, 2022). Due to limitation of the algorithm in distinguishing between spectral signatures of the different types of green vegetation (woody vegetation, grass, or trees), shrubs (*Rhododendron ferrugineum* and *Juniperus communis*) were mapped manually in QGIS (QGIS Development Team, 2020) from the "SwissImage" pictures with a 10-cm resolution. We also did so for artificial rockpiles and walls in the study area. Mean values of raster variables within each plot were extracted in R using the *extract* function from the *terra* package (Hijmans et al., 2022).

Table 1. List of predictors used to model species-specific abundance in the 93 plots of 250m x 250m. "Transformation" is the transformation used in the linear model, and z = centering and scaling to sd = 1.

Category	Variable	Data source	Description	Unit	Transformation	mean	range
Topographic variables	Elevation	SwissAlti3D DEM	Mean elevation above sea level	m	*z*	2023	1854 - 2262
	Slope	SwissAlti3D DEM	Mean inclination of the slope	%	*z*	26.8	8.5 - 45.5
	Northness	SwissAlti3D DEM	cos(aspect)*pi/180 from the mean aspect value		*z*	-0.7	-1 - 0.3
Productivity	NDVI May	Sentinel-2 satellite image	Mean normalized difference vegetation index for mid-May 2021	Index	*z*	0.13	-0.05 - 0.41
	NDVI June	Sentinel-2 satellite image	Mean normalized difference vegetation index for mid-June 2021	Index	*z*	0.56	0.17 - 0.74
Habitat composition	Non-vegetated ground	Supervised image classification SwissImage 10 cm	Non-vegetated mineral ground (bare soil, stones and rocks)	%	*z*	1.5	0 - 6.3
	Shrub	Swissimage 10 cm and on-site mapping	Proportion of shrub	%	*z*	0.2	0 - 0.8
	Rockpiles	Swissimage 10 cm and on-site mapping	Number of rockpiles per plot		*z*	11.8	0 - 119
Offset	Area	QGIS	Area of the plot	ha		5.16	1.5 - 6.25

Statistical analysis

To investigate fine-scale niche partitioning in the most common species, we first extracted the value of all predictors (Table 1) in a 25-m radius for each individual observation. To investigate partitioning in fine-scale habitat use between species, we then carried out a principal component analysis for the four most common insectivorous breeding birds: Water Pipit, Northern Wheatear, Whinchat and Black Redstart, which all have a similar size, and of which the last three are closely related Muscicapidae.

In a second analysis, we modelled the effects of environmental predictors on the density of the six most abundant species (Water Pipit, Northern Wheatear, Whinchat, Black Redstart, Common Linnet, Dunnock) using generalized linear mixed-effect models with zero-inflated negative binomial distribution and the log of the plot area as offset. Species-specific abundances were used as response variables, and models were fitted with the same predictors to allow direct inter-specific comparison (Table 1).

Models were run per species and fitted in a Bayesian framework (Gelman et al., 1995; McElreath, 2018). All predictors were standardized (mean = 0, SD = 1). There was no strong collinearity among explanatory variables (all Spearman's correlation coefficients $|r_S| < 0.5$). To account for repeated survey counts in the same plots, plot ID was included as random effect in the models (Korner-Nievergelt et al., 2015; Rime et al., 2020). To correct for the non-independence of plots located next to each other, we included a Gaussian process with default parameters accounting for spatial autocorrelation between plots. We used the function *brm* from the R package *brms* (Bürkner, 2017) with default settings (i.e., vague priors, Berger, 2006; Kass & Wasserman, 1996). Non-linear effects were tested based on biological reasoning for the first three species, but no relevant effect was detected, and we therefore decided to not include non-linear effects. All analyses were conducted in R, version 4.2.0 (R Core Team, 2023).

To visualize and quantify the effects of predictors on the density of the bird species, we present effect plots for each predictor with all other variables set to their means (Korner-Nievergelt et al., 2015). We obtained the regression lines for each of 4000 draws from the joint posterior distribution and present its median as a point estimate and the 2.5 % and 97.5 % quantiles as 95 % credible intervals (Korner-Nievergelt et al., 2015).

Results

We counted 3480 individual birds (1086, 1085 and 1309 during the three rounds, respectively) of 32 species (Table 2). The most common species were Water Pipit (n = 2057), Northern Wheatear (n = 406), Whinchat (n = 255), Common Linnet (n = 177), Black Redstart (n = 133), Dunnock (n = 105), Rufous-tailed Rock-Thrush *Monticola saxatilis* (n = 71), Eurasian Wren *Troglodytes troglodytes* (n = 34), Lesser Redpoll *Acanthis cabaret* (n = 30), and Lesser Whitethroat *Curruca curruca* (n = 28). Other Alpine birds were reported in smaller numbers, such as Alpine accentor *Prunella collaris*, Yellow-billed Chough *Pyrrhocorax pyrrhocorax*, Rock Partridge *Alectoris graeca*, Ring Ouzel *Turdus torquatus*, White-winged Snowfinch *Montifringilla nivalis*, and Wallcreeper *Tichodroma muraria*. Red-spotted Bluethroat *Luscinia svecica svecica*, a rare species in the Alps, was also present. The bird community was largely dominated by insectivorous species, highlighted in bold in Table 2.

Table 2. List of species surveyed, with the total count (sum of individuals counted during the three rounds within the 93 plots) and the total number of territories estimated in the study area (not used in the statistical analyses). Birds that rely mostly on insects or other invertebrate prey are highlighted in bold.

Species		**Total count**	**Territories**
Water Pipit	*Anthus spinoletta*	2057	681
Northern Wheatear	*Oenanthe oenanthe*	406	124
Whinchat	*Saxicola rubetra*	255	95
Linnet	*Linaria cannabina*	177	59
Black Redstart	*Phoenicurus ochruros*	133	57
Dunnock	*Prunella modularis*	105	59
Rufous-tailed Rock-Thrush	*Monticola saxatilis*	71	27
Eurasian Wren	*Troglodytes troglodytes*	34	18
Lesser Redpoll	*Acanthis cabaret*	30	21
Lesser Whitethroat	*Curruca curruca*	28	19
Garden Warbler	*Sylvia borin*	22	11
Common Chaffinch	*Fringilla coelebs*	22	10
Grey Wagtail	*Motacilla cinerea*	19	10
Yellow-billed Chough	*Pyrrhocorax graculus*	16	11
White Wagtail	*Motacilla alba*	15	7
Ring Ouzel (Alpine)	*Turdus torquatus*	14	6
Alpine Accentor	*Prunella collaris*	12	11
Tree Pipit	*Anthus trivialis*	11	5
Eurasian Blackcap	*Sylvia atricapilla*	8	5
Rock Partridge	*Alectoris graeca*	8	8
Common Blackbird	*Turdus merula*	7	6
Eurasian coot	*Fulica atra*	4	1
Red-spotted Bluethroat	*Luscinia svecica svecica*	4	2
Mistle Thrush	*Turdus viscivorus*	4	2
Dipper	*Cinclus cinclus*	3	2
Common Kestrel	*Falco tinnunculus*	3	3
Willow Tit (Alpine)	*Poecile montanus alpestris*	3	1
White-winged Snowfinch	*Montifringilla nivalis*	2	2
Common Chiffchaff	*Phylloscopus collybita*	2	2
Common Cuckoo	*Cuculus canorus*	1	2
Coal Tit	*Periparus ater*	1	1
Wallcreeper	*Tichodroma muraria*	1	1

Fine-scale niche partitioning in the most common insectivorous species

The results of the principal component analysis of all observations of the four most common insectivorous species (Figure 2) suggest partial fine-scale niche partitioning in the four most common insectivorous species. Given the common shared part of the habitat, there is overlap in the habitat preferences. Water Pipits showed no clear preference at this scale, i.e. they appeared to use all habitat types. Northern Wheatears preferred rockpiles and higher elevations, while avoiding shrub, a high NDVI in June, and North-exposed slopes. Whinchats showed preferences for high NDVI in May and June, for denser shrub cover and steeper slopes with more North-exposed aspect. Steeper slopes seemed to be the main driver shaping Black Redstart preferences compared to Whinchats and Wheatears. Non-vegetated ground did not seem to influence any of the four most common species.

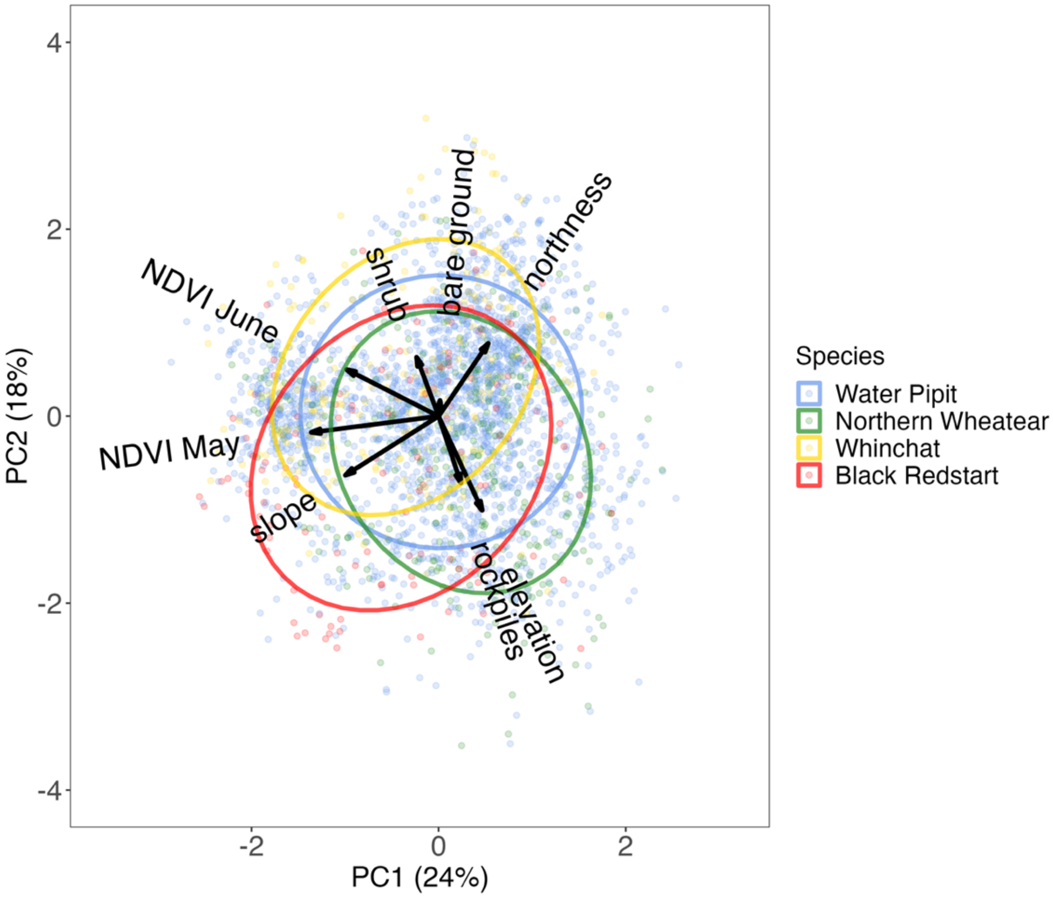

Figure 2. Results of the Principal Component Analysis (first and second principal component, with the percentage of variance explained) including all habitat predictors on a 25-m radius for the four most common insectivorous bird species. Ellipses represent the clusters that contain the 95 % confidence interval of all data from the four species on the first two components. The proportions of variance explained were: PC1 0.24, PC2 0.18, PC3 0.17, PC4 0.13, PC5 0.11, PC6 0.08, PC7 0.07, PC8 0.03.

Landscape-scale effects of the topography on species densities

Results from the linear mixed effect models analysing density on the 93 study plots (i.e., landscape-scale) were mostly species-specific (Table 3). Environmental predictors were divided into three categories: topography, vegetation productivity, and habitat composition. The effects of topography are summarized in Table 3 and Figure 3. Elevation had negative effects on the density of Water Pipits, Whinchats and Linnets. The effect on Northern Wheatear was not clear, while results suggested no effect for Black Redstarts and slightly negative effects for Dunnocks. Slope had negative effects on Water Pipits, Northern Wheatears, Whinchats and Common Linnets, no clear effect for Black Redstarts, and strong positive effects for Dunnock. The effects of northness in a mostly south-exposed landscape were uncertain; Water Pipits, however, seemed to have higher densities in plots with higher Northness values, i.e., in plots that were East- or West-exposed.

Table 3. Summary output (estimates and 95-% credible intervals) of the species-specific zero-inflated negative-binomial models including plot ID as a random effect for repeated counts and plot area as an offset to account for different plot sizes. The other variables were included as fixed effects in the models.

		Water Pipit			**Northern Wheatear**			**Whinchat**		
Category	**Predictor**	**Est.**	**2.5 %**	**97.5 %**	**Est.**	**2.5 %**	**97.5 %**	**Est.**	**2.5 %**	**97.5 %**
Topography	Elevation	-0.52	-0.89	-0.15	0.14	-0.33	0.54	-0.56	-1.04	-0.08
	Slope	-0.24	-0.51	0.02	-0.37	-0.85	0.08	-0.24	-0.78	0.28
	Northness	0.15	-0.01	0.31	0.02	-0.26	0.30	-0.08	-0.41	0.26
Productivity	NDVI May	0.08	-0.10	0.24	-0.07	-0.38	0.23	0.25	-0.13	0.66
	NDVI June	0.29	-0.03	0.61	0.23	-0.28	0.75	0.37	-0.25	1.00
Habitat Composition	Mineral	-0.02	-0.16	0.13	-0.09	-0.34	0.16	0.22	-0.04	0.51
	Proportion of Shrub	-0.17	-0.31	-0.03	-0.18	-0.44	0.06	0.52	0.26	0.81
	Rockpiles	0.08	-0.05	0.21	0.37	0.15	0.60	0.32	0.06	0.60

		Black Redstart			**Common Linnet**			**Dunnock**		
Category	**Predictor**	**Est.**	**2.5 %**	**97.5 %**	**Est.**	**2.5 %**	**97.5 %**	**Est.**	**2.5 %**	**97.5 %**
Topography	Elevation	-0.10	-0.61	0.40	-0.56	-1.07	-0.04	-0.24	-0.67	0.20
	Slope	0.23	-0.35	0.77	-0.60	-1.23	-0.05	0.57	0.14	1.02
	Northness	-0.10	-0.50	0.30	-0.21	-0.59	0.16	-0.18	-0.52	0.15
Productivity	NDVI May	-0.03	-0.43	0.38	0.03	-0.40	0.49	0.30	-0.06	0.67
	NDVI June	-0.11	-0.73	0.51	0.64	-0.05	1.36	-0.65	-1.21	-0.09
Habitat Composition	Mineral	0.18	-0.12	0.49	0.50	0.14	0.87	0.16	-0.08	0.39
	Proportion of Shrub	-0.42	-0.81	-0.07	0.03	-0.25	0.31	0.42	0.19	0.69
	Rockpiles	-0.21	-0.57	0.13	0.18	-0.12	0.48	0.04	-0.21	0.29

Landscape-scale effects of vegetation productivity on species densities

Vegetation productivity, measured by the mean NDVI values per plot in May and June (Table 3, Figure 4), seemed to have positive effects on the density of Water Pipits and Whinchats at the landscape scale. NDVI in May and June had unclear effects on Northern Wheatears and Black Redstarts. The effects of NDVI on Linnets seemed to be positive in May, and there was no clear effect in June. A clear negative effect of the NDVI in May on the density of Dunnocks contrasted with an apparent positive effect in June.

Landscape-scale effects of habitat composition on species densities

Habitat composition at the landscape scale had diverse effects on the density of the most common species (Table 3, Figure 5). Non-vegetated ground had strong positive effects on the density of Common Linnets and seemed to positively influence the density of Whinchats. Effects seemed to be positive but were rather uncertain for Black Redstarts and Dunnocks. No clear effect was detected for Water Pipits and Northern Wheatears at the landscape scale. The proportion of shrub had contrasting effects: a clear negative effect on density was found for Water Pipits, and shrub cover also seemed to have negative effects for Northern Wheatears and Black Redstarts. However, shrub cover had a strong positive effect on the density of Whinchats and Dunnocks. Rockpiles had a strong positive effect on Northern Wheatears and seemed to positively influence the density of Whinchats and Common Linnets. We found no clear correlation between the number of rockpiles and the density of the other species in our models.

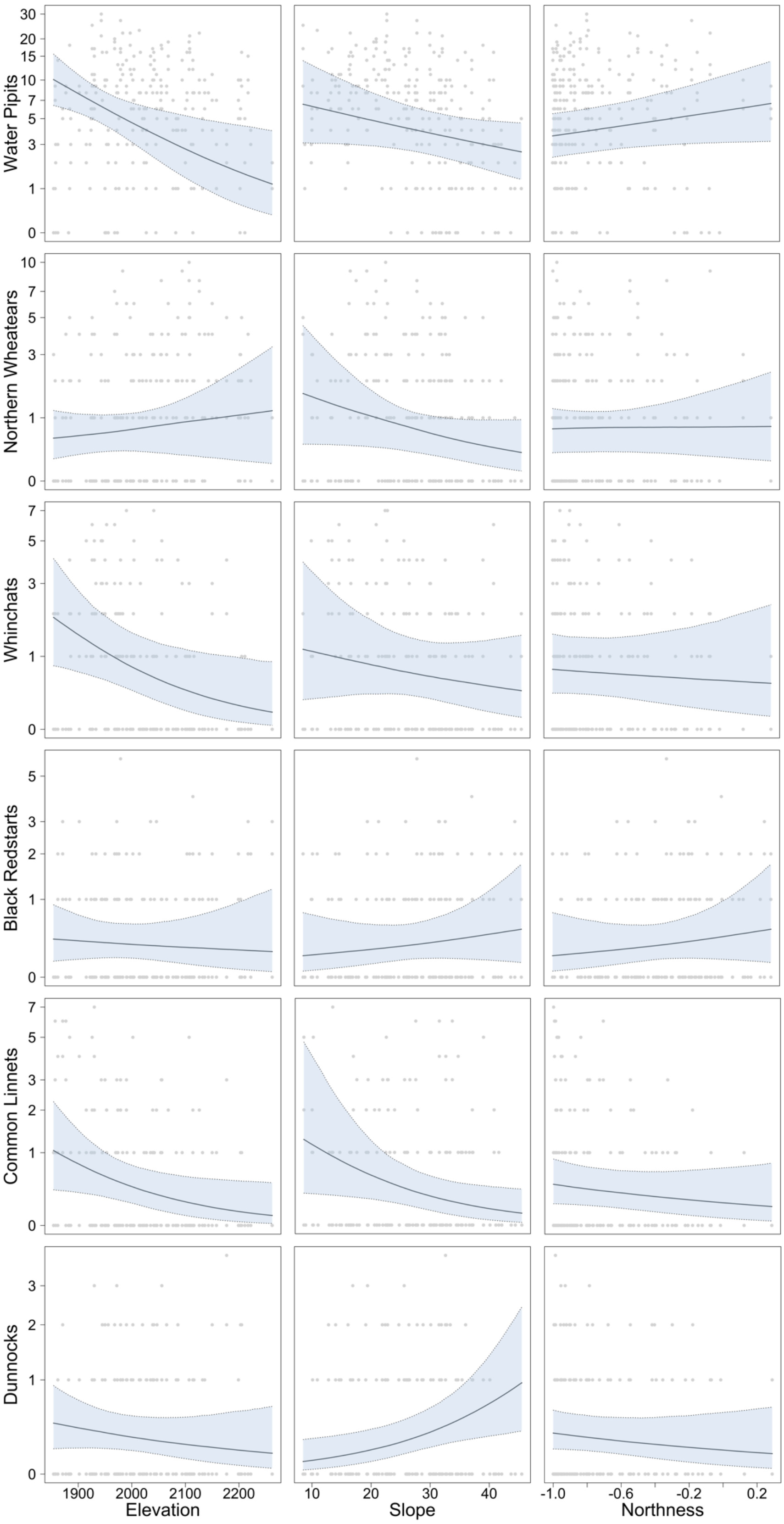

Figure 3. Topographic predictors: predictions from the zero-inflated negative binomial models showing the average effect (solid line) of predictors on the density of the six most common bird species in the study area, when other predictors were set to their mean. The coloured areas represent the 95% credible intervals, and the grey dots show the raw data.

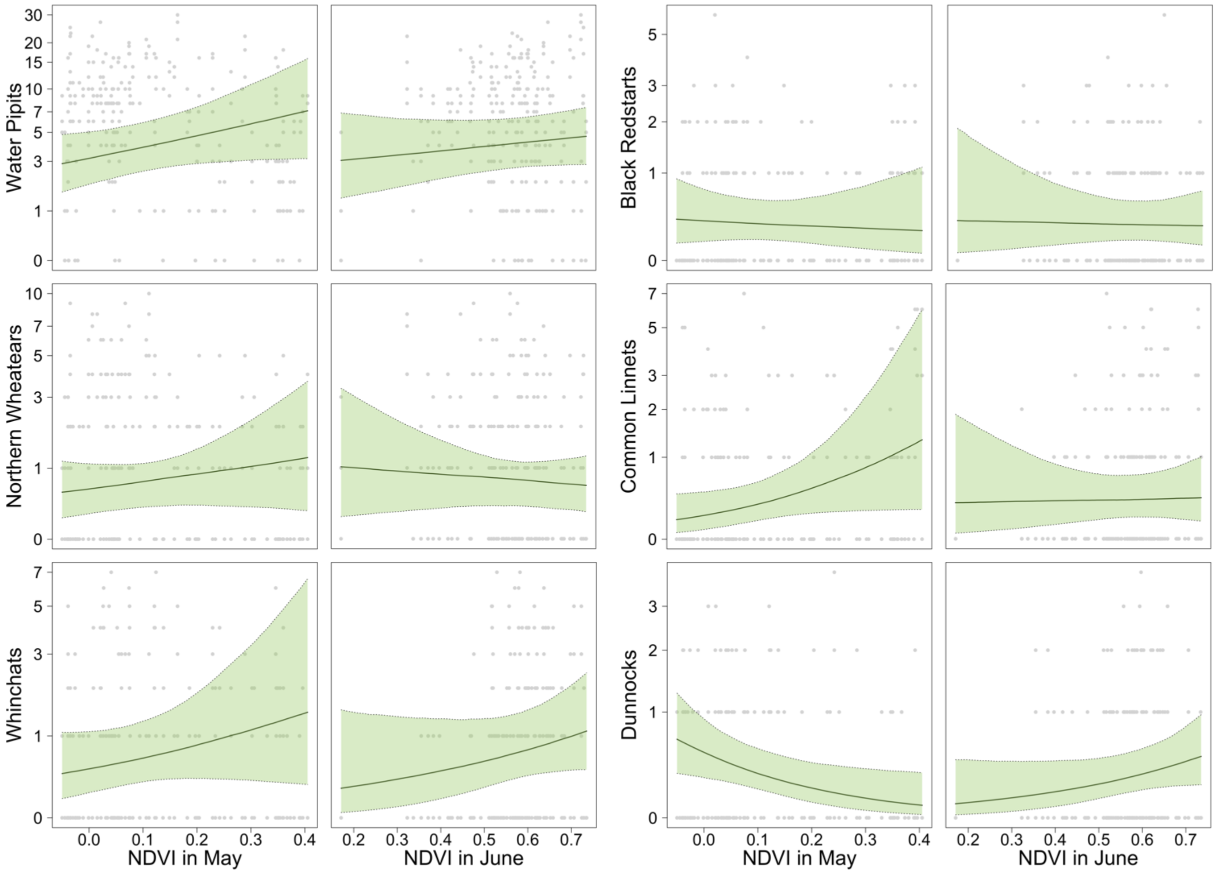

Figure 4. Spring vegetation productivity: predictions from the zero-inflated negative binomial models showing the average effect (solid line) of predictors NDVI in May and NDVI in June, which are related to seasonally shifting vegetation productivity, on the density of the six most common bird species in the study area, when other predictors were set to their mean. The coloured areas represent the 95% credible intervals, and the grey dots show the raw data.

