JOURNAL OF AVIAN BIOLOGY

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

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)
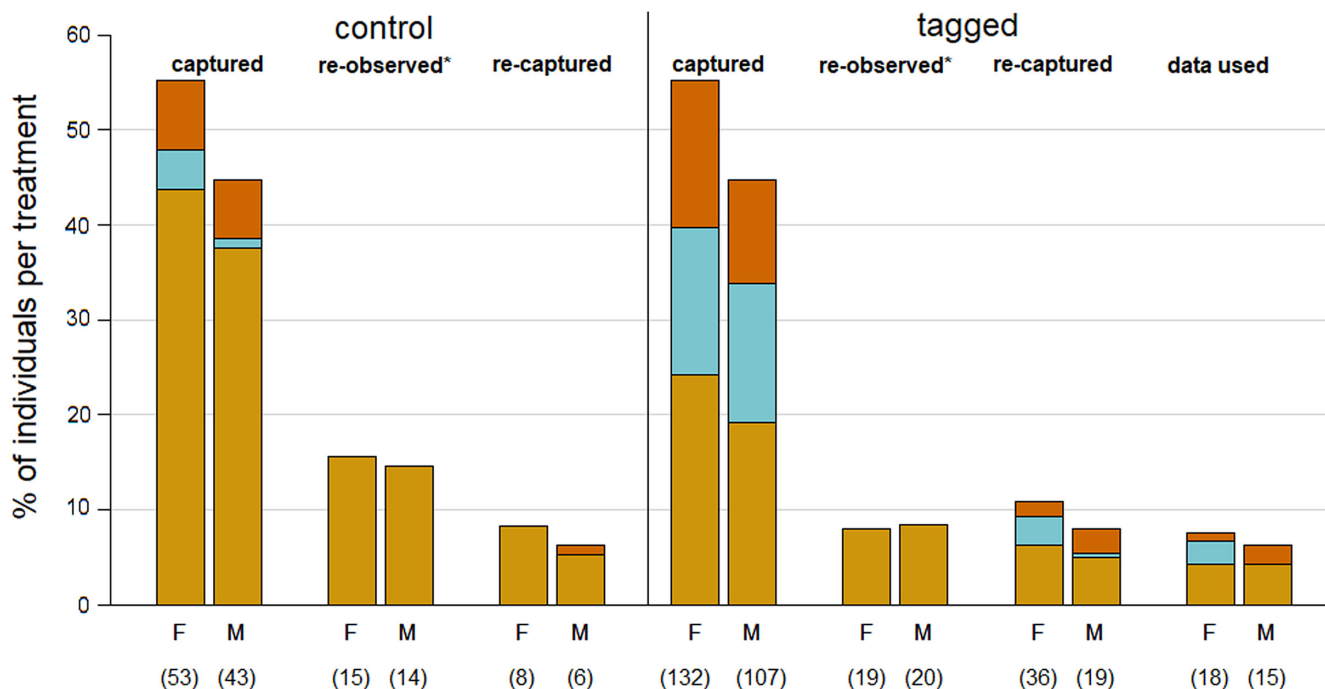

Figure 1. Distribution of the sample sizes between the control (left) and the tagged treatment (right) according to sex, population and treatment, relative to the total number (= 100%) of birds caught . Populations are indicated by the colours: Switzerland (dark gold), Germany (turquoise) and Austria (brown). The total absolute numbers per category are indicated in parentheses. The category * 'Re-observed' highlighted includes only the Swiss population.
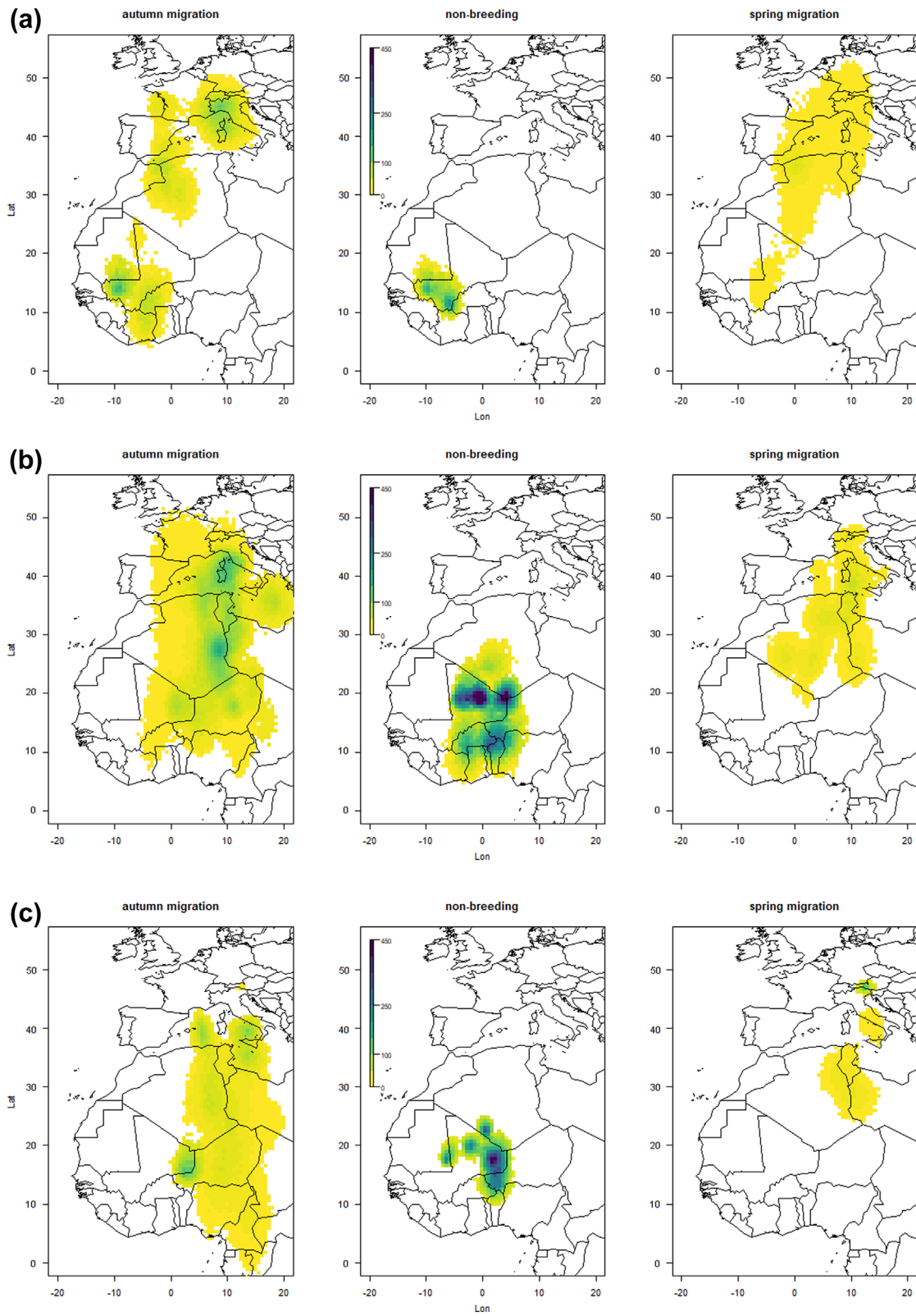
Figure 2. Combined tracks of all birds from Germany (a), Switzerland (b) and Austria (c) divided into three periods: autumn migration, non-breeding period and spring migration. The coloured area presents the cumulative probability of SGAT position predictions summed over the year for all individuals. The colour scale was adjusted to give every individual track the same weight; see main text for details.