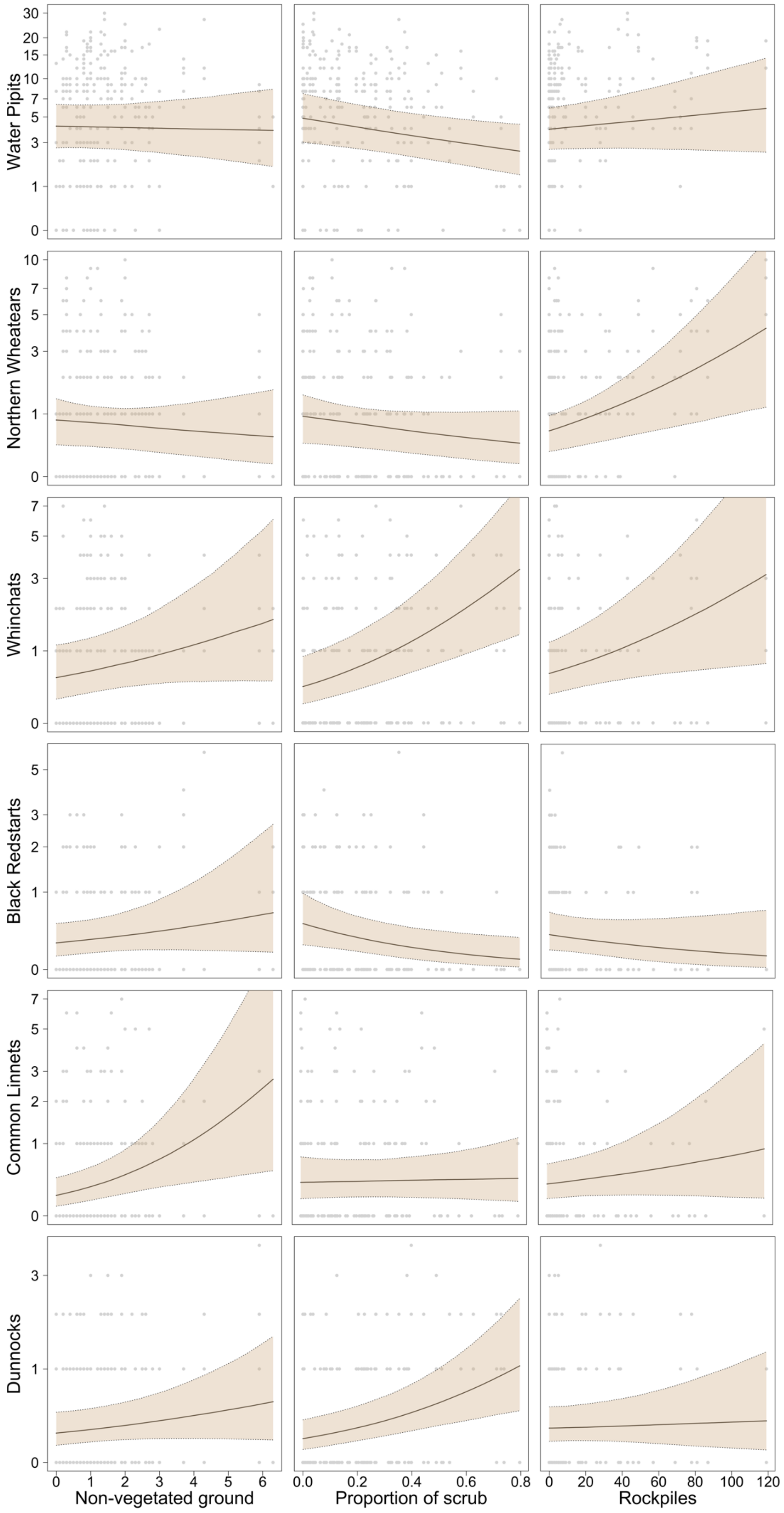

Figure 5. Habitat composition: predictions from the zero-inflated negative binomial models showing the average effect (solid line) of predictors describing effects of habitat composition on the density of the six most common bird species in the study area, when other predictors were set to their mean. The coloured areas represent the 95% credible intervals, and the grey dots show the raw data.

Discussion

Our results highlight insectivorous birds as the most abundant guild of the high-Alpine grassland bird community, with species-specific habitat preferences both at a fine scale and at the landscape scale. The insectivorous bird guild was largely dominated by one ground-breeding, open-land, and high-Alpine specialist, the Water Pipit (Bollmann & Reyer, 2001; Knaus et al., 2018), followed by the Northern Wheatear and the Whinchat, two widely declining species in Europe (Fay et al., 2020; Keller et al., 2020; van Oosten et al., 2015). Other abundant birds were Common Linnets, Black Redstarts and Dunnocks, which are all non-threatened species that are increasing at high elevations (Hallman et al., 2022; Knaus et al., 2018).

The fine-scale individual habitat (25-m radius) used by Water Pipits as shown in the principal component analysis suggested that they do not have clear niche preferences at a small scale, in contrast to Northern Wheatears, Whinchats and Black Redstarts. At the landscape scale, the density of Water Pipits was higher in plots located at lower elevations and gentle slopes. Northern Wheatears, Whinchats, and Black Redstarts had divergent habitat preferences, both at the individual, small-scale level of habitat use and when considering density at the landscape scale. This suggests high levels of niche partitioning in these three insectivorous Muscicapidae species. Northern Wheatears preferred rockpiles and higher elevations, while avoiding shrub, a high NDVI in June, and North-exposed slopes, confirming previous findings in the Alps (Alba et al., 2023; Müller et al., 2023). Whinchats showed preferences for high NDVI in May and June, denser shrub cover, and steeper slopes with more North-exposed aspect, which differed from habitat preferences in hay meadows (Britschgi et al., 2006; Fay et al., 2020; Müller et al., 2005) and more similar to preferences in other regions such as British Highlands (Calladine & Jarrett, 2021; Stanbury et al., 2022). Steeper slopes seemed to be the main driver shaping Black Redstart preferences, in contrast to Whinchats and Wheatears. Non-vegetated ground did not seem to be relevant for niche partitioning in any of the four most common insectivorous species, which all need access to the ground for foraging (Müller et al., 2023; Murray et al., 2016).

The effects of topographic variables on the density of the most common species at landscape scale (250-m x 250-m plots) were species-specific. Water Pipits, Dunnocks and Common Linnets seemed to have higher densities in lower elevation pastures just above the elevation of the treeline. No effect of elevation on the density of Northern Wheatears was detected at this scale. This might be explained by the large altitudinal range among the plots. Furthermore, the total elevational range considered in our study area (1850 – 2450 m) does not account for the upper part of the range of this species at higher elevations above 2400 m, where the population increases (Hallman et al., 2022; Knaus et al., 2018).

The limited effect of NDVI on the density of the most common species at the landscape scale might be related to the size of the plots in our study area. Effects of NDVI in May and June on the density did not show temporal discrepancies within species, except for Dunnocks, for which NDVI in May (before the surveys) had negative effects, while NDVI in June (during the surveys) had positive effects, maybe due to a preference for areas that are still covered in snow in May. Northern Wheatears were shown to select areas with higher NDVI to forage and breed (Müller et al., 2023), but NDVI did not have a clear effect on their density at the landscape scale. Nevertheless, positive trends of NDVI in both May and June for Water Pipits and Whinchats suggest preferences for relatively productive areas, which is in line with a positive preference for gentle slopes. Such areas tend to undergo intensification of management practices in parts of the Alps, which can affect bird communities. Effects can be direct, for example due to nest destruction, or indirect, e.g., due to increased vegetation growth and denser vegetation structure (Chemini & Rizzoli, 2003; Maggini et al., 2014; Tasser et al., 2005), or changes in prey composition (Chiffard et al., 2023). Whinchats are particularly sensitive to intensive grazing (Douglas et al., 2017), and an extensive management, such as at our study site, is a prerequisite to ensure persistence of these populations. In our study, we did not survey abandoned or intensified landscapes, as they are described for other parts of the Alpine range (Graf et al., 2014; Mack et al., 2013; Tasser & Tappeiner, 2002).

Rhododendron and Juniper shrubs have previously been shown to be avoided by Wheatears (Müller et al., 2023). At landscape scale, shrub cover only had weak negative effects on Wheatear density, as well as on Water Pipit density. This might be due to the patchy distribution of shrub cover in the study area, with patches of open habitat interspersed in the landscape (Alba et al., 2023; Jähnig et al., 2020; Müller et al., 2023). Shrub cover, however, had a strong positive effect on Whinchat density, underlining the need for low-intensity management promoting the heterogeneity of vegetation structures (Calladine & Jarrett, 2021; Murray et al., 2016). This preference for perennial vegetation was observed in other, lower-elevation regions such as the United Kingdom (Calladine & Jarrett, 2021; Stanbury et al., 2022), where the habitat is different from hay meadows used by Whinchats in central Europe (Britschgi et al., 2006; Fay et al., 2020; Müller et al., 2005). Thus, for conservation management of the Whinchat in central Europe, it is necessary to consider high-Alpine grasslands.

The predominance of insectivorous migratory species in the studied high-Alpine bird community, including an Alpine specialist and two birds that are severely declining in Europe, underline the continent-wide importance of Alpine grasslands for nature conservation. Different species-specific habitat preferences indicate that maintaining habitat heterogeneity is necessary to ensure the conservation of this bird community, in which species have different requirements within the same Alpine landscape. Overall, the joint effects of climate and land-use change could transform the current role of Alpine grasslands as a refuge for declining bird species (Chamberlain & Pearce Higgins, 2013; de Gabriel Hernando et al., 2022; Scridel et al., 2018). However, appropriate land management might mitigate negative effects of climate change (Brambilla et al., 2018; Rolando et al., 2014), for example by mitigating tree-line shift and bush encroachment, and by moderating vegetation growth through low-intensity grazing (Chemini & Rizzoli, 2003; Tasser & Tappeiner, 2002). In large parts of the Alps, Alpine grasslands are still pastured under traditional, low-intensity management. In this context, Alpine grassland should be a priority for the conservation of insectivorous, ground-breeding birds that decline in temperate Europe, like the Northern Wheatear and the Whinchat.

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Chapter 4

Locally adapted migration strategies? Comparing routes and timing of Northern Wheatears from Alpine and lowland European populations

Study sites where Northern Wheatears *Oenanthe oenanthe* were equipped with light-level geolocators in the Swiss Alps (mid-May 2022) and in Rheinland-Pfalz, Germany (mid-April 2023, © Yann Rime)

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Research

Locally adapted migration strategies? Comparing routes and timing of northern wheatears from alpine and lowland European populations

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The northern wheatear *Oenanthe oenanthe* has an almost circumpolar breeding distribution in the Northern Hemisphere, but all populations migrate to sub-Saharan Africa in winter. Currently, tracking data suggest two main access routes to the northern continents via the Middle East and the Iberian Peninsula. These routes would require detours for birds breeding in the European Alps. Our aim was to map the migration routes and determine annual schedules for birds breeding in Switzerland and Austria, using light level geolocators. We compared their migration patterns with birds from a lowland breeding population in Germany. Birds from the Alps cross the Mediterranean Sea directly heading straight to their non-breeding sites. In contrast, birds from Germany travelled further west via the Iberian Peninsula. While the German population initiated autumn migration relatively early, arrival on the wintering sites was nearly synchronous across the three populations. During spring migration, German birds arrived earlier at their breeding grounds than birds from the Alps. A comparison with the literature indicated that the breeding populations in the Alps use their own route and are among the latest to arrive in spring, showing resemblance to the phenology of Arctic breeding populations. Our results indicate that the annual cycle of Alps-breeding wheatears is influenced primarily by breeding ground conditions, and not solely by migration distance.

Keywords: Alpine birds, barrier crossing, connectivity, evolutionary legacy, full annual cycle, geolocator, migration timing, population comparison

Introduction

The typical annual cycle of a migratory bird consists of a round trip between their breeding and non-breeding ranges that provide save conditions and abundant food resources for their annual survival (Lack 1968, Cox 1985). However, the route linking both ranges may deviate from the shortest geographical route (Alerstam and Lindström 1990). Birds may take longer routes to avoid barriers (Moreau 1972), minimize sea

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crossings (Fortin et al. 1999), utilize more favourable wind (Hedenström 1993, Kranstauber et al. 2015, Shamoun-Baranes et al. 2017), enhance safety (Pomeroy et al. 2006) or ensure resources (Hahn et al. 2013, Lisovski et al. 2021). Some flyways might also be the result of a species' 'evolutionary legacy', which arises from shifting in breeding range and birds iteratively follow as much as possible the former route (Cox 1968, Newton 2008). This can lead to detour via the former breeding range and the northern wheatear *Oenanthe oenanthe* (hereafter referred to as wheatear) has long been used as a textbook example supporting this hypothesis (Newton 2008). Wheatears have one of the largest breeding ranges in the Northern Hemisphere (Cramp 1988). Yet all known populations migrate to sub-Saharan Africa during the non-breeding period, using Mediterranean and Middle Eastern routes (Bairlein et al. 2012, Schmaljohann et al. 2012b). The radiation of the genus *Oenanthe* initiated at the Horn of Africa in the late Miocene (Alaei Kakhki et al. 2016) and the last glacial refuge of wheatear species might have been in the Mediterranean region (Wang et al. 2020). After the last glacial period, the nominate form of the species spread throughout temperate Eurasia, mainly occupying coastlines and mountain regions. Today, the breeding range of wheatears extends above the Arctic Circle, to Newfoundland (CA) in the west, and the Alaskan (USA) peninsula in the east (Cramp 1988, Panov 2005). Despite this large breeding range, all populations still spend the non-breeding period in Africa instead of flying towards their closest equatorial landmass. As a result, some populations have extremely long migration distances of up to 14 500 km roundtrip (Alaskan-breeding wheatears; Schmaljohann et al. 2012b).

While evolutionary legacy may explain the migratory behaviour of populations at the northern edge of their breeding range, little research has focused on describing the migration patterns of populations at the southern edge of their range. Since these are the refuge populations from the last ice age (Wang et al. 2020), we expect to find high heterogeneity in migration behaviour among birds breeding at the edge of the southern range.

Timing of the annual cycle is generally considered to be constrained by the availability of resources, consequently limiting birds in high latitude breeding areas to a shorter breeding season (Lack 1950, van Loon et al. 2017). In order to understand the effect of a shorter breeding season on the annual cycle of birds, Lack (1950) suggested the comparison of migration phenology between populations along a latitudinal gradient. From the few studies which have made this comparison, two main patterns stand out. First, timing of reproduction has a major influence on migration phenology, shifting the entire annual cycle with the onset of breeding (Conklin et al. 2010, Briedis et al. 2016, Gow et al. 2019, Meier et al. 2020). Second, birds continuously adjust timing to match resource availability along their routes (Thorup et al. 2017, Pedersen et al. 2020). The pattern that is used can be observed in individuals from latitudinally-different breeding populations which share the same non-breeding site. If reproductive timing has greater influence on migration phenology, arrival and departure should occur on a population-specific schedule, and if resource availability has greater influence, all birds should arrive and depart at similar time in synchrony with environmental conditions.

In the wheatear study system, most tracking studies have been conducted on individuals from populations with a migration distance of at least 4000 km (Arlt et al. 2015). To our knowledge, there are four published studies using geolocators, tracking wheatears from Central Europe. Breeding birds from the Netherlands and from Rhineland-Palatinate in Germany showed some heterogeneity in migration routes (Schmaljohann et al. 2012a, van Oosten et al. 2014) Five birds partly followed the European continent via the Iberian Peninsula, while two birds followed more direct routes across the Mediterranean basin. Similar heterogeneity in migration routes had been described for birds breeding in Sweden too (Arlt et al. 2013). In a comparative study on protandry during spring migration among populations, Schmaljohann et al. (2016) also included a few tracks of Swiss breeding individuals, however, no routes towards the non-breeding sites were identified. Most recently, Sander et al. (2021) presented six complete tracks from a population in the Italian Alps and showed that these birds homogeneously crossed the Mediterranean basin on a direct north–south route.

Here, we aimed to quantify the heterogeneity in migration routes of alpine wheatears and determine whether all individuals cross the Mediterranean directly or whether a detour is taken via the Iberian Peninsula. A high amount of heterogeneity would provide evidence that the effect of annual differences in environmental conditions en route might be balanced at population level by different individuals following different routes (Schmaljohann et al. 2016). We analysed the migration phenology of the full annual cycle of two populations breeding in the Eastern Alps and the Central Alps across four years and compared them with data from an outgroup population breeding in Rhineland-Palatinate, Germany. We investigated spatial and temporal differences between their migratory routes and non-breeding regions. We expected that the shorter vegetation period in the Alps poses a stronger time constraint for the schedule of the annual cycle, leading to an overall shorter period at the breeding site compared to the lowland population from Rhineland-Palatinate. In addition, we compared migratory schedules of our study populations with published data of migration timing in other wheatear populations.

Material and methods

Study sites

We conducted studies in three different wheatear populations; in two alpine sites, 1) Austria, Hohen Tauern (12.317°E, 46.917°N) and 2) Switzerland, Val Piora (8.687°E, 46.551°N), and one lowland site, 3) Germany, Rhineland-Palatinate, in Bad Durkheim (8.167°E, 49.467°N). The two sites in the Alps are located above the tree line at 1800–2200 m above sea level and consist of alpine meadows with sparse boulders. Nestlings in these sites typically hatch in mid-June (Wartmann 1985, Glutz von Blotzheim et al. 1988). Replacement broods are frequently observed but successful completion of second broods is rare. The site in Rhineland-Palatinate is situated in the lowland at about 130 m above sea level in an agricultural landscape dominated by vineyards (Buchmann et al. 2009). The ground is sandy, and birds rely on stone walls and gravel pits for nest sites. Nestlings hatch in early June and early July, in the first and second brood, respectively (Buchmann 2001). In contrast to the Alpine populations, second broods occur and are successful in a fifth of all pairs.

Field work at all three sites consisted of searching the entire area for displaying pairs and locating their nesting sites. In addition, we captured birds at the nests while they provided food to the chicks (mid-June to July in the Alps, May to mid-June in Germany). To calculate re-capture rates, we ringed all captured individuals with metal rings (National ringing scheme at each site) and in Switzerland also with three additional individually unique plastic colour rings (<www.cr-birding.org/node/2595>, A C Hughes, UK and Ecotone, PL). Metal rings allowed the calculation of re-capture rate and colour rings the calculation of re-sight rates, which allowed also a comparison between the two rates. Birds were also sexed, aged and weighed at every capture occasion. Geolocators were deployed between 2014 and 2017 (GDL2, mean weight 0.63 g including leg-loop harness (Rappole and Tipton 1991), manufactured by Swiss Ornithological Inst.) and distributed evenly between sexes (55% females) on mature birds (2nd year and older, see Supporting information for samples sizes). Tags were removed, and in two cases replaced (one case each in the Swiss and the German population, see Supporting information), at the next re-capture in the following year.

Geolocator analysis

We identified twilight events (sunrises and sunsets) based on light level data at 5-minute measurement intervals and a threshold of three light units using the R package TwGeos (Lisovski et al. 2015).

Identification of the migratory schedule required a classification of the bird's movement behaviour at every twilight events as either stationary or migratory. This can be done by analysing four separate times series for changes in: sunrise time, sunset time, day length and night length. Abrupt changes between consecutive days are a strong indicator for a change of location of the bird. Hence, stationary periods were identified when at least three consecutive twilight events showed no indication for changes at any of the four-time series. The method requires a tag specific gamma error distribution of twilight times (Supporting information). The two functions used ('invChanges' and 'extractMovements') are explained in the Supporting information.

Geolocation to estimate the birds' location requires calibration. We performed a Hill–Ekström calibration on the longest stationary period in Boreal winter, when we presume that the birds spend most time in the same open habitat (Lisovski et al. 2021). When tags comprised too little data during the non-breeding period, mostly because the battery was empty, we applied an 'in habitat' calibration at the breeding site (Supporting information). We used Bayesian framework provided in R package SGAT to calculate the most likely routes (Wotherspoon et al. 2013). Specifically, we used the groupedThresholdModel, which provides one set of coordinates with a 95% credibility interval (CrI) for each stationary site based on all the twilights recorded at this site. We report median longitude and the quartiles of the route in the Mediterranean and visualize the entire route including the CrI of all stationary sites for each population. Based on the coordinates, we assigned the sites to five different regions. We assigned all sites with less than 300 km greater circle distance from the breeding site as belonging to the breeding ground. The threshold is larger than the accuracy of geolocators and hence a conservative measure of the bird's arrival or departure (Lisovski et al. 2012). The same threshold was used to assign sites to the non-breeding range, where the coordinates of the longest attended site in winter were used as the centre of the range. The remaining stop-over sites, beyond the 300 km buffer zone around the breeding ground and the non-breeding ground, were divided according to their latitude in three categories: northern Mediterranean (> 38°N), southern Mediterranean (between 38°N and 23°N) and sub-Sahara (< 23°N). For each region we report the date of the first and last stationary twilight event.

All analysis were carried out with the R software ver. 4.0.2 (<www.r-project.org>).

Literature review of Central European wheatear migration pattern

We are aware of five geolocator studies describing the migration of wheatears from Newfoundland and Alaska (both, Canada and USA, in Bairlein et al. 2012), Uppsala (Sweden in Arlt et al. 2015), Aekingerzand and Vogelduin (Netherlands in van Oosten et al. 2014), Rhineland-Palatinate (Germany, data in Schmaljohann et al. 2012a from 2009 on the same population as in this study) and Italy (Sander et al. 2021). All studies, except Italy, tracked birds exceeding 4000 km in migration distance and breeding at 49° latitude or farther north. For comparison with our data, we extracted the latitude and timing at the breeding and the non-breeding site of each population. The studies from European populations (Schmaljohann et al. 2012a, van Oosten et al. 2014, Arlt et al. 2015, Sander et al. 2021) provided fine-scaled data on the passage in the Mediterranean region, allowing a comparison of the interim time during migration, since previously-tracked wheatears from Central Europe also crossed the same regions. Schmaljohann et al. (2012a) had used 50% kernel densities to define stop-over sites. Arlt et al. (2015) and van Oosten et al. (2014) used a change-point analysis of the function changeLight provided in the R package GeoLight (Lisovski et al. 2012). Sander et al. (2021)

derived timing using the same methods applied in our study. Arlt et al. (2015) used additional temperature recordings on the tags to identify the exact time when birds switch between stationary and migratory behaviour. In instances where it was not provided in the original publication, we calculated median date of arrival in and departure from the Mediterranean region (here defined as South of the Alps < 46° latitude and north of the Tropic of Cancer > 23° latitude), based on the timing provided by the authors on individual stop-over site visits.

Results

We retrieved 33 geolocators with data from 31 birds (Supporting information), resulting in 22 partial and 11 complete annual migration routes. Re-sighting rates for control birds and tagged birds in the Swiss breeding population were almost identical (37% and 38%), while recapture rate was slightly lower in control birds (17% and 26%), likely due to higher catching effort in tagged birds (Fig. 1; Supporting information).

For all three populations, we identified the Western Sahel region as the major non-breeding site. Birds from Switzerland (16 tracks) and Austria (7 tracks) showed a clear overlap in their distribution during the period between mid-October and end of March in east Mali and adjunct regions such as Niger, Algeria, Burkina Faso and Benin. In contrast, during the same period, birds from Germany (3 tracks) occupied sites in the southwest of Mali and south Mauritania (Fig. 2).

Migration in all populations occurred in two bouts. After leaving the breeding sites, birds stopped either north or south of Mediterranean Sea, before crossing the Sahara to reach the non-breeding site (Fig. 2, 3). This stop-over in the Mediterranean was shortest for birds from the German breeding population. They spent more time migrating north of 46° and before arriving in the Mediterranean, compared to birds breeding in Switzerland and Austria. This same stopover in the Mediterranean was used on the return spring migration by all populations. Longitude estimates revealed a main difference where birds of the breeding population from Germany and the Alps crossed the Mediterranean Sea, especially in spring. In autumn, the median (and quartile) longitudes of stop-over sites of Alpine population in the Mediterranean were for the Austrian breeding population at 10.4°E (9.3°E–10.5°E) and Swiss breeding population at 4.6°E (3.1°E–8.6°E). In spring, birds from the Austrian and Swiss populations returned at 10.1°E (7.5°E–13.3°E) and 8.8°E (7.3°E–10.3°E) longitude, respectively. In contrast, the German population crossed the Mediterranean region farther west past the Balearic Islands in autumn at 1.4°E (0.8°E–5.1°E), and in spring at 1.7°W (2.5°W–0.5°E) (Fig. 2).

Median duration of migration in the Austrian breeding population was 52 (quartiles: 46.5–70.5) days for autumn migration and 18 (16–20.5) days for spring migration. In the Swiss breeding population, autumn migration lasted 40 (22.5–60.3) days and spring migration lasted 29 (21.3–33.8)

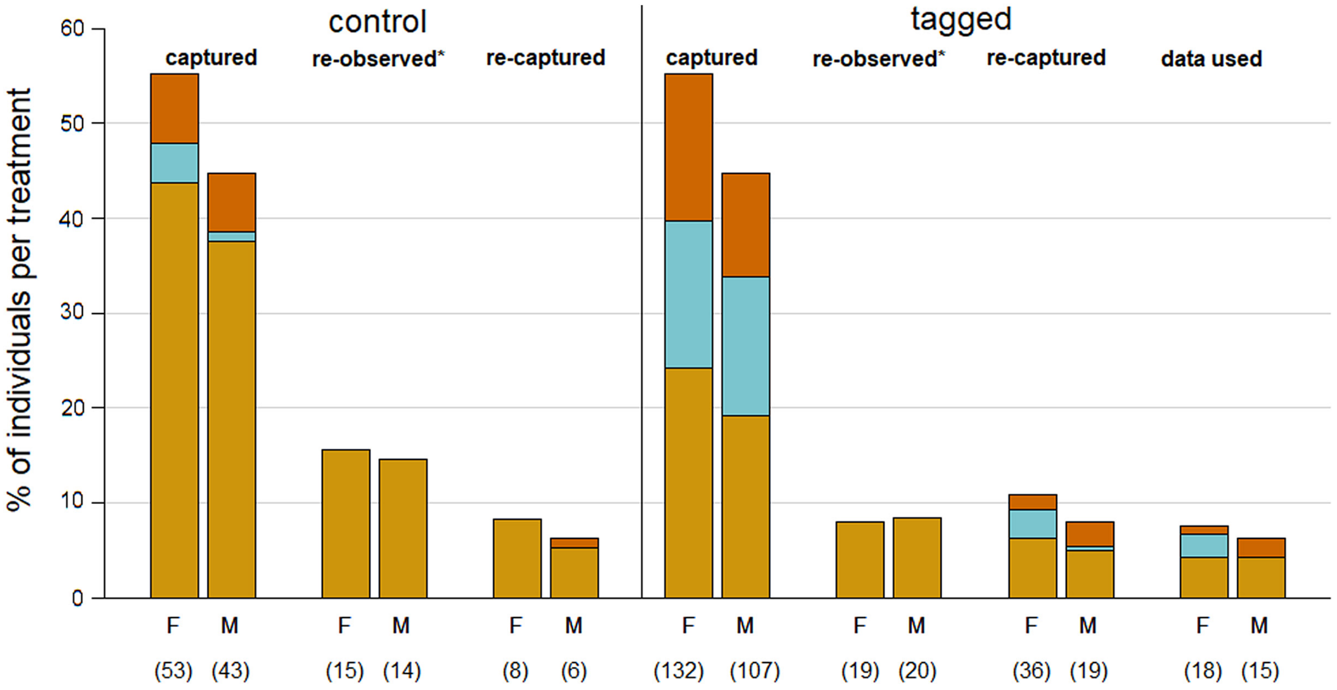

Figure 1. Distribution of the sample sizes between the control (left) and the tagged treatment (right) according to sex, population and treatment, relative to the total number (= 100%) of birds caught . Populations are indicated by the colours: Switzerland (dark gold), Germany (turquoise) and Austria (brown). The total absolute numbers per category are indicated in parentheses. The category * 'Re-observed' highlighted includes only the Swiss population.

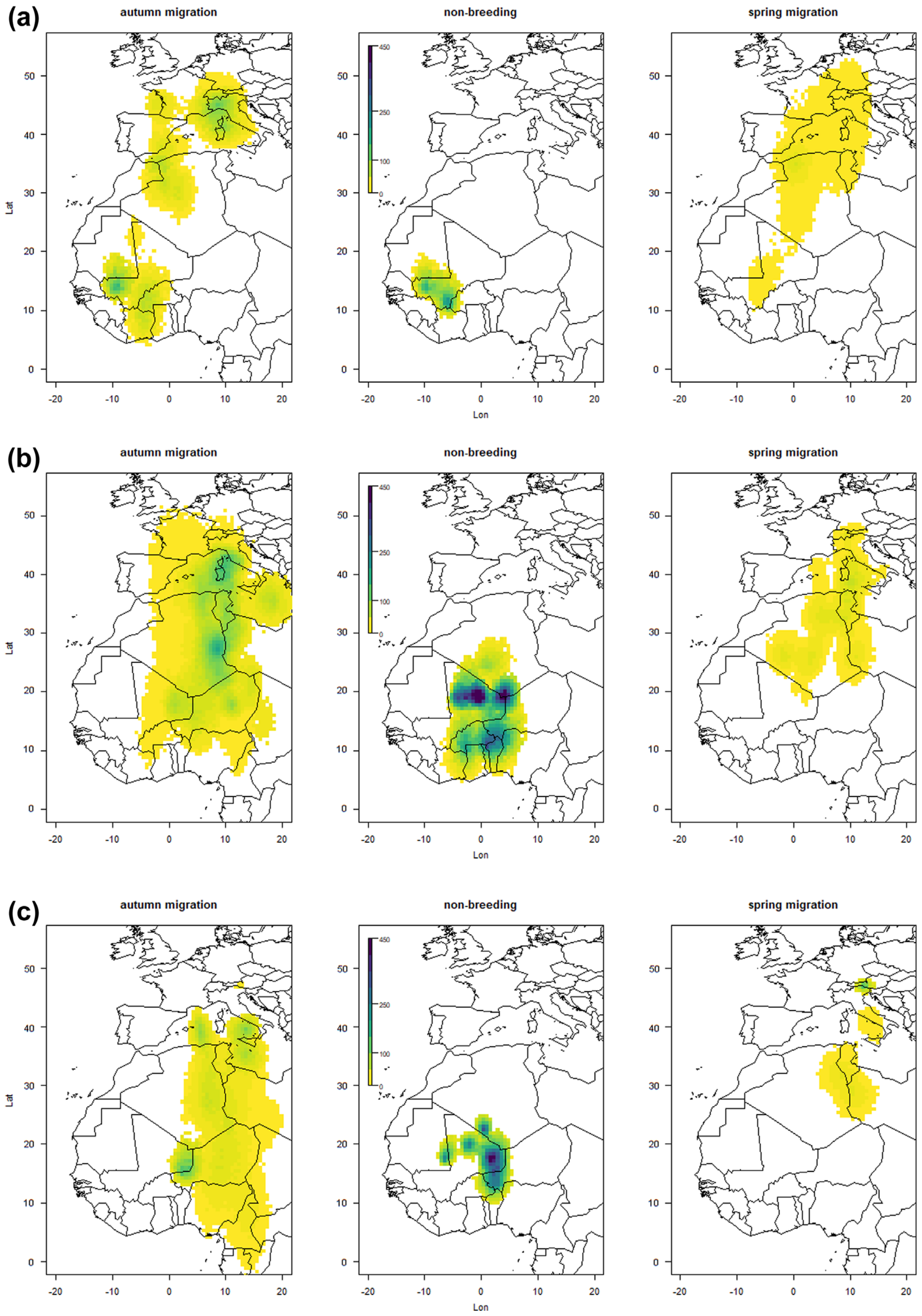

Figure 2. Combined tracks of all birds from Germany (a), Switzerland (b) and Austria (c) divided into three periods: autumn migration, non-breeding period and spring migration. The coloured area presents the cumulative probability of SGAT position predictions summed over the year for all individuals. The colour scale was adjusted to give every individual track the same weight; see main text for details.

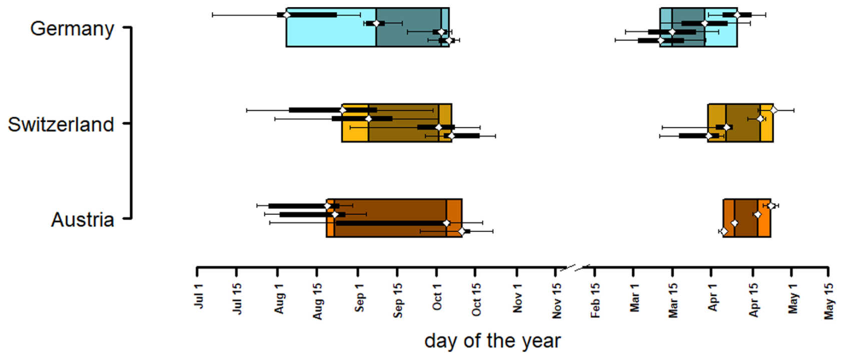

Figure 3. Comparisons of timing during autumn and subsequent spring migration in the three study populations (large squares by the colours: Switzerland, dark gold, Germany, turquoise, and Austria, brown). The colour shading within each square corresponds to three distinct "sub-periods" of each migration: In autumn, 1) Date of departure from the breeding site to crossing the Mediterranean at 38° latitude (light shade); 2) Crossing the Mediterranean to crossing the Sahara at 23° latitude (dark shade); and 3) Crossing the Sahara to arrival at the non-breeding site (medium shade). In spring, migration was divided into the same three "sub-periods" (in reverse order). The narrow horizontal bars represent the variation in timing between all individuals during these transitions between sub-periods. The median date (diamond), upper and lower quartile (bold line), and range of all dates (thin line) are shown.

days. The German breeding population spent 56.5 (41.3–63.5) days in autumn migration and 29.5 (26.3–32.8) in spring migration.

Timing of autumn migration was very similar across the three study populations. Median departure from the breeding site occurred on 21 August (quartiles: 29 Jul–25 Aug) in the Austrian population, 27 August (6 Aug–9 Sept) in the Swiss population and 5 August (2–24 Aug) in the German population (Fig. 3). Birds from the breeding population in Austria spent more than a month in the Mediterranean between the median dates of 24 August (3–28 Aug) to 6 October (24 Aug–7 Oct), and birds from the Swiss and German breeding population spent almost a month in the Mediterranean between 6 September (23 Aug–15 Sep) and 3 October (25 Sep–9 Oct), and between 9 September (5–12 Sep) and 4 October (1–6 Oct), respectively. Arrival at the non-breeding sites was similar across all three populations. Austrian birds arrived around 12 October (11–15 Oct), Swiss birds around 8 October (5–18 Oct) and German birds around 7 October (3–9 Oct).

Spring migration was shorter in duration than autumn migration and occurred in a clear order across populations. Birds from Germany departed first from the non-breeding site around 13 March (4–22 Mar), followed by the birds from Switzerland around 1 April (20 Mar–4 Apr), while Austrian birds departed last around 7 April (6–7 Apr) Similar to autumn migration, birds stopped for more than a week in the Mediterranean. German birds were present between 18 March (9–27 Mar) and 30 March (21 Mar–8 Apr), Swiss birds were present between 8 April (4–10 Apr) and 21 April (21–22 Apr) and Austrian birds were present between 11 April (10–11 Apr) and 20 April (10–20 Apr). The German birds and they reached their breeding site around 12 April (6–17 Apr). In contrast, both Alpine populations arrived two weeks later than the German population, with Swiss birds arriving on 26 April (26 Apr–26 Apr) and Austrian birds arriving on 25 April (23–26 Apr) to their breeding grounds.

Comparison of migratory timing of birds in this study with former studies

A comparison with published data showed that timing of migration was similar between birds from the alpine breeding populations and individuals from populations breeding farther north. In autumn, the birds from the breeding populations in the Alps departed after the birds in the Dutch breeding populations. In spring, Alps-breeding birds returned to their breeding grounds later than the arrival of Swedish-breeding birds back to their breeding grounds (Fig. 4). For all populations, arrival date at the breeding site was correlated with departures from the non-breeding site (Spearman's rank correlation r = 0.84, df = 5, CI 0.24–0.98), and distance between non-breeding site and breeding site had no influence on the entire duration of migration between these two sites (Spearman's rank correlation r = 0.43, df = 5, CI –0.47–0.89). Stop-over period at the Mediterranean lasted in all populations between 17 and 35 days.

The annual phenology of German breeding population found in this study was different from the previously published migratory schedule of the same population. However, it is important to note that migration dates in the previous study were derived from different individuals using a different method (Schmaljohann et al. 2012a). Nevertheless, median dates in our study for all migration events across the year overlapped with the interquartile range of the previous study. The main difference was that we found an earlier departure date in autumn and a slower migration to the Mediterranean stop-over site compared to the previous study. However, the arrival date at the non-breeding site across both studies only differed by two days. In spring, the previous study found an advanced median departure by 11 days, which resulted in 6 days earlier median arrival date at the breeding site in Rhineland-Palatinate.

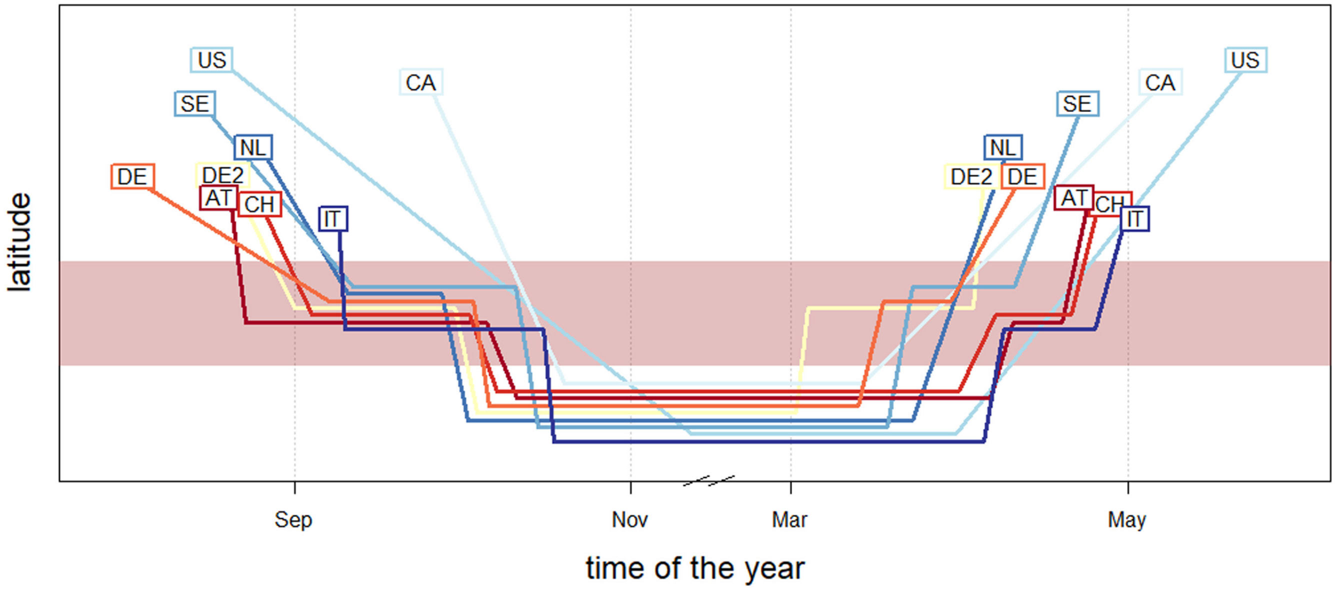

Figure 4. Comparison of the timing between all wheatear populations for which geolocator tracks exist. Lines show the median timing in each population along a proxy for latitude, indicating whether the birds were either north of the Mediterranean (>46°N), within the Mediterranean region between 46°N and 23°N, or south of the Mediterranean (<23°N). The labels of the populations are DE = Germany, CH = Switzerland, AT= Austria (populations in this study), DE2 = Germany (birds published in a previous study), NL = Netherlands, SE = Sweden, CA = Canada, US = Alaska, and correspond to studies reported in the main text.

Discussion

The wheatear has been used as a model to highlight the influence of ancestral expansion patterns on current migration routes. Following the migratory routes of their ancestral Mediterranean refuge population, nearly the entire world population of wheatears was presumed to migrate using two routes via Gibraltar and the Middle East to reach non-breeding sites in Africa (Newton 2008, Bairlein et al. 2012). However, our study revealed that migration behaviour is more variable, particularly for populations from central Europe carrying out short-distance migrations of less than 4000 km per season. Populations from the Alps consistently used central routes directly crossing the Mediterranean Sea in contrast to the German lowland population which opportunistically chose between those central routes and the more westerly routes across the Iberian Peninsula.

Many migrants overcome the Mediterranean Sea in a direct non-stop self-powered flapping flight, suggesting that the sea does not constitute a strong barrier (Grattarola et al. 1999, Biebach et al. 2000). For example, northern wheatears of the subspecies leucorhoa cross the North Atlantic during migration in more than 3500 km non-stop flight. Thus, they are well adapted to store a high amount of energy in advance (Bairlein et al. 2012, Corman et al. 2014). In addition, the nominate subspecies also shows remarkable accumulation in fuel load prior to migration (Maggini and Bairlein 2010). For smaller passerines, tracking studies have also provided evidence for crossing the Mediterranean Sea at a broad front (Briedis et al. 2016, 2018, Klvaňa et al. 2018). Therefore, the straight crossing at the central Mediterranean Sea fits our expectation for the two wheatear populations of this study breeding at the southern extent of their range.

Wheatears from breeding populations north of the Alps all seem to opportunistically follow either a western or a central Mediterranean route, and mostly circumvent the Alpine barrier (Bruderer and Jenni 1990, Bruderer and Liechti 1990, Schmaljohann et al. 2012a, Arlt et al. 2015, Bruderer et al. 2018). Mountains are an obstacle as birds must rise up and then are confronted with different wind conditions once crossing the ridge (Aurbach et al. 2018). Furthermore, the composition of habitats might differ at higher altitudes (Ćiković et al. 2021).

While the routes between all tracked European wheatear populations to date might partially overlap in space, the phenology of migration differed between populations. Among individuals tracked in this study, birds from Germany were first to start migrating in spring, followed by birds from Switzerland and Austria. Upon arrival at the breeding site, German birds had an advance of two weeks compared to the Alpine populations. This order of magnitude corresponds well with the reported difference in early onset of vegetation period at the Rhineland-Palatinate site and sites at higher altitudes in the Alps (Rodriguez-Galiano et al. 2015). This matches the hypothesis that migration phenology is ruled by the optimal timing of reproduction at each breeding site (Lack 1950, van Loon et al. 2017). Notably in spring, the correlation between the departure date and the arrival date fits the general expectation that departure is adjusted to conditions at the breeding site (Schmaljohann 2019). This has led to the conclusion that departure at the non-breeding site might be a hard wired genetic program well adapted to the constraints within each breeding population (Gwinner 1986, Tøttrup et al. 2010, Bairlein et al. 2015). Such an adaptation could also be present in wheatears. When lowland German birds return in early April (Buchmann et al. 2009), the alpine habitats above the tree line are usually still covered in snow (Klein et al. 2016, Sander et al. 2021), which may explain why Alps-breeding birds may have evolved such a late departure date from the non-breeding site.

In autumn, the difference in timing between populations was less apparent and the duration of migration varied more between individuals within populations. Partly, this variation might be a technical artefact because the error in estimates of latitude by geolocation increase around the time of equinox, making detection of north-south movement less obvious (Ekström 2004, Lisovski and Hahn 2012). However, arrival date at the non-breeding site was close between all individuals tracked in this study despite the large phenological variation between individuals. The same increase in synchrony towards the arrival date at the non-breeding site was also revealed in our literature review for all previously tracked populations. Since the non-breeding sites of all birds are centred around Mali, the synchrony of arrival time might be the result of birds tracking the peak of resources in Mali (Thorup et al. 2017, Pedersen et al. 2020). This may be supported by the onset of more moderate temperatures temperature in Mali in mid-October, providing good climatic conditions until February (Nicholson 2013).

On a larger scale, the Alpine populations showed a late arrival at the breeding site compared to the other tracked populations across Europe. In particular, the birds breeding in Italian Alps with the most southern breeding site and the shortest migration route showed the latest median return date in spring. At the extreme, this divergence in phenology has the potential to affect speciation (Pons et al. 2016). The shorter breeding season in the Alps might also affect population dynamics. Later arrival can reduce fecundity since late broods usually have lower survival (Kokko 1999, Lerche-Jørgensen et al. 2018), and the short season reduces the chance for successful second broods or replacement broods (Buchmann 2001, Morrison et al. 2019, but see Low et al. 2015). In addition, in arctic and mountain habitats, strong extreme weather events are more frequent compared to low-land habitats (Schmidt et al. 2019, Schano et al. 2021). This could hamper the bird's ability to predict favourable breeding conditions and challenges the possibility to adapt their annual cycle to local habitat (McNamara et al. 2011). As a result, the phenology of alpine populations could be subject to more inter-individual variation (Schano et al. 2021). In this study, the phenology in spring is more different between individuals of the German low-land population, although samples size might have been too small for reliable detection. Alternatively, alpine birds might also evade extreme weather events by altitudinal movement (Barras et al. 2021). The new development of bio-logging tools using air pressure might have the potential to reveal such behaviour in the future (Meier et al. 2018, Sjöberg et al. 2018, Barras et al. 2021).

The congruent arrival dates in spring of the birds breeding in the Alps compared to the birds breeding in Sweden, which migrated almost twice as far between the non-breeding and the breeding sites, is interesting. Swedish birds arrived simultaneously because they departed more than three weeks earlier from the non-breeding site compared to their conspecifics breeding in the Alps. This is almost twice the duration for an approximately 1800 km longer route than one could expect according to the model by Schmaljohann (2019). This example adds evidence to an ongoing discussion suggesting expenses in energy and travel of long-distance migratory birds are not the main constraint to the organisation of a species' annual cycle (Marra et al. 2005, Briedis et al. 2020, Buchan et al. 2020).

In conclusion, wheatears breeding in the Alps deviate from the major species-specific access routes from Africa to Europe. Timing of their annual schedule is delayed by more than two weeks in spring compared to neighbouring populations due to the late-starting vegetation growth at high alpine habitats. Both findings suggest that the migration routes and timing of Alpine populations is less the result of an expansion from the ancestral refuge population during the last glacial period, but rather an adaptation to the cooler climate at high elevation. The similarity in timing of migration between populations at high altitude and high latitude is another example of how the local environment might have strong selective power in this species, leading to homologous adaptations which make disentangling the evolutionary relationships between populations all the more challenging (van Oosten et al. 2016, Wang et al. 2020).

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Author contributions

Christophe M. Meier: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Project administration (equal); Writing – original draft (lead). **Yann Rime**: Data curation (equal); Validation (supporting); Writing – review and editing (equal). **Simeon Lisovski**: Software (lead); Validation (equal); Writing – review and editing (equal). **Martin Buchmann**: Data curation (equal). **Felix Liechti**: Conceptualization (equal); Funding acquisition (lead); Project administration (equal); Writing – original draft (equal).

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Data availability statement

The datasets generated during and/or analyzed during the current study are available in the Movebank Data Repository,

Austria study: <https://doi.org/10.5441/001/1.tn4h3kt0> (Meier et al. 2022)

Germany study: <https://doi.org/10.5441/001/1.b285q8gh> (Meier et al. 2022)

Switzerland study: <https://doi.org/10.5441/001/1.vp61g6gd> (Meier et al. 2022)

Supporting information

The Supporting information associated with this article is available with the online version.

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Chapter 5

Multi-sensor geolocators unveil global and local movements in an Alpine-breeding long-distance migrant

Male Northern Wheatear *Oenanthe oenanthe* at the breeding site and the breeding habitat after arrival from migration in the study area of Val Piora (© Yann Rime)

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Movement Ecology

RESEARCH **Open Access**

Multi-sensor geolocators unveil global and local movements in an Alpine-breeding long-distance migrant

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Abstract

Background To understand the ecology of long-distance migrant bird species, it is necessary to study their full annual cycle, including migratory routes and stopovers. This is especially important for species in high-elevation habitats that are particularly vulnerable to environmental change. Here, we investigated both local and global movements during all parts of the annual cycle in a small trans-Saharan migratory bird breeding at high elevation.

Methods Recently, multi-sensor geolocators have opened new research opportunities in small-sized migratory organisms. We tagged Northern Wheatears *Oenanthe oenanthe* from the central-European Alpine population with loggers recording atmospheric pressure and light intensity. We modelled migration routes and identified stopover and non-breeding sites by correlating the atmospheric pressure measured on the birds with global atmospheric pressure data. Furthermore, we compared barrier-crossing flights with other migratory flights and studied the movement behaviour throughout the annual cycle.

Results All eight tracked individuals crossed the Mediterranean Sea, using islands for short stops, and made longer stopovers in the Atlas highlands. Single non-breeding sites were used during the entire boreal winter and were all located in the same region of the Sahel. Spring migration was recorded for four individuals with similar or slightly different routes compared to autumn. Migratory flights were typically nocturnal and characterized by fluctuating altitudes, frequently reaching 2000 to 4000 m a.s.l, with a maximum of up to 5150 m. Barrier-crossing flights, i.e., over the sea and the Sahara, were longer, higher, and faster compared to flights above favourable stopover habitat. In addition, we detected two types of altitudinal movements at the breeding site. Unexpected regular diel uphill movements were undertaken from the breeding territories towards nearby roosting sites at cliffs, while regional scale movements took place in response to local meteorological conditions during the pre-breeding period.

Conclusion Our data inform on both local and global scale movements, providing new insights into migratory behaviour and local movements in small songbirds. This calls for a wider use of multi-sensor loggers in songbird migration research, especially for investigating both local and global movements in the same individuals.

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Keywords Multi-sensor loggers, Geolocators, Atmospheric pressure, Migratory behaviour, Local movements, Trans-saharan migrant

Background

Understanding movements and identifying positions of migratory animals throughout their annual cycle is a prerequisite to assess the spatial and temporal aspects relevant to species conservation [1–3]. Annual movements allow migratory species to optimize the use of spatially and temporally limited resources [4]. However, migration across biomes involves vulnerability to various environmental changes during the annual cycle, especially in the case of long-distance migratory birds [5, 6]. Environmental conditions at the non-breeding site, such as drought and land-use changes in the Sahel region, impact populations of palearctic-breeding species [7–9]. Nevertheless, habitat and climate changes at the breeding site are also prime drivers of population trends in long-distance migrants [10–13]. While connecting breeding and non-breeding sites at a population level allows the assessment of sensitivity to site-specific changes, migration represents a critical phase. It is thus essential to describe individual migratory flights and stopover behaviour to fully understand the entire annual cycle of migratory species.

Landbirds migrating between Europe and Sub-Saharan Africa face major spatial and temporal challenges. First, they must cross the Mediterranean and the Sahara Desert, which are major ecological barriers between their breeding and non-breeding sites [14–16]. Barrier-crossing strategies vary within and between species [17–19]. Non-stop flights between breeding and non-breeding sites occur in some trans-Saharan migrants [20], even in small passerines [21]. While some large soaring birds tend to prioritize longer diurnal flights and avoid crossing broad surfaces of sea [22], direct or partial sea crossings are common in many wing-flapping species [23, 24], especially in songbirds [25, 26]. In this case, Mediterranean islands serve as important stopover sites for birds crossing large waterbodies [27] and many species land during the day when crossing the Sahara [28]. However, even small songbirds can cross the desert in a single non-stop flight [29]. Prolonged nocturnal migratory flights into daytime are common [30–32] and lead to behavioural adjustments, such as increased flight altitude during the day [33]. Similarly, flight altitudes tend to be higher over the Sahara Desert than during the rest of migration [34]. Nevertheless, due to technical limitations, vertical flight behaviour remains poorly understood in small songbirds.

Studying the full lifecycle of alpine species is crucial to understand their responses to environmental change, especially given the recent marked climate and habitat changes at high elevations [35]. In birds inhabiting mountain habitats, altitudinal movements occur not only during migration, but also at stationary sites. Typically, species breeding in highly seasonal environments, such as alpine habitats, must adjust their migratory and breeding timing to snowmelt and optimal availability of food resources [36–38]. In this regard, seasonal local altitudinal movements allow shifting resources across an elevational gradient to be tracked [39]. Diel altitudinal movements may also be aimed at tracking food resources or at coping with adverse meteorological conditions [40].

In the Northern Wheatear *Oenanthe oenanthe*, all populations migrate to sub-Saharan Africa, including those breeding in the Alps, but also those in Greenland or Alaska [41–43]. Populations from continental Europe have a shorter journey to Africa with longer stopovers [44, 45]. Light-level geolocation previously allowed the identification of non-breeding regions of Central European populations in the western Sahel [45, 46]. The Mediterranean has been identified as an important stopover area [26, 45]. However, due to a north-south migration around the time of equinox, when light recordings are not latitudinally informative, light-level geolocation has often resulted in poor estimates of the stopover locations, which calls for new methods to describe migration patterns (e.g., [47]).

In the Alps, Northern Wheatears face variable snowmelt and weather conditions upon arrival and tend to breed later than other central European populations [48, 49]. A potential mis-adaptation to a changing phenology of spring green-up has been suggested [45, 49], and the species is currently undergoing a broad-scale upward elevational shift [50, 51]. The phase between arrival and breeding is critical in high elevation birds [52, 53] and remains poorly understood. This advocates the investigation of movements not only during migration, but also at the breeding site.

Here, we studied migratory and local movements of Northern Wheatears from the Alps throughout the annual cycle using multi-sensor loggers recording light intensity and atmospheric pressure. Such devices have recently opened up new opportunities for research on the migration of small-bodied birds [32, 54, 55]. While informing on the altitude and duration of the stationary phases and of migratory or local flights [32, 54, 55], atmospheric pressure data also allow the geographic position of birds to be located during their stationary periods with a higher precision than light-level geolocation [56, 57]. We used atmospheric pressure to describe migration routes, stopover, and non-breeding locations as well as individual migration timing with an unprecedented precision in a small songbird. Furthermore, we analysed flight behaviour in relation to barrier-crossing migratory flights. We also detected two types of local movements at the breeding site: pre-breeding local altitudinal movements were undertaken in response to meteorological conditions and, more surprisingly in this territorial species [58–60], unexpected small-scale altitudinal movements occurred at the breeding site. In this study, we showcase that atmospheric pressure data can simultaneously unravel both global- and local-scale movements in small songbirds.

Methods

Geolocators and deployment

We fitted multi-sensor geolocators (GDL3-PAM, Swiss ornithological institute, 1.2 g with harness) on Northern Wheatears at two study areas: one in the Swiss Alps (Val Piora, 46°33'N, 8°42'E, 1850 to 2200 m a.s.l.) and one in the Italian Alps (Val Troncea, 44°57′N, 6°56′E, 1900 to 2700 m a.s.l.). These devices mounted using a leg-loop harness[61] record ambient light intensity, atmospheric pressure, and temperature. In this species, both males and females usually return to the same breeding territories, allowing recapture in subsequent years [58, 62–64]. All birds were individually marked with a colour combination of three plastic rings and a metal ring. Birds were trapped with a trap placed at the entrance of the nest cavity while feeding the chicks (both for the first capture and recapture), or with baited spring traps in the territory (recapture only). Between 2016 and 2020, we ringed 301 adult birds in June and July at the Swiss site. We equipped 54 individuals with GDL3-PAM geolocators (2016, 2018, 2019 and 2020). 140 birds were ringed but not tagged and served as a control group. 47% of the control birds (66/140) and 37% of the GDL3 PAM (20/54) were observed in the year after tagging. In addition, we equipped 40 adults in 2019 and 2020 in the Italian Alps, with a control group of 23 birds; here, 48% of the control birds (11/23) and 22.5% of the GDL3 PAM (9/40) were observed in the year after tagging. The mean ± standard deviation body mass of adults at the Swiss site was 24.6 ± 1.6 g (range 20.0–30.0 g) and 23.6 ± 1.9 g at the Italian site (range 19.8–32.0 g). The device always amounted to less than 5% of the body mass of the tagged birds [65]. We compared return rates of the tagged and control individuals, under the same resighting effort and handling procedure except for fitting the loggers, using a Fisher's exact test ($p=0.47$ for the Swiss site, $p=0.19$ for the Italian site) and a 2-sample test for equality of proportions with continuity correction ($X^2=1.23$, $p=0.27$ and $X^2=3.23$, $p=0.072$, respectively). A high proportion of these experimental devices failed a few weeks after tagging because of battery issues ($n=16/24$, mostly those fitted in 2016, 2018 and 2019), resulting in recording of only partial tracks. Here, we considered only the tracks with at least a full autumn migration ($n=8$ for autumn migration, $n=6$ for non-breeding site data, $n=4$ for spring migration; Table 1).

Trajectory reconstruction

We modelled the trajectory of each track following the approach presented in Nussbaumer et al. (2023, [66]) and using the R package GeoPressureR (version 2.7, [67]. All analyses were performed in R version 4.2.0 [68]. We briefly describe the main steps of the approach below.

First, we identified stationary periods, when a bird was presumed to remain at the same location at the resolution of our model (0.25°, i.e. 27 km). We manually labelled the geolocator pressure measurements: stationary periods were characterized by a limited variation in consecutive pressure measurements indicating an absence of change in altitude, while migratory flights typically displayed a clear drop in atmospheric pressure, corresponding to altitude gain in-flight.

Second, we constructed separate probability maps based on atmospheric pressure and light intensity data (sunrise and sunset times) for position estimates of each bird during each stationary period. For the pressure-based maps, the time series of the geolocator pressure measurements during stationary periods were matched with the one-hour ERA5 surface level reanalysis dataset (spatial resolution: 0.25×0.25°) to produce a likelihood map of the geolocator's position [57]. The likelihood map produced included the information of both the temporal variation of pressure and the absolute values of pressure corresponding to the altitudinal range within each grid cell.

For the light-based maps, we calculated likelihood estimates following Nussbaumer et al. (2022a, [57]). We used an "in-habitat" calibration from the equipment and retrieval periods [69–71], fitting the distribution of zenith angle with a kernel density estimation. The likelihood maps of twilights belonging to the same stationary period were aggregated with a log-linear pooling.

Finally, we constructed the trajectories of each bird following the Hidden Markov Model presented in Nussbaumer et al. (2023, [66]). The observation model consisted of the likelihood maps generated from pressure and light data. The movement model used the information of flight duration derived from the labelling together with wind data, so that the parametric equation of movement was defined on airspeed. This parametric equation was defined as the cubic root of the mechanical power required for the average airspeed computed for a transition, accounting for a typical Northern Wheatear size and shape. A low airspeed threshold of 20 km/h was used to account for potential short local or exploratory flights. Using this model, we generated (1) the marginal

Table 1 Summary of the general information, migration schedule and flight performance of Northern Wheatears tagged with multi-sensor geolocators showing full annual cycle (n = 4) and fall migration (n = 8)

ID	26IM	26IL	26HS	20TJ	16IQ	24IS	24TJ	24EA
Sex	M	M	F	F	F	M	M	F
First data	14.07.20	14.07.20	07.07.20	01.08.18	01.07.17	01.08.19	31.07.20	20.07.19
Breeding site	CH	CH	CH	CH	CH	CH	IT	IT
Last data	28.05.21	30.06.21	23.06.21	08.11.18	28.01.17	16.10.20	05.06.20	31.10.19
Autumn migration								
Departure breeding site	16.09.20	10.09.20	16.09.20	10.09.20	12.09.20	15.09.20	12.09.20	15.09.20
Duration (days)	23	26	48	32	25	-	37	-
Duration of stopover in N Africa	9	11	24	21	12	10	16	25
Arrival non-breeding site	09.10.20	06.10.20	03.11.20	12.10.18	07.10.16	-	19.10.20	-
Mediterranean stopover site	Spanish coast	Sardinia	Corsica, Sardinia	None	None	None	Sardinia	Baleares
Number of migratory flights	15	13	17	11	20	12	17	12
Total migration distance	4625	4055	4716	4032	4241	4296	4121	3733
Cumulative flight hours	87	69.5	103.5	79	90	85.5	73	79.5
Mean ground speed per flight	45.3	54.5	39.7	47.2	39.4	42.8	48.4	46.2
Mean flight altitude per flight	1287	1478	1270	1559	1276	1554	1229	1287
Max flight altitude	4120	4530	4157	4764	4250	4475	4600	3662
Spring migration								
Departure from the NB site	01.04.21	04.04.21	04.04.21	-	-	-	05.04.21	-
Duration (days)	32	22	39	-	-	-	29	-
Duration of stopover in N Africa	18	13	13	-	-	-	16	-
Arrival at the B site	03.05.21	26.04.21	13.05.21	-	-	-	04.05.21	-
Mediterranean stopover site	None	Baleares	Sardinia	-	-	-	None	-
Number of migratory flights	11	15	14	-	-	-	13	-
Total migration distance	4581	4873	3736	-	-	-	4415	-
Cumulative flight hours	78.5	104.5	74	-	-	-	78	-
Mean ground speed per flight	46.4	42.8	42.4	-	-	-	52	-
Mean flight altitude per flight	1387	1667	1631	-	-	-	1454	-
Max flight altitude	4567	5148	3725	-	-	-	4306	-

probability map of the position of each stationary period, (2) the most likely migration trajectory of the birds, and (3) 100 random simulations of the trajectories. We refer readers to Nussbaumer et al. (2023, [66]) for further details on the implementation of this method.

Data, code and parameter values used in this study are available under the DOI: 10.5281 at https://zenodo.org/record/7471405 [72].

Description of flight behaviour

For each migratory flight, we extracted (1) flight duration, (2) maximum and mean flight altitude, as well as (3) positive altitudinal change during the flight using a standard barometric equation while correcting for the temporal variation of pressure from the ERA 5 data at the most likely location. We then calculated (4) ground speed, wind support and flight distance for each of the 100 random simulations. We then classified the flights in five categories (above continental Europe, the Mediterranean Sea, the Atlas region, the Sahara Desert, and the Sahel region) and calculated the mean and standard deviation of the different variables for each of these flight categories. We also distinguished between flights during autumn and spring migration.

Results

Migration patterns: timing and locations

Tracks and migration timing are summarized in Fig. 1, and general information is given in Table 1. An example of a full annual altitudinal profile based on atmospheric pressure data is given in Fig. 2a. The tagged individuals stayed at the breeding site in the post-breeding period until departure to migration. In all years, they departed from the breeding sites between the 10th and the 16th of September (n = 8, Fig. 1). They spent 0 to 9 days (mean ± sd = 3.5 ± 3.2) between the breeding site in the Alps and the Mediterranean coast (Liguria, Italy) before starting to cross the Mediterranean. In 2020, a female from Switzerland (26HS, Fig. 1) spent several days at high elevations in the western Alps (3040 to 3200 m) before flying over the Mediterranean to Corsica directly from this alpine site. One bird from Italy (24TJ, Fig. 1) crossed the Mediterranean directly from the breeding site and another one stopped on the coast over the day. Four birds landed

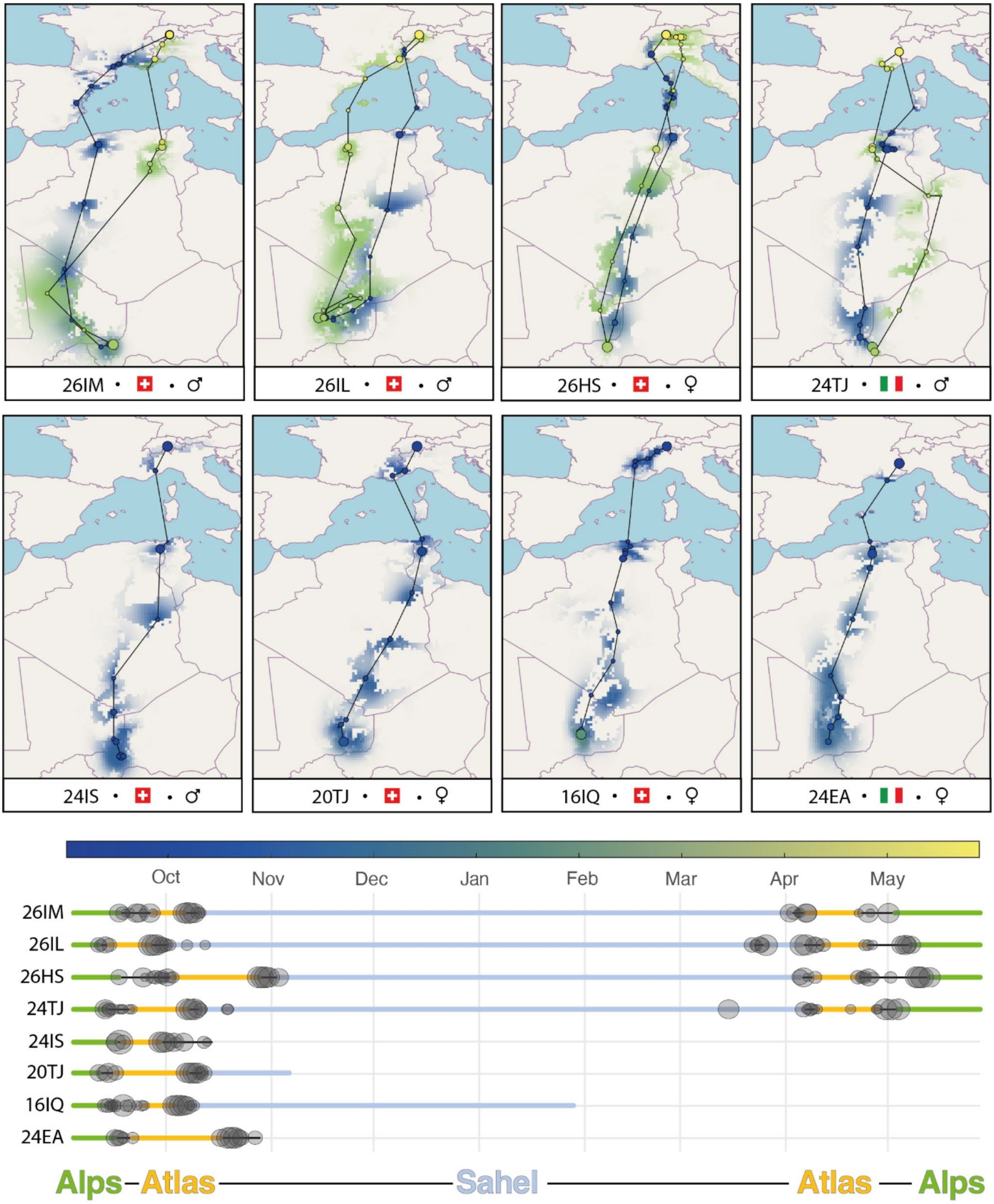

Fig. 1 a. Most likely trajectories and stationary locations of the Northern Wheatears equipped with multi-sensor geolocators in the Swiss Alps (26IM, 26IL, 26HS, 24IS, 20TJ, 16IQ) and Italian Alps (24TJ, 24EA). For visual purposes, the colour scale for all stationary sites was normalized to a maximal value of 1 and represents the marginal probability of the position of the bird. Autumn migration appears in blue and spring migration in green

b. Time series of the individuals with breeding site (green), migration (yellow) and non-breeding sites (blue). The grey circles show migratory flights. The size of the circles is proportional to the flight duration

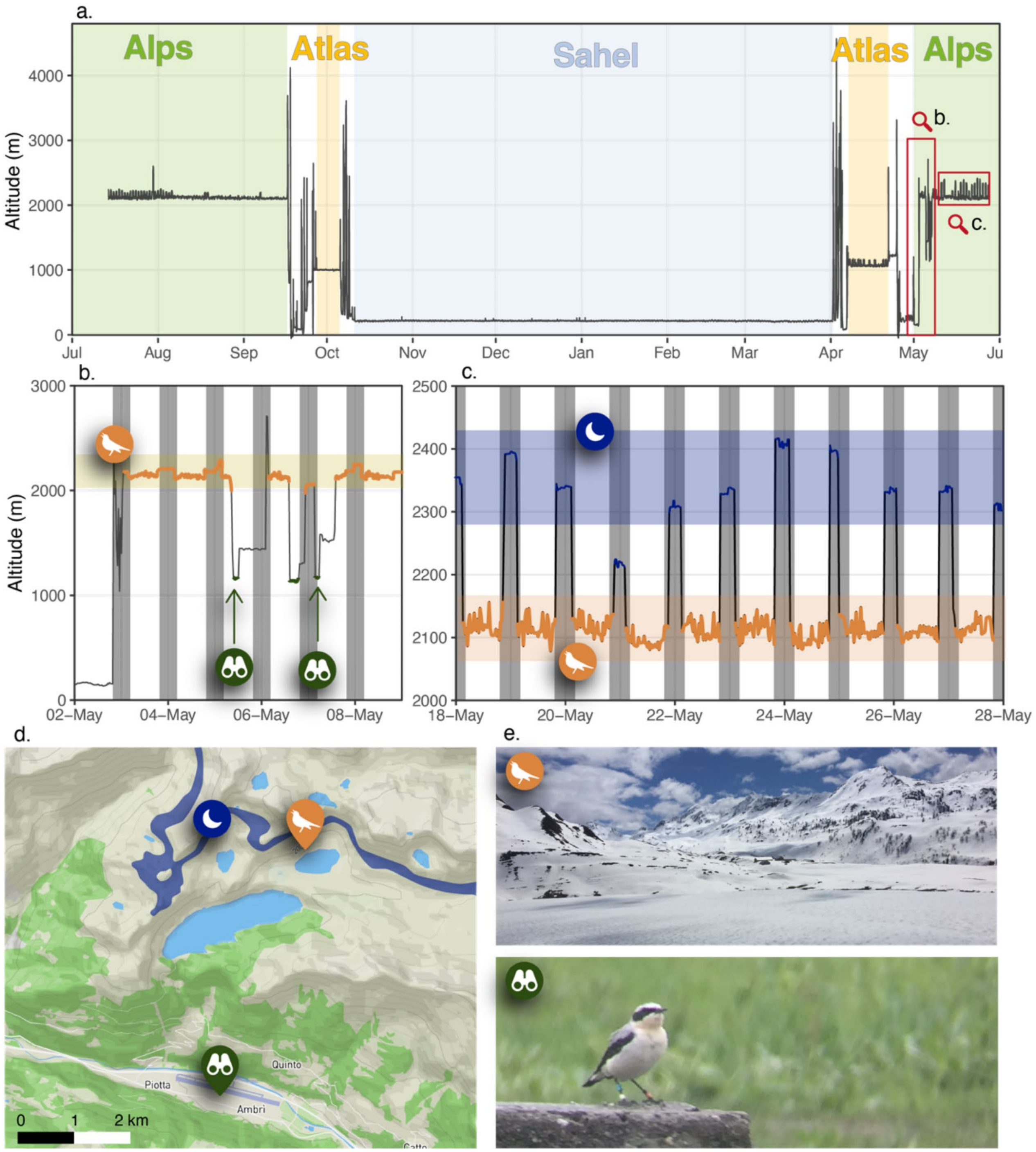

Fig. 2 a. Altitudinal profile of the male 26IM during the annual cycle. The green transparent area shows the breeding site, yellow the stopover in the Atlas, and blue the non-breeding site. The red box b. refers to the zoom on Fig. 2b and the red box c. to the zoom on Fig. 2c

b. Altitudinal profile of the bird 26IM between 2 May and 9 May 2021 (red box b on Fig. 2a). The orange line is the measured position of the bird when it was at the breeding territory. The dark-green line shows the residency at lower elevation in the nearby valley, highlighted with the binocular symbol for the two occasions when the bird was observed directly

c. Altitudinal profile of the bird 26IM between 18 May and 28 May 2021 (red box c on Fig. 2a). The orange shade shows the area of the breeding territory and the orange line the measured position of the bird within the territory. The blue lines show the measured position of the bird at night. The shaded blue area with the moon symbol shows the area where the bird roosts, corresponding to the blue area on Fig. 2d

d. Map of the study region showing the breeding territory (orange), the roosting elevational area near the breeding territory (blue) and the area where the bird was observed in the nearby valley during bad weather events (Fig. 2b)

e. Breeding territory at the time of arrival and photography of the male 26IM in the nearby valley on 5 May 2021 briefly in Sardinia, Corsica or the Balearic Islands in the Mediterranean in autumn, and four birds crossed the Mediterranean without stopping over. A female briefly landed on both Corsica and Sardinia (26HS, Fig. 1). Overall, birds crossed the Mediterranean quickly (mean ± sd = 2 ± 2.4 days, median = 1 day), but then spent a long stopover of 9 to 25 days (mean ± sd = 16 ± 6.5) in the Atlas highlands of northern Africa before crossing the Sahara in the second phase of autumn migration. The crossing of the Sahara was direct in autumn, consisting of 4 to 6 typically long nocturnal flights, with stops during the day. The birds thereafter spent a few days in the Sahel, interspersed with shorter flights (further details about flight durations are given under the "flight performance" result section), before settling at a single site for the entire non-breeding period. The four individuals that provided data for a full cycle were stationary for 165.3 ± 9.4 days on sites located close to each other between eastern Mali and western Niger (Figs. 1 and 3).

Spring migration (n = 4, year 2021) started between April 1st and 5th. However, one male (26IL, Fig. 1) initiated two earlier migratory-like flights to the North-East (duration of 8 h with 27 km/h perpendicular wind from the North-West and 10 h with 48 km/h supporting wind from the South-West), but then returned to the non-breeding area (duration of 6 h with 25 km/h perpendicular wind from the North-East and 8 h with 35 km/h supporting wind from the North-East), before departing finally on April 4th. The four birds crossed the Sahara in a similar way in spring compared to autumn, in 3 to 5 nights with daytime stopovers. A main stopover again took place in the highlands of Northern Algeria in spring, with a duration of 15 ± 2.4 days. Mediterranean Islands were used for short stops in two cases (Table 1; Fig. 1).

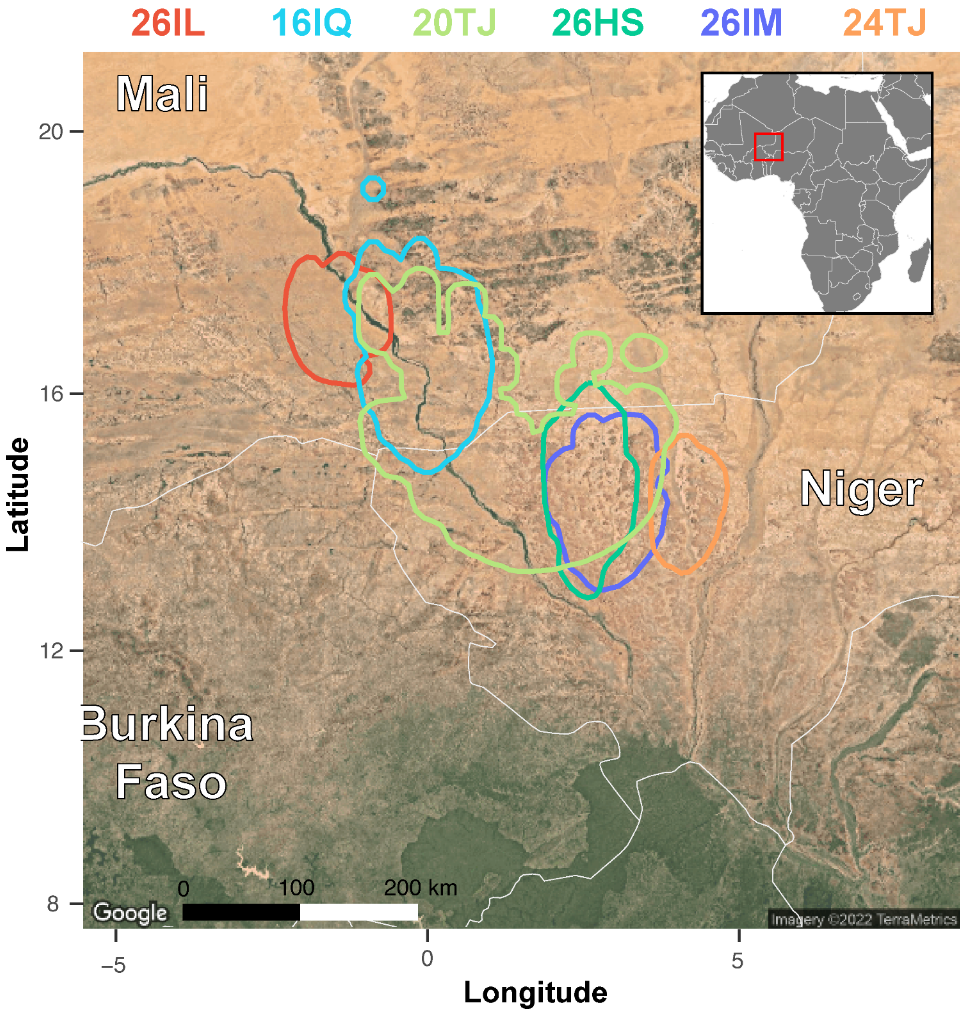

Fig. 3 Most likely locations of the non-breeding sites of six individuals between E Mali, W Niger and N Burkina Faso in Western Africa. The delineated areas correspond to the 99th quantile of the marginal probability distribution of stationary locations extracted from the hidden Markov model. Because the device was operational for a shorter duration, the estimated area for the individual 20TJ is larger

Migratory flight performance

During autumn (n=8 individuals) and spring migration (n=4 individuals), we described 167 migratory flights (117 in autumn and 50 in spring) that were initiated at dusk and were only rarely prolonged into the following day (n=11 flights longer than 12 h and 4 flights longer than 14 h, maximum=21 h). The flights had the following characteristics (mean ± sd): duration 5.9 ± 4.6 h, maximum altitude per flight 2294 ± 1172 m and up to 5150 m, average altitude per flight 1409 ± 796 m, positive altitudinal change 2298 ± 1902 m, positive altitudinal change per flight hour 405 ± 239 m, ground speed 45 ± 16 km/h, wind support 7 ± 10 km/h and distance 302 ± 296 km. Flight duration (Fig. 4c) was longer over the Mediterranean and Sahara (n=45) than over continental Europe (n=40), the Atlas (n=27) and the Sahel (n=34). Maximum and mean flight altitude (Fig. 4a, b) were higher above the Sahara and Europe than above the Atlas and the Sahel, but more variable above the Mediterranean. Ground speed (Fig. 4d) was faster above the Mediterranean and Sahara than above Europe, the Atlas and the Sahel. Positive altitudinal change was higher above the Mediterranean (3116 ± 836 m) and the Sahara (3992 ± 1659 m) than above Europe (1303 ± 1233 m), the Atlas (836 ± 607 m) and the Sahel (1811 ± 1578 m), but positive altitudinal change rate per hour did not show any particular pattern between long barrier-crossing flights and other flights (Europe 352 ± 254 m/h, Mediterranean 415 ± 178 m/h, Atlas 469 ± 345 m/h, Sahara 369 ± 126 m/h, Sahel 456 ± 259 m/h). Wind support was generally used above the Mediterranean (10 ± 10 km/h) and the Sahara (12 ± 11 km/h), but less above Europe (1 ± 4 km/h), the Atlas (6 ± 9 km/h) and the Sahel (7 ± 9 km/h). Flight distances were longer over the Mediterranean (481 ± 317 km) and over the Sahara (609 ± 261 km) and much shorter in Europe (122 ± 109 km), the Atlas (69 ± 56 km) and the Sahel (169 ± 136 km).

Local altitudinal movements at the breeding site

Individuals arrived at the breeding territory between April 26th and May 13th (n=4). The behaviour upon arrival in the breeding region differed between

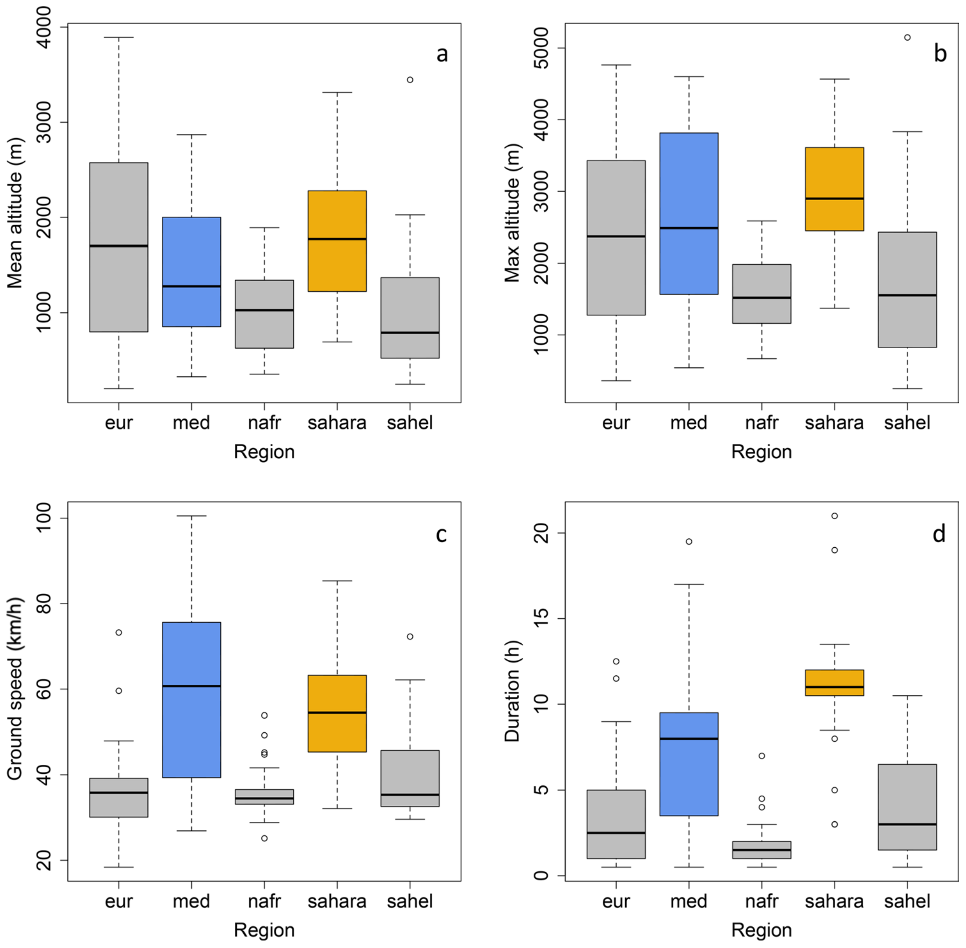

Fig. 4 Mean flight altitude per flight (a), maximum flight altitude per flight (b), ground speed (c) and flight duration (d) over continental Europe (eur), the Mediterranean Sea (med), the Atlas region in Northern Africa (nafr), the Sahara Desert (sahara), and the Sahel region (sahel)

individuals. One Swiss male (26IM) moved on three occasions from the breeding site to the adjacent valley, 5 km further and 1000 m lower than the breeding territory. This coincided with an adverse weather event with snowfall at the breeding site (Fig. 2b, d and e). This behaviour was confirmed twice with visual observations in the field. The bird came back to the territory between these foraging excursions, with one flight measured at 2600 m a.s.l. The third male also performed altitudinal movements in the nearby Alps. The latest arrival was recorded for the female, which stayed at high elevation sites (1640 to 2085 m) in the Alps between April 25th and May 8th before reaching the breeding site on May 13th. The male from Italy (24TJ) did not undertake local altitudinal movements to the valley upon arrival (Fig. 1).

During their presence at the breeding site, all four birds undertook diel altitudinal movements from the breeding and foraging territories towards roosting sites, located between 50 and 300 m higher (example for the male 26IM, Fig. 2c). In the female 26HS, this behaviour occurred in the post-breeding season 2020, as well as in the pre-breeding season 2021, but was interrupted when she started incubating in June. The tag was retrieved when the female was feeding the chicks. The males continued to commute at night while breeding.

Discussion

We used atmospheric pressure measurements, combined with light-level geolocation, to describe local and global movements of Alpine Northern Wheatears, one of the few long-distance migrants breeding in high-alpine habitats, throughout the annual cycle. We located the main stopover area in the northern African highlands, underlining the importance of this region in autumn and spring. We refined the knowledge of the location of non-breeding sites in the Alpine population, within a restricted area in the Western Sahel and detected residency at a single site during winter. While migration timing showed synchrony between the tagged birds, we highlighted faster and longer flights over migratory barriers, especially the Sahara, compared to areas with favourable stopover opportunities. Flight altitude was typically higher above the desert. Moreover, we described local altitudinal movements at the breeding site, with occasional movements to an adjacent valley in response to weather conditions in the pre-breeding season, as well as unexpected regular diel commuting behaviour at the nesting site.

The time window for the initiation of autumn migration across different years was surprisingly narrow compared to short-distance high-elevation migratory species with higher variability in departure date [39, 73]. Compared to previous results from light-level geolocation suggesting a main stopover of the Alpine population in the central and western Mediterranean [26, 45, 46], the identification of a major stopover region in the Atlas highlands of Northern Africa underlines the advantages of using atmospheric pressure to estimate stationary locations [57]. The open agricultural and pastoral land uses typical of these regions obviously serve as refuelling habitats between barrier crossings. This complements the findings of Maggini and Bairlein (2011, [74]), who described Northern Wheatears at a lowland spring stopover on the edge of the Sahara as not having sufficient body condition to subsequently cross the Mediterranean without refuelling. These birds however did not remain at this site, but most likely continued towards further stopover sites, probably in the Atlas highlands further north.

All four individuals tracked for an entire annual cycle stayed at a single location throughout the boreal winter, without any altitudinal movement detected in the pressure time series within the non-breeding region. However, previous light-level geolocation studies identified movements in some individuals within the non-breeding region [26, 45]. Other Afro-Palearctic migrants, especially species linked to wetlands such as the Great Reed Warbler *Acrocephalus arundinaceus*, shift between successive non-breeding sites to track resources [75, 76]. The residency at a single non-breeding site in the Wheatears we tracked is likely related to the site-fidelity and territorial behaviour of the species on the wintering grounds [77].

Migration of the Central European populations of the Northern Wheatear is north-south oriented, resulting in flights above the Mediterranean as the shortest route [26, 44, 45]. The species can fly non-stop for more than 2500 km over the Atlantic Ocean [43, 78], and Cyprus Wheatears *Oenanthe cypriaca* can reach their non-breeding sites in a non-stop flight [21]. Hence, one could expect non-stop Mediterranean crossing in Northern Wheatears. However, in autumn and spring some birds landed on the Mediterranean islands, or flew further west towards the Iberian Peninsula, where the sea is narrower. This underlines the role of small islands for migratory songbirds in the central Mediterranean [27], although it remains unclear whether these short stopovers were intentional (the bird knew about the land mass and directed its flight towards it) or happened opportunistically (the bird saw the land mass and decided to stop).

Northern Wheatears adapted their migratory flights in relation to barrier crossing. Some migratory songbirds, such as Tawny Pipits *Anthus campestris* and Great Reed Warblers, regularly prolong their nocturnal migratory flights into the following day [32, 33]. Nevertheless, the tracked Wheatears mostly performed nocturnal migratory flights interspersed with stopovers during the day. These flights were, however, notably longer and faster while crossing barriers such as the Mediterranean and the Sahara, than were the flights performed closer to the breeding and non-breeding sites and above the favourable Atlas region in Northern Africa. Barrier-crossing flights were generally wind-supported. They showed altitudinal fluctuations and hence a higher total positive altitudinal change than shorter migratory flights, but not a higher climb rate per hour. Müller et al. (2018), Schmaljohann et al. (2011) and Schmaljohann & Naef-Daenzer (2011) [79–81] described departures earlier in the evening in the case of barrier-crossings flights towards the Atlantic Ocean and Greenland. Here, the nature of the barrier differed: while crossing the Mediterranean and the Sahara, birds can stop over when needed, which is not possible over the ocean. Numerous short flights interspersed with daily stopovers took place before reaching the non-breeding site in the Sahel region at the end of autumn migration, as well as before returning to the breeding site in spring. Such short flights also occurred in the Atlas region of Northern Africa, as suggested by Maggini and Bairlein (2011, [74]). Some birds also stayed at different locations in the Alps before autumn migration and after spring migration. More surprisingly, one individual performed migratory flights and returned to the non-breeding area before undertaking the actual spring migration (this event was apparently linked with wind support conditions); using only light-level data in this case would cause imprecision of several days when inferring migration timing from changes in light-level stationary locations [26]. Birds generally flew at higher elevations above the Sahara than during the rest of the migration and remained stationary in the heat of the day. As an open-ground species, the Northern Wheatear is more likely to stop over in the desert than are wetland species [30] or forest species [29]. High elevation flights were recorded at night and took advantage of supportive winds, thereby suggesting that heat avoidance during daylight hours would itself not be sufficient to explain high-altitude flights over the desert in songbirds [33].

Our data also unveiled local altitudinal movements in Northern Wheatears. Such movements typically occurred in two distinct phases in the pre-breeding and breeding seasons. First, occasional local altitudinal movements of larger amplitude were undertaken in the pre-breeding period. Similar early-season altitudinal movements occur in other alpine migratory species such as the Ring Ouzel *Turdus torquatus alpestris* [39]. However, in the case of the Northern Wheatear, the movements were irregular and appeared to be an emergency response to extreme meteorological events such as late and intense snowfalls upon arrival at the breeding site. One bird flew at 2600 m between the foraging site in the valley and the breeding territory, indicating that the individual did not minimize the elevational difference while commuting between alternative foraging sites and the breeding territory.

A second type of altitudinal movement, unexpected in this territorial and breeding-site-faithful species [48, 59, 82], occurred at night, while birds flew up to roost, most likely in nearby cliffs, sometimes changing location after one to three nights at the same elevation. This behaviour was halted by the female during breeding but continued throughout the breeding season in males. It is unclear whether commuting aims to optimise temperature at night or to avoid predation, or a combination of both – such behaviour is a typical strategy to cope with cold nights in high-alpine passerines such as the White-Winged Snowfinch *Montifringilla nivalis* roosting in cliff crevices where the temperature remains higher than outside [40]. During the post-breeding season, Northern Wheatears remained at the breeding site until departure for migration, including the period of moult, as previously demonstrated for lowland populations [83]. This stresses the importance of suitable habitat throughout the period of presence at the breeding site.

Conclusion

Our study provides novel insight into migration strategies, flight behaviour, barrier crossing and local altitudinal movements in a small songbird, including life history stages such as the transition between arrival and breeding, the post-breeding season, and moult. Movement behaviour was surprisingly variable in the Northern Wheatear, with almost no movement over more than five months at the non-breeding site, opposed to locally mobile behaviour at the breeding site and broader-scale movements during migration. This overview of the annual cycle calls for a wider use of pressure loggers to investigate the three-dimensional movements of songbirds at different spatial scales, especially using the method of positioning by correlating the atmospheric pressure measured on the bird with global atmospheric pressure data [57, 66].

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Author Contribution

YR, CMM and FL designed the study, YR and MMS conducted fieldwork, YR and RN performed data analyses, YR wrote the original draft with support of CMM, RN, MB, VA and BH. All authors provided editorial advice.

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Data Availability

Data, codes, and parameter values used in this study are under the DOI: 10.5281 at https://zenodo.org/record/7471405 [72]

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Publisher's Note

Chapter 6

Long-distance movements driven by rainy seasons across the equator in an intra-African migratory bird

Rainstorm in Africa and Woodland Kingfisher *Halcyon senegalensis* (© Yann Rime)

Long-distance movements driven by rainy seasons across the equator in an intra-African migratory bird

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Abstract

Our fundamental knowledge of bird migration is biased as research mostly focused on migrants from the northern hemisphere. Conservation challenges call for a more global understanding of migration, including movements within tropical regions, especially in Africa, which is subject to major changes in habitat and seasonal weather patterns. For the first time, we used multi-sensor loggers to track the long-distance migration of a small-sized intra-African migrant, the Woodland Kingfisher. Based on atmospheric pressure, light levels and acceleration data, we retrieved all their stationary sites and modelled their complete migratory trajectory. This also allowed to describe migration timing and flight behaviour. We described how these precisely timed movements matched with patterns of rainfalls, temperatures, vegetation greening and habitat composition throughout the annual cycle. Woodland Kingfishers used similar open woodland landscapes and climatic conditions while breeding in the South African rainy season and at non-breeding sites 4000 km away in the northern hemisphere. Migratory flights were relatively short (3.7 hours in average) and strictly nocturnal, reaching up to 2890 m a.s.l.. The Congo Basin rainforests were avoided by longer flights and shorter stopovers compared to wooded savanna, a behaviour similar to that of barrier-crossing adaptations in other migratory systems. All birds individually reached single non-breeding sites within a small area in South Sudan (<100 km of each other), an unprecedented report of migratory connectivity in an austral migrant. These contrasting results and the large gaps in the knowledge of intra-tropical migration underline the importance of further fundamental research alongside with the ongoing conservation efforts.

Keywords: *Halcyon senegalensis*, intra-African migration, Austral migrant, multi-sensor geolocator, atmospheric pressure, *geopressureR*

Introduction

Bird migration is a diverse phenomenon worldwide, consisting in periodic movements between two or more locations (Dingle & Drake, 2007). Migration is usually defined from a high-latitude perspective, where it aligns with photoperiodic changes in environmental seasonality (Newton, 2023). However, conservation challenges call for understanding the diversity of migratory systems globally. In particular, intra-tropical migration remains very poorly studied compared to the movement ecology of birds breeding in the Northern Hemisphere (Chesser, 1994; Dingle, 2008; Huber et al., 2005; Jahn et al., 2020). We aimed at filling this research gap by focusing on migration within Africa, a continent subject to major changes in habitat and seasonal weather patterns (Collier et al., 2008; Dunning et al., 2018; Maitima et al., 2009).

Within tropical regions, migration is considered a response to environmental seasonality that is different from that faced in high latitude regions. The annual cycle of locally breeding and moulting birds and their intra-tropical migration patterns largely depend on rainfall seasonality (Lloyd, 1999; Moreau, 1950; Nwaogu et al., 2019; Nwaogu & Cresswell, 2016, 2021). The climate of sub-Saharan Africa is mostly driven by the fluctuation of the inter-tropical convergence zones, with tropical areas north of the Equator receiving rainfall during the boreal summer and tropical to subtropical areas south of the equator receiving rainfall mostly during the austral summer (Nicholson, 2018b; Schneider et al., 2014). In addition to these annual patterns, tropical Africa undergoes pluri-annual cyclic rainfall variations (Biasutti, 2019; Lucio et al., 2012; Nicholson et al., 1998). Most bird species in the Afrotropic, depending on their diet, breed before or during the rainfalls, followed by a post-breeding moult (Moreau, 1950; Westwood & Murton, 1977). Species higher in the food chain such as raptors usually breed earlier to anticipate the peak abundance of their prey (Hau, 2001; Lloyd, 1999; Moreau, 1950).

Intra-African migration consists of seasonal movements of African-breeding birds within the Afro-tropical biogeographic realm, ranging from nomadism tracking temporary resources to typical migration featuring seasonally distinct breeding and non-breeding sites (Cresswell et al., 2008; Dingle, 2008; Hockey, 2000; Ivande & Cresswell, 2016). Migratory and resident populations often co-occur within the same species that are described as resident, partial migrant or nomadic. This is the case with the Red-billed Queleas *Quelea quelea*, the most abundant bird in the world, whose swarms move short-distances, affecting agriculture (Cheke et al., 2007; Dallimer & Jones, 2002). Movement ecology of larger Afrotropical birds within the continent has been increasingly investigated, including resident and nomadic species, typically raptors (Diekmann et al., 2004; Garcia-Heras et al., 2019; Zvidzai et al., 2020), and some other species that are large enough to carry a GPS device (Iwajomo et al., 2018; Jensen et al., 2006; Lenz et al., 2011, 2015). Intra-African seasonal movements often span over short distances of less than 1000 km (Garcia-Heras et al., 2019; Iwajomo et al., 2018). However, several species perform long-distance, trans-equatorial migration. Abdim's Storks *Ciconia abdimii* breed in the Sahel and migrate to Central, Eastern and Southern Africa, hereby benefitting from rainy seasons of both hemispheres (Jensen et al., 2006). Few austral migrants, such as the Pennant-winged Nightjar *Caprimulgus vexillarius* (Del Hoyo et al., 1999), undertake long-distance migration to spend the non-breeding season north of the Equator. Various strategies exist by which birds link breeding and migration. The ground-breeding Dusky Larks *Pinarocorys nigricans*, for example, nest during the dry season in Southern-Central Africa and spend the non-breeding season further south during the austral summer rains (Dean, 1974; Ryan, 2020).

In contrast to the Afro-Tropics, the migration behaviour and ecology of Afro-Palearctic species in Africa has been intensively studied (Jones, 1995; Salewski & Jones, 2006; Thorup et al., 2017). In some Palearctic-breeding migrants, intra-African movements have been described, whereby these species track seasonal rainfall and vegetation greening (Briedis et al., 2018; Thorup et al., 2017). Yet, other Afro-Palearctic birds are stationary at a single site, once they reached their non-breeding goal areas (e.g., Rime et al., 2023). Some Afro-Palearctic migratory species use population-specific non-breeding grounds, i.e., showing high migratory connectivity (Marra et al., 2006; Webster et al., 2002), whereas others spread over large areas that are not population-specific, i.e., showing low migratory connectivity (Finch et al., 2017; van Wijk et al., 2018). Most palearctic species that use flapping flight migrate at night. Their journey between breeding and non-breeding sites often crosses suboptimal or hostile habitats, so called migratory barriers that are typically seas, mountains and deserts (e.g., Bruderer et al., 2000; Jiguet et al., 2019; Zhao et al., 2024). Diverse species- and trait-specific behavioural adjustments of migratory flights and stopover behaviour allow migratory birds to cover sometimes large distances over such unhospitable habitats (Adamík et al., 2016;

Åkesson et al., 2016; Lavallée et al., 2021; Malmiga et al., 2021; Ouwehand & Both, 2016; Rime et al., 2023).

The links between breeding, movement ecology and seasonality of African-breeding birds were mostly described from observational approaches so far (del Hoyo, J., Elliott, A., & Sargatal, 2001; Moreau, 1950). It is still unclear how most of the small birds in the Afrotropic time their annual cycle and how they respond to environmental changes. Light-level geolocation typically produce poor positioning in the tropics, where variations in day-lengths across latitudinal gradients are limited (Lisovski et al., 2012, 2018, 2020). The development of multi-sensor loggers now allows to use atmospheric pressure for positioning and opened new opportunities to study intra-tropical movements of small birds (Nussbaumer et al., 2022, 2023; Rhyne et al., 2024; Rime et al., 2023). This method provides precise information on flight and stop over behaviour that have never been described before in small intra-tropical migrants (Lathouwers, Artois, et al., 2022; Lathouwers, Nussbaumer, et al., 2022; Rime et al., 2023). The current understanding of intra-African movements is still very incomplete and species-specific fundamental knowledge is lacking.

To address these gaps, we used multi-sensor geolocators for the first time in an intra-tropical migrant, the Woodland Kingfisher *Halcyon senegalensis cyanoleuca.* This small-sized species has been described to carry out long-distance migration from breeding sites in South Africa, which was supported by an earlier study locating the non-breeding sites of two birds from light-loggers (Tarboton & Tarboton, 2014). Woodland Kingfishers breed during the rainy season (del Hoyo, J., Elliott, A., & Sargatal, 2001; Mwale et al., 2022), and little was known about their whereabouts in the non-breeding season. We aimed at locating non-breeding and stopover sites and at describing how local habitat and climatic conditions, especially rainfall patterns, compared to the breeding site. Furthermore, we explored if these birds had high migratory connectivity, which has not been reported before in an intra-tropical migrant. We described flight behaviour and stopover strategy and expected stopovers to be longer in suitable habitat, with adjusted flight behaviour while crossing the dense Congo Basin rainforest, that could act as a “green” or “soft” barrier (Alerstam, 2001; Lathouwers, Artois, et al., 2022). By building fundamental knowledge in a poorly known migratory system, we aimed here at setting a standard anticipating a future, broader use of multi-sensor geolocators in intra-tropical migrants.

Methods

Study species

Woodland Kingfishers use a wide range of open wooded habitats, from Savanna to forest clearings and gardens, with a preference for riverine woodland. They prey on terrestrial, large arthropods and small vertebrates. Three subspecies are described: *H. s. cyanoleuca* from Southern Africa and *H. s. senegalensis* from the Sahel and Western Africa have migratory and resident populations, while *H. s. fuscopileus* from central to western African equatorial forests is considered as sedentary (del Hoyo, J., Elliott, A., & Sargatal, 2001; Fry et al., 1988).

Geolocators and deployment

Tagging was carried out during the breeding seasons between December 2016 and January 2019 at Mogalakwena Research Centre, South Africa (22° 43' 35" S, 28° 46' 30" E). In three years, 20 adult individuals were equipped with 27 multi-sensor geolocators (GDL-3 PAM, Swiss ornithological institute, Switzerland, weight 1.6 g) mounted on a leg-loop harness (Rappole & Tipton, 1991). Six individuals were equipped twice. One individual was equipped three times during two breeding seasons but lost all tags. Five geolocators were successfully retrieved from four individuals (Table 1). The geolocators 16 LN and 22 NO were fitted on the same bird in 2017 and 2019. The male 16 LO and female 16 LP were a breeding pair. All other birds from which the tags were retrieved were females.

Analyses

We modelled trajectories from pressure, light and wind data following Nussbaumer et al., 2022, 2023, using the associated R Package GeoPressureR (Nussbaumer & Gravey, 2022). First, we identified migratory flights periods based on accelerometer (i.e., high activity for a prolonged period of time) and pressure data (i.e., sharp change in pressure indicating change of altitude). Birds were considered to be at a single stationary location (<10km) between two migratory flights. Second, we constructed pressure likelihood maps by matching geolocator pressure measurements of each station periods with data from the ERA5-LAND reanalysis

(0.1° x 0.1°, Muñoz-Sabater et al., 2021). Third, we built light likelihood maps using the threshold method and a calibration from the equipment and retrieval periods (Lisovski & Hahn, 2012). The likelihood maps of all twilights from the same stationary periods were aggregated using a log-linear pooling function (Nussbaumer et al., 2022). Finally, we modelled the trajectory of each individual with a Hidden Markov Model using pressure and light likelihood maps as well as wind data (Nussbaumer et al. 2023). Based on this model, we produced 1) a probability map for the position at each stationary period, 2) the most likely individual trajectory for each bird and 3) 100 random simulations of the trajectories. All analyses were conducted in R version 4.3.2 (R Core Team, 2023).

Remote-sensing data

Daily temperature and precipitation data for the breeding site, as well as for the estimated non-breeding sites, were obtained from the ERA5-Land between 1979 and 2020 (Muñoz-Sabater et al., 2021). We then calculated the mean precipitations and temperatures for each day of the year. NDVI values were retrieved from the MODIS Terra Vegetation (Didan, 2021). We used the median NDVI value per 16-day period of the year along the latitudinal gradient covered by the birds, for the entire dataset (2000-2024). To describe landscape-scale habitat at stationary sites (stopover, breeding and non-breeding sites), we extracted landcover proportion on a 20-km radius around each most likely location from the Copernicus Global Land Cover Layers (100-m resolution, Buchhorn et al., 2020).

Description of flight behaviour and stopover use

For each migratory flight, we extracted flight distance, flight duration, maximum and mean flight altitude above ground and above sea level. We calculated ground speed, wind support and flight distance for each of the 100 random simulations (Nussbaumer & Gravey, 2022). We then classified the migration bouts in two habitat-based categories (Congo Basin equatorial forests between -3° and +3° latitude and savanna or wooded savanna otherwise). We calculated the mean, median and standard deviation of the different variables above the Congo Basin rainforest compared to migration above favourable savanna habitats.

Results

Migration timing and routes

The tracked Woodland Kingfishers left the breeding site between 22 March and 17 April (Figure 1a). This timing aligned with the end of the rainy season (Figure 1c), when the average temperatures fall below 25°C (Figure 1b). The north-bound post-breeding migration covered on average 4080km over 73 days (Figure 2 and Supplementary material, Figure S1), for a total of 86.5 flight hours (see minor individual variation in Table 1). All five tracks showed long stopovers in Zambia, where vegetation greening remains higher at the end of the rainy season compared to the breeding site. Migration through the equatorial rainforest was faster, with only short stopovers (Figure 1a and Figure 2). Four individuals arrived close to the final non-breeding site but resided southward at sites presenting higher long-term NDVI than the non-breeding site at that time (Figure 1a). In 2019, one individual (22 NO) migrated through the equatorial region a month later and directly reached the final non-breeding site without preliminary residency at another site. Three out of four birds initiated pre-breeding migration almost at the same date. The departure from the non-breeding sites corresponds to the average end of the rainy season, coupled with a decrease in vegetation greening. Compared to post-breeding migration, pre-breeding migration was shorter (mean = 26.9 days) with slightly more time in flight (93.6h, Figure 1a, Table 1). Three birds arrived at the breeding site mid-November, among them the breeding pair (16LP, 16LO) within two days, and one in early December, just before the long-term onset of the rainy season and vegetation greening.

Table 1. Summary of the general information on migration schedule, flight performance and stationary periods of Woodland Kingfishers tagged with multi-sensor geolocators during an entire annual cycle, divided between post-breeding (n = 5) and pre-breeding migrations (n = 4). Wind support is the mean weighted relative to flight duration.

	Tag ID	**16LN**	**16LO**	**16LP**	**20IK**	**22NO**
Post-breeding	**Departure breeding site**	05.04.17	26.03.17	15.04.17	22.03.18	17.04.19
	Arrival non-breeding site	07.06.17	01.06.17	15.06.17	21.06.18	08.07.19
	Migration duration (days)	63.72	67.69	61.70	90.95	81.89
	Number of flights	26	26	22	25	38
	Days in the Congo Basin	3.82	2.75	1.64	4.76	15.78
	Flights in the Congo Basin	3	3	2	2	6
	Cumulative flight distance	4228	3914	4057	3998	4220
	Cumulative flight hours	83.00	85.83	83.75	91.42	88.58
	Mean flight altitude a.s.l.	1023	1139	953	1000	922
	Mean flight altitude a.g.l.	238	229	275	202	199
	Max flight altitude a.s.l.	2455	2714	2352	2587	2890
	Max flight altitude a.g.l.	1670	2151	1732	1159	1661
	Wind support (km/h)	8.72	7.98	8.34	7.10	5.01
	Mean stopover duration	2.43	2.59	2.79	3.64	2.13
	Median stopover duration	0.90	0.92	0.89	1.00	1.03
Pre-breeding	**Departure non-breeding site**	27.10.17	17.10.17	27.10.17	26.10.18	-
	Arrival breeding site	17.11.17	14.11.17	13.11.17	04.12.18	-
	Migration duration (days)	21.57	28.65	17.56	39.90	-
	Number of flights	17	24	14	26	-
	Days in the Congo Basin	2.67	0.54	0.55	1.59	-
	Flights in the Congo Basin	3	1	1	3	-
	Cumulative flight distance	4129	4655	4038	4309	-
	Cumulative flight hours	90.17	102.75	82.50	99.08	-
	Mean flight altitude a.s.l.	1315	1134	1365	1011	-
	Mean flight altitude a.g.l.	496	258	388	189	-
	Max flight altitude a.s.l.	2688	2459	2677	2352	-
	Max flight altitude a.g.l.	2002	1545	2021	1688	-
	Wind support (km/h)	6.10	6.37	6.43	4.93	-
	Mean stopover duration	1.15	1.09	1.15	1.45	-
	Median stopover duration	0.77	0.91	0.71	0.88	-

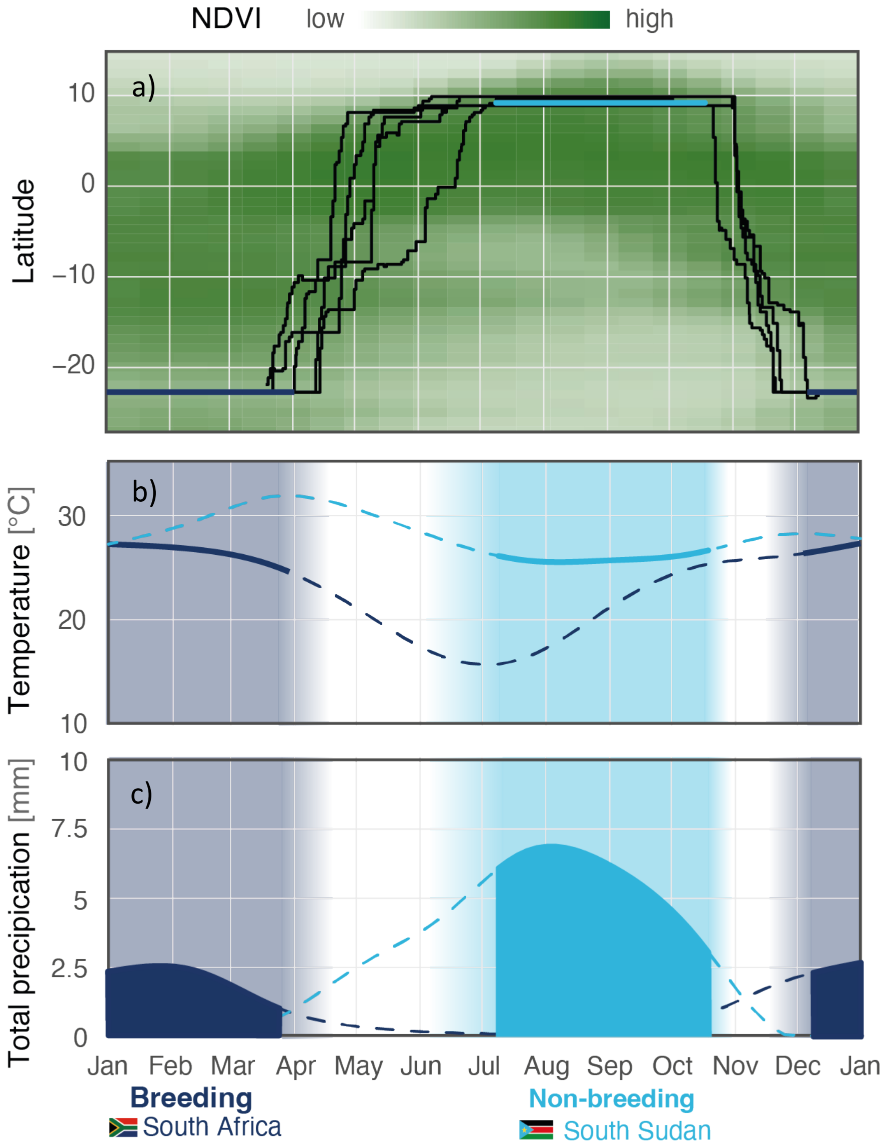

Figure 1. Presence of birds relative to long-term patterns of vegetation greening (a), temperature (b) and rainfall (c). Breeding sites are marked by pale blue lines and shading, non-breeding sites by dark blue lines and shading.

a. Latitudinal distribution of the birds during the entire annual cycle (black solid line) with the multi-year (1979-2020) annual seasonal pattern of vegetation greening (Normalized Difference Vegetation Index) at the corresponding latitudes in background. The data indicate that birds stay in habitats with substantial seasonality, using both Southern and Northern hemisphere rainy seasons but avoiding equatorial regions where vegetation greening is more constant year-round.

b. Average temperature in °C (1979-2020) at the breeding site (dark blue line) and most likely non-breeding site (pale blue line). The solid line indicates the period when the bird is present, suggesting the use of a similar thermal niche in both the breeding and non-breeding areas and avoidance of extreme (both low and high) temperatures.

c. Average precipitations in mm (1979-2020) at the breeding site (dark blue line) and non-breeding site (pale-blue line). The coloured areas indicate the presence of the birds at the breeding site and non-breeding site. While the amount of precipitation differed, the birds stayed at the respective sites during the relative local peaks of the rainy season.

Non-breeding site and migratory connectivity

The birds tracked over three years spent the non-breeding seasons in the same area of South Sudan, within less than 100 km distance of each other (Figure 3). Birds migrated individually to this area, even in the case of the breeding pair (16 LP and 16 LO). Landscape-scale habitat structure (20-km radius) was similar at the breeding site (tree cover = 17.9 %) and at the most likely non-breeding sites (median = 17.3 %). Tree cover was denser, but more variable, at migratory stopover sites (median = 41.1 %). Thermal niche was similar between the breeding site and non-breeding sites, and so was the relative peak of precipitation at the two sites (Figure 1b and c).

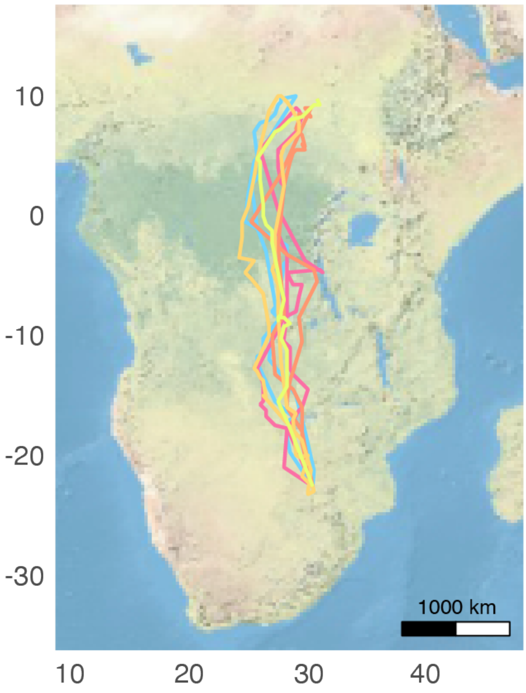

Figure 2. Most likely trajectories of the four Woodland Kingfishers including one repeated track equipped with multi-sensor geolocators in South Africa.

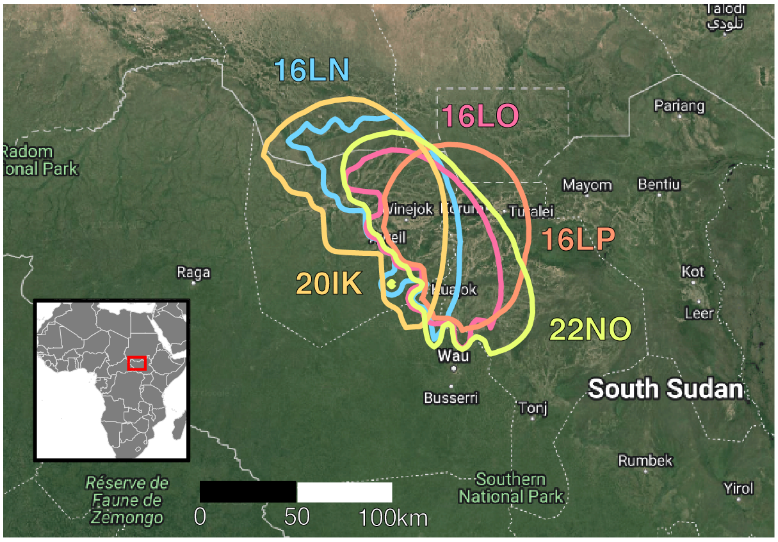

Figure 3. Most likely locations of the five final non-breeding sites in Northern-central South Sudan. This area is located at the edge of the Sahel zone, with similar seasonal weather patterns and habitat as the breeding region. The overlap of non-breeding areas indicates a high degree of migratory connectivity. The delineated areas correspond to the 99th quantile of the marginal probability distribution of stationary locations extracted from the hidden Markov model. Male 16LO and female 16LP were a pair, loggers 16 LN and 22NO were repeated tracks of the same birds.

Flight behaviour and barrier-crossing adjustments

Migratory flights occurred exclusively at night. Departure time was variable, with a mean at 22:38 ± 02:39 (UTC+2), i.e. more than 4 hours after dusk (supplementary material, Figure S2). Woodland Kingfishers migrated with frequent (median of 25 flights per migration) but short flights (50% of the flights lasted less than 2.7 hours). They still performed a few longer flight (max flight duration per individual was between 10.5 and 11.4 hours, supplementary material, Figure S3). Flight duration and distance were generally shorter in the post-breeding migration but with more wind support than in the pre-breeding migration (Table 1). Flight altitude varied between 417 to 2890 m above sea level and between 0 m to 2151 m above ground level (Table 1). This suggests that flight altitude was often adjusted to the underlying ground topography (Supplementary material, Figure S4). While crossing the Congo Basin, birds shortened the duration of stopovers (median = 0.7 days, Figure 4) compared to savanna areas (median = 0.9 days, Figure 4). Flights were also much longer above the Congo Basin (median = 5.2 hours, n = 33) compared to savanna habitats (median = 2.4 hours, n = 185, Figure 4). Tree cover was higher at stopover sites in the Congo Basin, (median = 98.7 %), compared to other stopover sites (median = 35.5 %).

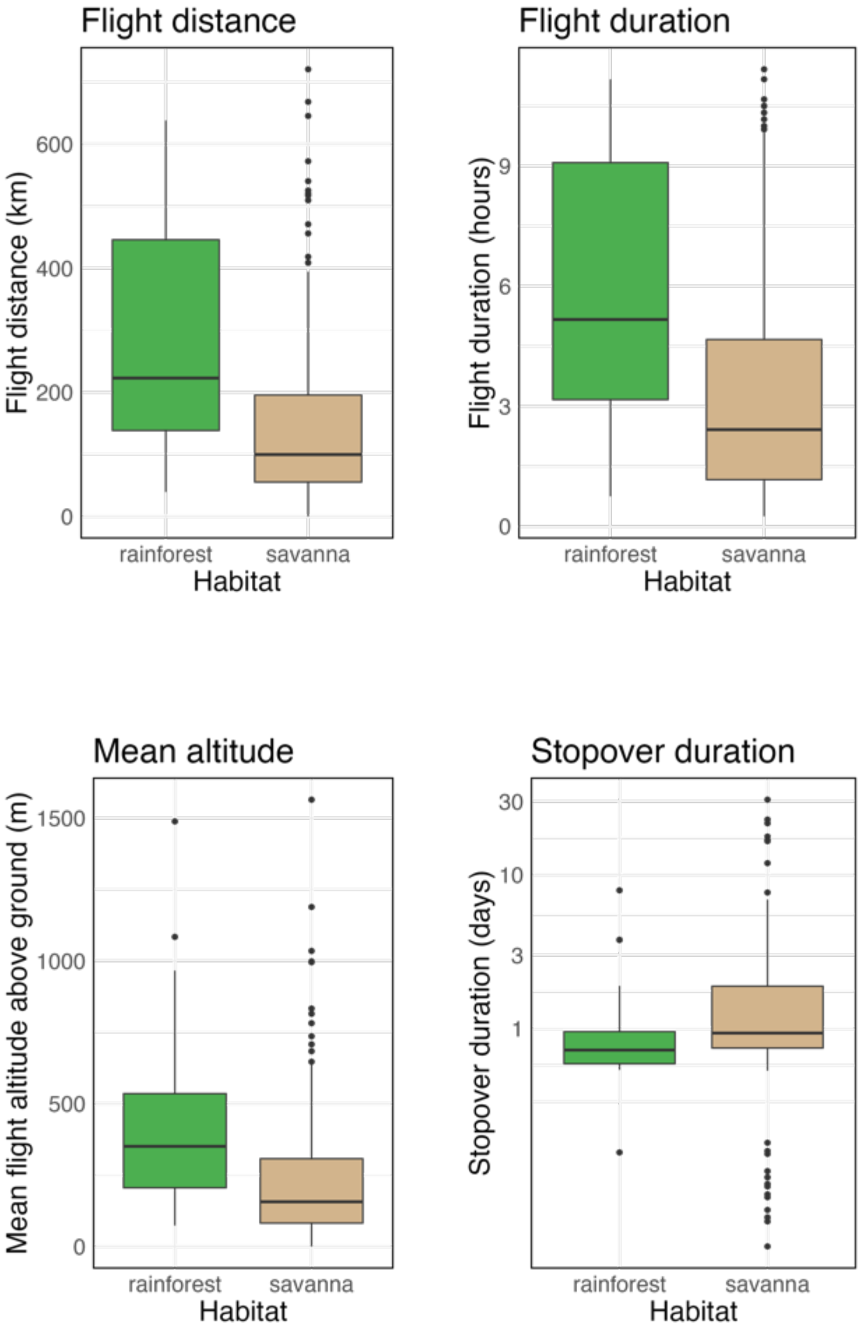

Figure 4. Flight performance (distance, duration and mean flight altitude above ground) and stopover behaviour for flights above the Congo Basin equatorial rainforest (n=33), i.e., between -3° to +3° latitude, and above the Savanna habitats (n=185). This suggests that the equatorial rainforest is treated like a barrier, crossed by longer flights interspersed with shorter stopovers.

Discussion

Woodland Kingfishers breeding during the austral rainy season in South Africa performed 4000 km of migration to spend the non-breeding season in the same region of South Sudan, where they benefitted from the northern hemisphere rainfalls in habitats that were similar to the breeding site. This suggests evidence of migratory connectivity, which has never been reported previously in intra-tropical migrants. Furthermore, South-African breeding Woodland Kingfishers reach South Sudan when the local subspecies is breeding. For the first time, we report data on flight behaviour and flight altitudes in a Kingfisher: the tracked birds adjusted their behaviour during migration through the Congo Basin rainforests, compared to wooded savanna, in a similar way as barrier-crossing adaptations in Afro-Palearctic migrants.

For insectivorous birds breeding during southern African rainy season, subequatorial regions with lower seasonal variation in rainfall and temperatures are within close reach. During the post-breeding migration, birds had prolonged stopovers in tropical Savannas of Zambia, where vegetation was still greener than at the breeding site. However, the tracked Woodland Kingfishers then migrated across the Equator to a specific area in South Sudan. This is the first documented case suggesting high migratory connectivity in austral or intra-tropical migrants. However, the general lack of individual tracking studies in intra-African migrants does not allow comparisons and it is unclear if such a high connectivity is an exception or the rule for an intra-African long-distance migrant. The cost of long-distance movements seems to be compensated by a gain from temporary food abundance related to seasonal rainfalls at the non-breeding site, with less competition compared to subequatorial regions where food availability and inter-specific competition are more stable (Karr, 1976; Moreau, 1950; Mulwa et al., 2013; Sinclair, 1978). Interestingly, the first prolonged stopover after crossing the rainforest were about 100 km south of the final non-breeding sites. This is in line with the onset of the rainy season which moves into the northern Savanna from the equator at the beginning of the boreal summer, followed by increases in vegetation greening and food abundance (Karr, 1976; Nicholson, 2018a; Omotosho, 2008; Proud & Rasmussen, 2011). Such fine-tuned migratory movements following the advance of vegetation greening have also been reported in several Palearctic migrants (Briedis, Bauer, et al., 2020; Van der Graaf et al., 2006). Post-breeding migration of the Woodland Kingfishers was notably longer than pre-breeding migration, a common pattern in other migration systems (Briedis et al., 2019; Jahn et al., 2016; Kokko et al., 2006). Woodland Kingfishers stayed in South Sudan until the end of the rainy season and migrated back to Southern Africa in a journey of less than a month (most of the nights were spent flying). The arrival at breeding sites at the beginning of the rainy season coincided with the onset of vegetation greening, later than other migrants such as Pennant-winged Nightjars that start breeding before the first rains (Del Hoyo et al., 1999). Hence, the large difference in the duration of post- versus pre-breeding migratory periods might be due to favourable conditions at the non-breeding site, at the end of the Sahel rainy season (Biasutti, 2019; Lucio et al., 2012). Many Palearctic migrants on the Eastern flyway use this area in the boreal autumn for prolonged stationary periods before to continue their migration to South-Eastern Africa (Adamík et al., 2024; Korner-Nievergelt et al., 2012; Pearson et al., 2014; Stach et al., 2012; Thorup et al., 2017; Tøttrup et al., 2012).

Surprisingly, the non-breeding range of the tracked austral Woodland Kingfishers (*H.s. cyanoleuca*) lies within the breeding range of the closely related subspecies *H. s. senegalensis*, where it is reported to simultaneously breed (Mwale et al., 2022). The tracked birds did not breed, and overlap might be made possible by a high temporary food abundance, reducing intra-specific competition, or a subtle niche partitioning between these two subspecies reported to share similar habitats (del Hoyo, J., Elliott, A., & Sargatal, 2001; Mwale et al., 2022). A clearer distinction between breeding and non-breeding range exists in other austral migrants such as Pennant-winged Nightjars (Del Hoyo et al., 1999). The Woodland Kingfisher migration strategy compares to systems on other continents, especially in the Neotropics, with the example of Vermilion Flycatchers *Pyrocephalus rubinus*, in which austral populations can migrate north of the Equator and overlap with other conspecific subspecies (Carmi et al., 2016; Ridgely & Tudor, 1994). The Fork-tailed Flycatcher *Tyrannus savanna* from South America is another example of austral-breeding migrant using open landscapes in both hemispheres and overlapping with locally breeding populations (Jahn et al., 2013, 2016). Such range overlaps imply limitations in the observational understanding of intra-tropical migration phenology (e.g., Nussbaumer et al., 2021), highlighting the advantage of tracking to disentangle the multiple origins of observed birds.

Our tracking data provide the first confirmation for nocturnal migration in an intra-tropical migrant, a flight strategy which is realized by many other migrants across Palearctic and Nearctic (Alerstam, 2009; Newton, 2023). Flights occurred exclusively at night, with late flight departures compared to palearctic migrants (Briedis, Beran, et al., 2020; Müller et al., 2016; Rime et al., 2023). This contrasts with the strategy of prolonging flights into the day almost always observed in species from the northern hemisphere, especially above migratory barriers (Adamík et al., 2016; Briedis, Beran, et al., 2020; Rime et al., 2023; Sjöberg et al., 2021). Flight altitude profiles have not been reported before in any kingfisher species. Altitude varied, reaching 2890 m a.s.l., and often followed ground elevation. Hereby, accounting for altitude above ground level, rather than above sea level, is essential in regions of higher elevation plateaus that prevail in large parts of Southern and Eastern Africa. Maximal altitudes are not exceptional compared to Afro-Palearctic migratory songbirds that migrate above 5000 m over migratory barriers (Rime et al., 2023; Sjöberg et al., 2018, 2021) and other small non-passerines that can reach elevations above 8000 m (Klaassen et al., 2011).

Flights above the Congo Basin equatorial forests were longer, and stopovers usually lasted only one day. Longer and higher flights are a common strategy in birds crossing barriers such as sea or desert (Ouwehand & Both, 2016; Rime et al., 2023). Barrier-crossing flights occur in closely related species: Sacred Kingfishers *Todiramphus sanctus* from Australia undertake sea-crossing flights at least as long as Woodland Kingfishers above the Congo Basin (del Hoyo, J., Elliott, A., & Sargatal, 2001; van Balen & Johnstone, 1997). The equatorial forests may act as a barrier, explaining the similarity between flight patterns of our tracked birds and these barrier-crossing flights in Afro-Palearctic migrants. A similar avoidance of "green" barriers has been described in European Nightjars *Caprimulgus europaeus* (Lathouwers, Artois, et al., 2022).

Our study constitutes the first evidence linking trans-equatorial long-distance migration and rainy seasons in two hemispheres and the first report of migratory connectivity in an intra-tropical migrant. Using the same habitat and local climatic conditions at two locations across the equator involves sensitivity to climate and land use changes in breeding and non-breeding areas: while long-distance migrants decline in the northern hemisphere, fundamental knowledge on migrants in intra-tropical migratory systems and their status is still lacking to address their conservation (Both et al., 2010; Morrison et al., 2013; Ockendon et al., 2012, 2013; Sanderson et al., 2006; Vickery et al., 2023). Deforestation in the Congo Basin could create open habitats that may be suitable as stopover or non-breeding sites for Woodland Kingfishers and other birds of open landscapes (Catterall et al., 1998; Kofron & Chapman, 1995). In the context of rapid changes in climate and land use throughout sub-Saharan Africa, there is a critical lack of data informing on the constraints faced by intra-African migrants, which calls for further research using multi-sensor loggers. Due to the advantages of geolocation using atmospheric pressure, especially in tropical regions with limited variations in day length across the year, we recommend establishing this method for studying small intra-tropical migratory birds (Nussbaumer et al., 2022, 2023; Rhyne et al., 2024). To envision the effects of habitat and climate changes on tropical bird communities, studies addressing the effects of seasonality on the movement ecology of intra-tropical migrants should be priority in global bird migration research.

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Supplementary material

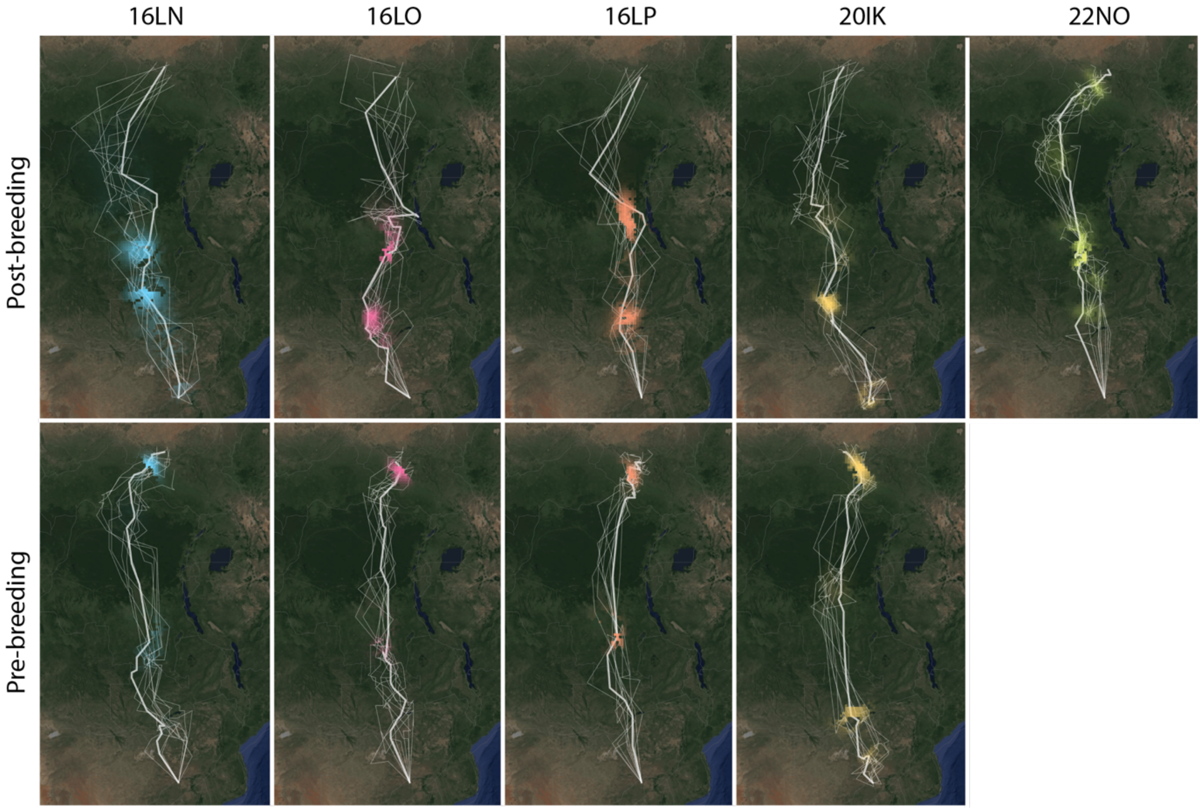

Figure S1. Modelled tracks and stationary sites of four Woodland Kingfishers in post-breeding and pre-breeding migrations (geolocators 16 LN and 22 NO were fitted on the same bird in 2017 and 2019). The main white solid line shows the shortest simulated migratory path for each bird, the other white lines indicate 9 more simulated path. The stationary sites are shown as the probability of the bird being at a location at a given time based on atmospheric pressure data (coloured areas). Male 16LO and female 16LP were a pair, loggers 16 LN and 22NO were repeat tracks of the same birds.

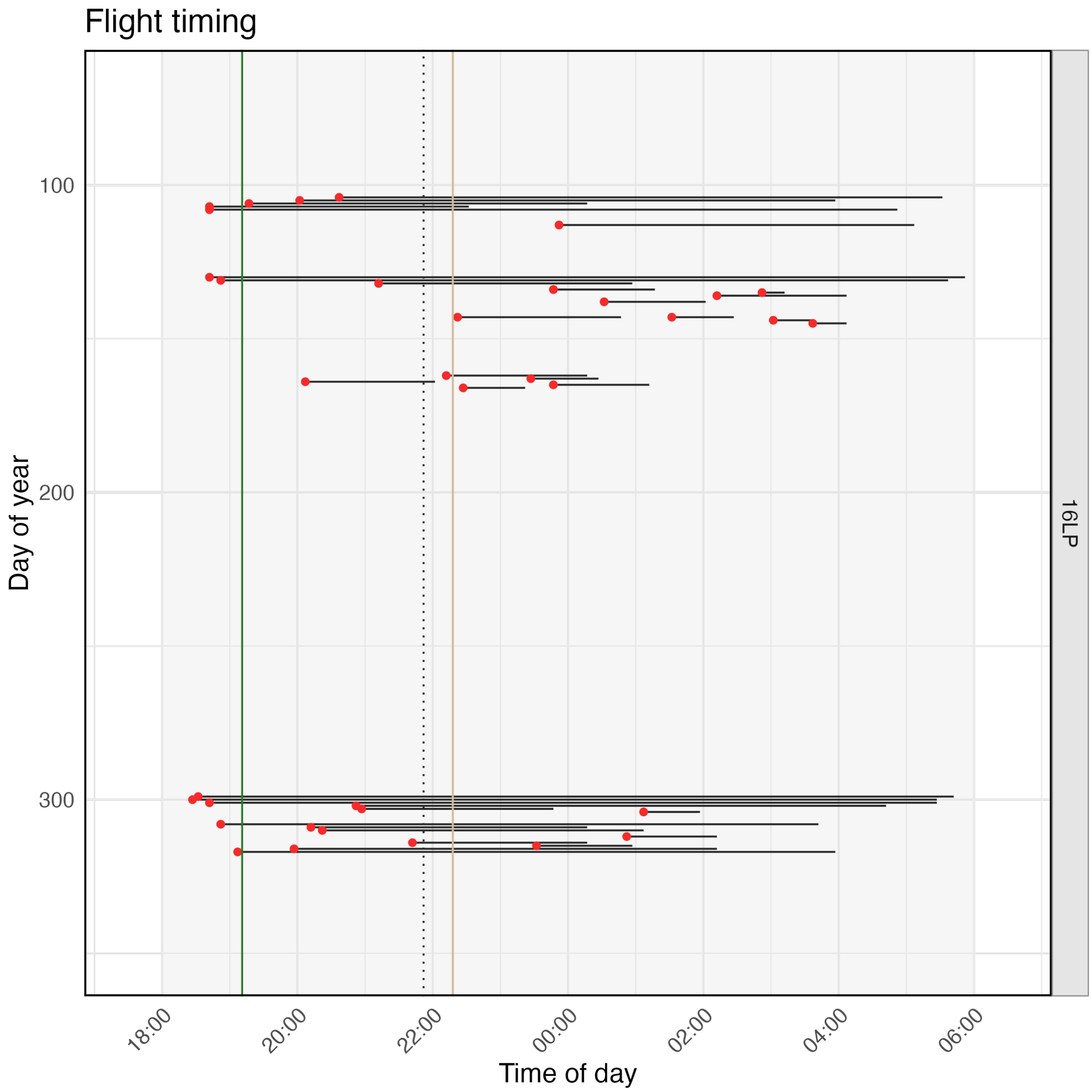

Figure S2. Flight timing of the bird 16 LP during the annual cycle showing flight departure (red dot) and the durations of migratory flights (black horizontal line). Overall mean flight departure is shown as a vertical dotted line, mean flight departure above the Congo Basin rainforest as a dark green vertical solid line and mean flight departure above savanna habitat as a pale brown vertical solid line. Take off generally occurred several hours after dusk, with an earlier flight departure above the Congo Basin rainforest compared to Savanna habitat.

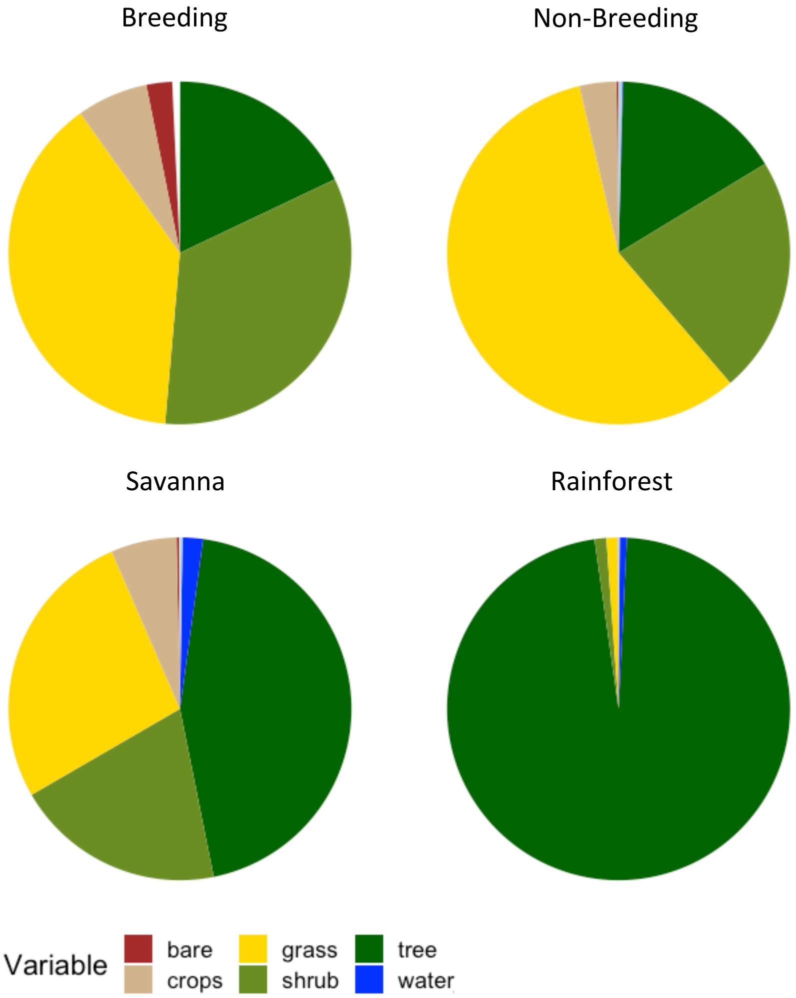

Figure S3. Land cover on a 20-km radius around the breeding site, and mean land cover values around the most likely locations of the non-breeding sites and stopover sites in savanna and Congo Basin rainforest.

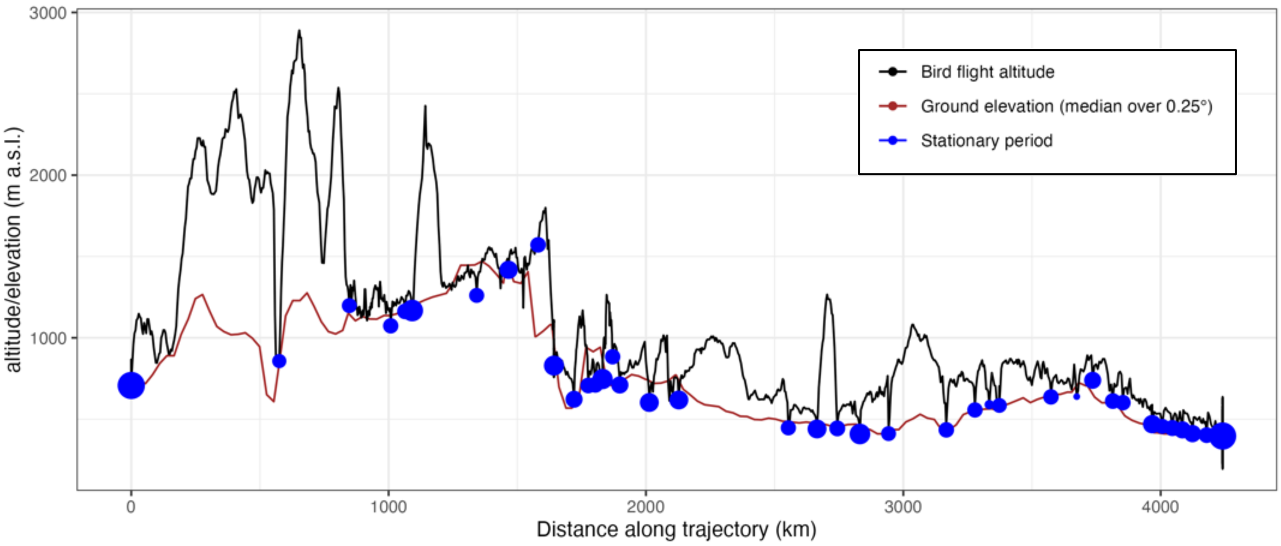

Figure S4. Flight altitudinal profile of the bird 22 NO during the post-breeding migration (black line = altitude in m a.s.l.), and average ground-level elevation at the most likely location (red line) along the distance of the journey. The Blue dots represent stationary periods. Minor, local imprecision where stationary sites or flights are below the estimated ground level are due to the coarse resolution of digital elevation model (mean elevation per 0.25° cell).

General discussion

Our understanding of the ecological constraints faced by long-distance migratory birds is currently insufficient, despite a consensus calling for research to address population declines in these species (Bairlein, 2016; Sanderson et al., 2006; Vickery et al., 2014, 2023). Such a lack of knowledge also holds for Alpine ecosystems, under pressure of land-use and climate changes at an increasing pace (Chamberlain et al., 2023; Scridel et al., 2018; Sekercioglu et al., 2008). This thesis aimed at filling these general research gaps by focusing on the Northern Wheatear, an Afro-Palearctic migrant breeding at high elevations. The first three chapters focused on breeding-site ecology of a population of Northern Wheatears in the Alps. In the first chapter, I determined habitat preferences for selecting a nest-site, and how this influenced breeding success. The second chapter described the foraging micro-habitat on a fine scale throughout the presence at the breeding site, including pre- and post-breeding periods. The third chapter considered the avifauna community sharing the same Alpine grassland habitat. Chapter four and five concerned migration of the Northern Wheatear, unveiling migration routes and timing, flight behaviour and local movements at the breeding site. I broadened the scope of this work by considering another, reverse migration system from the southern hemisphere in a sixth chapter, applying similar methodological approaches as for Northern Wheatears for the first time in an intra-tropical migrant. In this discussion, I discuss the results of this thesis and present their implications. The first part of the discussion concentrates on breeding-site ecology and the second part on migration behaviour, before ending with overall conclusions.

Discussion of the results and limitations: breeding-site ecology

The results on nest site selection, breeding success and foraging habitat preferences in the first two chapters highlight preferences of Northern Wheatears for open areas with high heterogeneity in ground cover composition and habitat structures on a small scale. Wheatears need an eased access to prey with short vegetation or bare ground, throughout the presence at the breeding site. As in other parts of the Alps (Sander et al., 2023; Wartmann, 1985), nest survival in our population was mostly influenced by predation, an important driver of reproductive success (Martin, 1995; Martin & Briskie, 2009). Here, the influence of habitat quality on breeding success therefore needs to be mainly interpreted as the influence of habitat on the risk of predation. The surrounding habitat played a prime role in the selection of a nest site in Northern Wheatears. This is the case for other alpine species like the White-winged Snowfinch, which however undertakes longer foraging trips for provisioning food to nestlings in nest-sites that are better protected against predators (e.g. Niffenegger et al., 2023). In our study, most of the drivers of nest site selection by Wheatears seemed related to the suitability of the habitat for foraging, that were detailed in chapter two. Topography influenced the choice of a nest-site as well as the breeding success: South-exposed locations on gentle slopes were preferred and we found a strong negative correlation with north-exposed aspect. In previous studies on lowland populations, predation risk was shown to increase at lower temperatures, when provisioning rates increased (Low et al., 2008; Moreno, 1989; Öberg et al., 2015; Schneider et al., 2012).

The presence of rockpiles was preferred by Wheatears to nest, underlining the important role of these human-made elements in Alpine grasslands. According to our observations, these rockpiles often hosted nests, but also served as a shelter where fledglings could hide. However, nest survival before the time of fledgling was negatively correlated with rockpiles in the surroundings. Higher breeding densities around rockpiles might increase intra-specific competition (Maurer, 1984), but also the vulnerability to predators targeting areas with high densities of nests (Andersson & Wiklund, 1978; Larivière & Messier, 1998; Taylor, 1976).

As in other ground-dwelling insectivorous birds, access to prey (Rime et al., 2020; Schaub et al., 2010; Tagmann-Ioset et al., 2012) is most likely explaining the preference for locations with bare ground described for nesting in chapter one, and for foraging in chapter two. Dense shrub alters access to the ground and was thereby avoided for foraging. Non-vegetated ground was positively correlated with nest survival. Predation risk was previously shown to increase in low-quality foraging habitats in a Swedish lowland population (Pärt, 2001). Birds breeding in habitats with enhanced access to ground-dwelling prey in short vegetation and patches of bare ground might need less frequent but more effective provisioning visits to the brood, hereby reducing predation risk (Arlt et al., 2008; Arlt & Pärt, 2007; Low et al., 2010; Müller et al., 2023).

In chapter one, I found that nests were more likely located in relatively productive vegetation. In chapter two, birds similarly preferred to forage at locations with higher NDVI compared to the pseudo-absence locations. Greenness in May, when birds arrived from migration (Rime et al., 2023; Sander et al., 2021) did not influence nest-site selection. According to our observations, vegetation grew earlier on steep slopes that were first snow-free and therefore had higher NDVI but were not selected by Wheatears for establishing their nest. I thus presumed that Wheatears did not select a territory based on the vegetation at arrival but used other cues, maybe gathered in the previous post-breeding season (Pärt et al., 2011). In chapter two, Wheatears foraged near the snow front after arriving at the breeding site. Other species in the Alps, such as Ring Ouzels *Turdus torquatus* (Barras et al., 2020) and White-winged Snowfinches *Montifringilla nivalis* (Brambilla et al., 2017; Resano-Mayor et al., 2019) rely on melting snow for brood provisioning. Northern Wheatears mostly bred after snowmelt, hence they did not use the snow front for brood provisioning, but only for sustaining themselves. In addition to habitat quality, greater distance to conspecific nests positively affected nest-site selection. This is likely the result of a trade-off between breeding in favourable habitat while keeping a sufficient distance to conspecifics to minimize energy expenditure in defending the surroundings of the nest against competitors (Arlt & Pärt, 2007; Brooke, 1979; Conder, 1989).

In chapter one, I described breeding phenology among three years. Breeding success was similar between years, but the laying dates varied in response to strong inter-annual variations in weather conditions and spring onset between the study years. This adjustment of the breeding period may buffer the negative effects of shifting spring phenology (e.g., Taff & Shipley, 2023). Although the effect was weak in our model, the observed success within year was higher in late nests. This corroborates previous findings in the Italian Alps (Sander et al., 2021, 2023). Due to a short breeding season, second broods are rare in Northern Wheatears breeding in the Alps (Müller et al., 2023; Wartmann, 1985), and consisted of attempts to re-nest after predation in our study area. A better success late in the season contrasted with results from lowland populations, where late breeding resulted in a general decrease in fitness (Öberg et al., 2014). Sander et al. (2023) found a reduced weight of chicks in late breeders in the Alps, which could therefore face other disadvantages such as delayed moult and reduce survival after the breeding season (Buchmann et al., 2009; Magrath, 1991; Sander et al., 2023; Streby et al., 2014; Tinbergen & Boerlijst, 1990).

With time-limited food resources for brood provisioning in seasonal habitats (Chamberlain et al., 2023; Martin & Wiebe, 2004), many species of birds face a mismatch between the timing of breeding and the optimal availability of food resources (Both & Visser, 2001; Jones & Cresswell, 2010; Saino et al., 2011; Visser et al., 2004). Such mismatch has been described in Alpine bird species (e.g., Schano et al., 2021; Wann et al., 2019) and mentioned as a potential cause of inter-annual variation in breeding success in the Northern Wheatear (Sander et al., 2021). We did not measure food availability or food provisioning in chapter one and two but found no evidence of change in breeding success in years with varying meteorological conditions and spring onset. Laying dates were delayed in spring 2021, a year with late snowmelt, cold weather and heavy rains. The probability of nest survival did not decrease later in the season, which would be expected if birds were not able to time their laying dates adequately relative to the availability of food resources (Jones & Cresswell, 2010; Saino et al., 2011; Wann et al., 2019). Nevertheless, the relationships between the fluctuations of predators among years and the cycles of their alternative prey may also influence breeding success, with possibly more complex interactions with weather conditions (Ibáñez-Álamo et al., 2015; Maag et al., 2024).

Regarding breeding-site ecology, this thesis brought new insight on habitat preferences of Northern Wheatears in the Alps, but more investigation is needed to complete the picture. The relative effects and potential interactions between land-use and climate changes are complex and difficult to disentangle (Barras, Braunisch, et al., 2021; Chamberlain et al., 2013; Chamberlain & Pearce Higgins, 2013; Maggini et al., 2011, 2014). The interplay between climate change and land use modifications and the effects on the Northern Wheatears in the Alps is still to be defined. Future research using data from citizen science (Schano et al., 2021), or long-term monitoring or breeding bird atlases (e.g. Knaus et al., 2018; Schmid et al., 1998), could allow to model the effects of habitat changes on the populations of Northern Wheatears and other Alpine species at a broader scale. Such models were recently presented for the Ring Ouzel, another mountain songbird (Barras, Braunisch, et al., 2021). A wider understanding of resource availability is still needed for the Northern Wheatear and other species sharing the same landscapes, including the temporal distribution of arthropod abundance throughout the breeding season and how this varies between years. Diet could be characterized, especially for the purpose of detecting habitat-dependent selection of food items (Chiffard et al., 2023). This could be done by analysing faecal samples (Chiffard et al., 2023; Deloria-Sheffield et al., 2001; Jedlicka et al., 2013), and alternatively or complementarily by an observational approach using camera recorders (Barras, Niffenegger, et al., 2021; Goodbred & Holmes, 1996). Furthermore, a better mechanistic understanding of coping strategies of birds to inter-annual variations in weather and spring onset further requires a survival analysis. This could be addressed based on the colour-ringed data from our study. Individual data on within-year survival (2020-2022) and between-year survival (2015-2022) may inform on the relative effects of yearly conditions at the breeding site compared to mortality during the non-breeding season.

In a conservation context, the conclusions drawn from these first two chapters were limited to the Northern Wheatear. A more general, multi-species approach is important when results are used to formulate recommendations for the conservation of bird species and their habitat. Hence, the third chapter of this thesis extended to bird communities sharing the same Alpine grassland habitat as the Northern Wheatear. Most of the birds observed in our study area of Val Piora were insectivorous and migratory species. On a fine scale, the Water Pipit *Anthus spinoletta* seemed to use all the available habitats. For three, closely related Muscicapidae species, niche partitioning occurred with a partial overlap due to the shared general grassland habitat. Northern Wheatears preferred south-exposed, gentle slopes with rockpiles, as shown in previous chapters, while Whinchats *Saxicola rubetra* were more likely at lower elevations, where dense Rhododendron or Juniper shrubs occur. Black Redstarts *Phoenicurus ochruros* preferred steeper slopes. While Northern Wheatears avoided shrubs (in particular, see Chapter two), this habitat positively influenced the abundance of Whinchats, a species of high conservation concern (Keller et al., 2020; Knaus et al., 2018). Thereby, based on the community-level data, I suggest that Alpine grassland can play a key role for the conservation of insectivorous birds that are declining elsewhere, but this can only be achieved by maintaining a mosaic of diverse and patchy habitats such as those in high-elevation pastures that are grazed with low intensity. This advocates for sourcing conservation recommendations from results taking into consideration bird communities beyond single study species. The results from the first three chapters present a picture on the current situation in Val Piora, a valley of the Alps under low-intensity management with grazing milk cows, which may not be entirely representative of other parts of the Alpine range. If similar studies take place in the future, I recommend considering broader elevational gradients (our study area did not cover the upper range of some of the studied species above 2400 m) and including habitats with varying land use (i.e., intensive, extensive, or abandoned).

Overall, the findings of the first three chapters suggested positive effects of low intensity grazing on the micro-habitat used by Northern Wheatears, spatially but also temporally. Grazing especially played a role during the post-breeding season, keeping a lower grass layer where birds can forage. Such a positive role of low intensity grazing on bird communities of open landscapes is generally acknowledged (Bazzi et al., 2015; Brambilla et al., 2018; Braunisch et al., 2016; Jähnig et al., 2018; Laiolo et al., 2004; Loe et al., 2007; Mermillon et al., 2021; Schwarz et al., 2018). Pastoralism is key to keep the landscape open but is also an important economic sector in mountain regions, which allows joint efforts to conserve the cultural, economic, and ecological value of this habitat (Mack et al., 2013). However, few studies addressed the direct and indirect effects of grazing on breeding birds in alpine pastures. Trampling by cattle was identified as a main cause of nest failure in ground-breeding birds such as Water Pipits, Meadow Pipits *Anthus pratensis* and Skylarks *Alauda arvensis*, suggesting that grazing could be detrimental at high intensity (Pavel, 2004). An increased grazing intensity has been linked to shifts in diet in Northern Wheatears and Water Pipits (Chiffard et al., 2023) and to alteration of foraging habitat in Whinchats (Murray et al., 2016). Conversely, grazing abandonment can be detrimental for Whinchats (Calladine & Jarrett, 2021). Further research would be required to identify optima and thresholds to achieve adequate biodiversity-promoting grazing. Other taxa, such as plants and invertebrate, should also be included as indicators in an attempt to describe the effects of grazing on the organisms of changing mountain ecosystems (Cislaghi et al., 2019; Komac et al., 2014; Labaune & Magnin, 2002; Mayer & Erschbamer, 2017).

From a methodological point of view, these three chapters show that observational approaches can hold a central role in acquiring field-based fundamental information on the ecology of birds. Considering different spatial scales and including various aspects of habitat preferences, from the fine-scale micro-habitat to the landscape, remains necessary in a scientific domain that is increasingly dominated by approaches that are confined to remotely sensed modelling methods, which sometimes miss elements that appear obvious in the field.

Instead, this work therefore combines field-sourced data on a fine resolution with frontline statistical modelling methods.

Discussion of the results and limitations: migration

Our results on migration improve the understanding of long-distance movements between central Europe and Africa and of how small birds organize their journey across barriers such as the Mediterranean Sea and the Sahara. Moreover, we show that recently developed tracking methods based on atmospheric pressure can be used to unveil both global and local movement behaviour of small birds with unprecedented spatial and temporal precision, which opens wider research opportunities compared to light-level geolocation.

In the fourth chapter, we used light-level geolocator data and compared migration routes and timing of two Alpine populations in the Swiss and Austrian Alps with a lowland population, suggesting that Alpine birds can cross the widest parts of the Mediterranean Sea while birds from lowland Germany tend to fly through the Iberian Peninsula (Meier et al., 2022). Migration across the Mediterranean was the most direct route for Alpine-breeding Wheatears. While large, soaring birds often try to follow land masses during their migratory flights (Evans & Lathbury, 1973; Mellone, 2020; Verhelst et al., 2011), previous studies suggest crossing the sea rather than taking a detour as a common strategy in wing-flapping long-distance migrants (Briedis et al., 2016, 2018; Koleček et al., 2016; Lemke et al., 2013). Migration timing also differed between Alpine and lowland Northern Wheatears, with lowland birds arriving earlier in spring compared to high-elevation populations. The schedule of Alpine birds was more similar to that of Arctic-breeding populations that undertake much longer migratory distances (Bairlein et al., 2012; Meier et al., 2022). This means that the elevation of the breeding site, with different timing of spring onset in the Alps compared to lowland Europe, influences migration timing, and not only the distance to the non-breeding site.

In Chapter five, I used atmospheric pressure logger data from Northern Wheatears breeding in the Swiss and Italian Alps to unveil the organization of migration in more detail (Rime et al., 2023). I highlighted how birds made non-obligatory use of Mediterranean islands (i.e., these islands were not used for all the recorded sea crossings) for very short stopover while crossing the sea. This confirms the importance of small islands for migratory songbirds (Ferretti et al., 2021; Pilastro et al., 1998) in a context where the burden of illegal, over-harvest of birds in the Mediterranean is still a serious threat for afro-Palearctic migrants (Brochet et al., 2016). Between the two main migratory barriers constituted by the Mediterranean Sea and the Sahara Desert, I precisely identified the habitats of longer stopovers in the Atlas highlands of Northern Africa that were used for refuelling between crossing the sea and the desert. Individual non-breeding sites in the Western Sahel, which were continuously used throughout the boreal winter, were located in close vicinity of each other, suggesting that Northern Wheatears from the Alpine population do not use an area as large as previously expected from light-level geolocation data (Meier et al., 2022; Sander et al., 2021; Schmaljohann et al., 2016). I also showed that flight behaviour was adjusted when flying above barriers, with longer, higher, and faster flights above the Sahara and the Mediterranean compared to favourable habitats. I also described how Wheatears cross the desert with mostly nocturnal flights interspersed with one-day stopovers in the desert before reaching their non-breeding sites. Wheatears thus did not perform non-stop crossing of the desert as do some other species: Wheatears are ground-foraging, open-land birds that might deal better with landing in the desert compared to forest or wetland species (Jiguet et al., 2019; Klaassen et al., 2011; Ouwehand & Both, 2016). The strategy of nocturnal flights prolonged into the day is often observed in passerines crossing the Sahara, such as Tawny Pipits *Anthus campestris* and Great Reed Warbler *Acrocephalus arundinaceus* (Briedis et al., 2020; Sjöberg et al., 2021) but was only occasionally observed in our tracked Wheatears. These prolonged flights into the day were not characterized in higher flight altitudes during the diurnal part compared to the nocturnal part as for Great Reed Warblers (Sjöberg et al., 2021). In addition to large-scale movements, I showed evidence of altitudinal movements to cope with snowfall upon arrival at the breeding site in early May. While pre-breeding daily altitudinal commuting has been reported in other mountain songbirds (Barras, Liechti, et al., 2021), Wheatears undertook this behaviour only as a response to extreme weather events in our study system (Rime et al., 2023). I reported a second, unexpected type of local, diel elevational movement at night, while birds flew up to roost, most likely in nearby cliffs, sometimes changing location after several nights at the same elevation. White-winged Snowfinches are known to show a similar behaviour, with roosts located at high elevations in cliff crevices where the temperature remains higher than outside (Heiniger, 1989).

To extend insights on long-distance migrants, we applied similar methods to different geographical contexts, allowing to highlight similarities and differences between migratory systems. A sixth chapter thus extended the scope of this work to a migratory species in the southern hemisphere with similar migration distances as those of Northern Wheatears from the Alps. Specifically, we studied a similar-sized intra-African migrant, the Woodland Kingfisher, with the same analytic framework used for Wheatears (Nussbaumer et al., 2022, 2023; Nussbaumer & Gravey, 2022; Rime et al., 2023). In Woodland Kingfishers, stop-overs were more frequent and migratory flights were also nocturnal, but shorter. Post-breeding migration was notably longer than pre-breeding migration, a common pattern in other migration systems, typically in birds breeding in the northern hemisphere (Briedis et al., 2019; Kokko et al., 2006). The Woodland Kingfisher's migration compares to systems on other continents, for example in South America where birds from the southern part of the continent cross the Equator to spend the non-breeding season north of the Amazon (Carmi et al., 2016; Jahn et al., 2013, 2016). However, it is the first time that data on migration behaviour of an Austral migrant using barometric sensors is presented, and that detailed flight and stopover behaviour is thereby described.

While Woodland Kingfishers also used single non-breeding sites, their migration routes did not overcome major apparent barriers as experienced by the Northern Wheatears but took the birds across habitat that can be considered a "soft", or "green", barrier (Alerstam, 2009; Lathouwers, Artois, et al., 2022). Nevertheless, Woodland Kingfishers adjusted their migration strategies over suboptimal habitats in similar ways as did barrier-crossing Northern Wheatears above the Mediterranean and the Sahara (Rime et al., 2023). Compared to systems in the Northern Hemisphere where birds undertake south-bound migration to escape harsh winter conditions, drivers of intra-African migration are diverse and poorly known. In the case of the Woodland Kingfisher, long-distance movements allowed the birds to align with multi-year patterns of rainfalls and vegetation greening across the Equator. The birds thus benefitted from seasonal abundance of food resources in both hemispheres, a similar case to Abdim's Storks that breed in the Sahel and migrate to Eastern and Southern Africa in the non-breeding season (Jensen et al., 2006). Our results shed light for the first time on the detailed migratory behaviour of a small intra-African migrant.

The research projects related to this PhD thesis contributed to the development of light-weight multi-sensor geolocator devices and new methods for analysing the collected data. Identifying altitude of birds flying at night, precisely locating their stationary locations during migration, and following their diel local movements was not possible until the recent technological and analytic advances used in these studies (Lathouwers, Nussbaumer, et al., 2022; Nussbaumer et al., 2022, 2023; Nussbaumer & Gravey, 2022; Rhyne et al., 2024; Rime et al., 2023). This however involved technical issues. Several geolocator batteries failed or birds lost the device, which impacts the expected results when dealing with small sample sizes and birds that require a large time investment to be captured. Still, geolocation using atmospheric pressure (Nussbaumer et al., 2022, 2023) surpassed the light-level technique: in birds migrating at equinox like the Northern Wheatear, our results suggest that light-level geolocation results should be considered with caution and that atmospheric pressure is much more reliable (Lisovski et al., 2012; Lisovski & Hahn, 2012; Nussbaumer et al., 2022). This method was confirmed to be equally appropriate on north-south oriented migration in tropical regions, where variations in day-lengths are minor. The two case studies in this thesis allowed to test the R package *GeoPressureR* (Nussbaumer & Gravey, 2022) and prove its efficiency in different contexts.

Conclusion

This thesis sheds light on various aspects of the annual cycle of the Northern Wheatears, with novel insight on breeding-site ecology and migration behaviour, using new methods that were also applied to an intra-tropical migration system. The Alpine population of the Northern Wheatear offered a unique opportunity to study an Afro-palearctic migratory bird that breeds in high-alpine habitats. To conclude, the main outcomes from this thesis can be synthesized in six take-home messages.

First, Northern Wheatears select a nest according to the foraging habitat in the direct surroundings of the nest, but breeding success is mostly driven by predation. Predation increases in nests that are north-exposed or without bare ground patches in the vicinity used to catch prey for brood provisioning. Furthermore, Wheatears seem to be able to adjust to inter-annual variations in weather conditions and spring onset, but they however may not be able to cope with much warmer temperatures in the future.

Second, the habitat of the Northern Wheatear is still widely available in the Alps but must be preserved from changes due to climate disruption, land use modifications and the development of infrastructure (Alba et al., 2022; Bazzi et al., 2015; Jähnig et al., 2018; Müller et al., 2023). Wheatears need suitable micro-habitats within their breeding territory during most of their presence in the Alps. These habitats might be altered by habitat homogenization.

Third, Alpine grassland habitats used by Northern Wheatears are shared with other species of conservation concern, such as Whinchats, which have different habitat preferences. Maintaining low-intensity management in Alpine grassland with a mosaic of habitats should be a priority for conservation strategies (Chamberlain et al., 2013; Laiolo et al., 2004; Mack et al., 2013; Rolando et al., 2014).

Fourth, the migration timing of the Alpine population of the Northern Wheatear and their migration routes is different from other population in Europe (Arlt et al., 2015; Bairlein et al., 2012; Meier et al., 2022; Schmaljohann et al., 2012, 2016). Birds from the Alpine population seem to spend the non-breeding season in a specific area of the Sahel, suggesting high migratory connectivity. Thereby, the entire Alpine population might be sensitive to changes such as repeated drought at the non-breeding site (Ockendon et al., 2012, 2014).

Fifth, migration behaviour of small songbirds can now be studied with a 30-minutes precision. In addition to this unprecedented temporal resolution, this method is opening the third dimension for our understanding of flight strategies to overcome migratory barriers in small birds (Lathouwers, Nussbaumer, et al., 2022; Nussbaumer et al., 2023; Rhyne et al., 2024; Rime et al., 2023; Sjöberg et al., 2018, 2021). In Northern Wheatears, migration behaviour of populations in Canada and Alaska, which overwinter in sub-Saharan Africa (Bairlein et al., 2012), could be re-investigated using atmospheric pressure, informing on their breath-taking sea-crossing strategies, and beyond.

Sixth, migration research should address intra-tropical migration systems in parallel to the effort in studying long-distance migrants from the northern hemisphere. Changes in seasonality are not limited to temperate and arctic regions and may also influence organisms with annual cycles driven by rainfall patterns in tropical environments. Our knowledge about the movements and seasonality of birds in the Afrotropic are still largely insufficient. New geolocation studies should target intra-tropical migrants, including long-distance migrants, but also short-distance migrants or supposedly resident species that constitute an underestimated part of the migratory organisms worldwide.

To conclude, Northern Wheatears breeding in high-alpine ecosystems and migrating across the sea and the deserts to reach their non-breeding site in arid savanna and Woodland Kingfishers migrating within Africa, offered two very different systems to study breeding ecology and migration behaviour. While nature around us changes at an increasing pace, the ecology and migration of these birds, and many more, will probably change in the next decades. However, our understanding of the migration phenomenon is still widely incomplete. As suitable technology is now available, this calls for studying migratory birds and their fascinating annual cycles.

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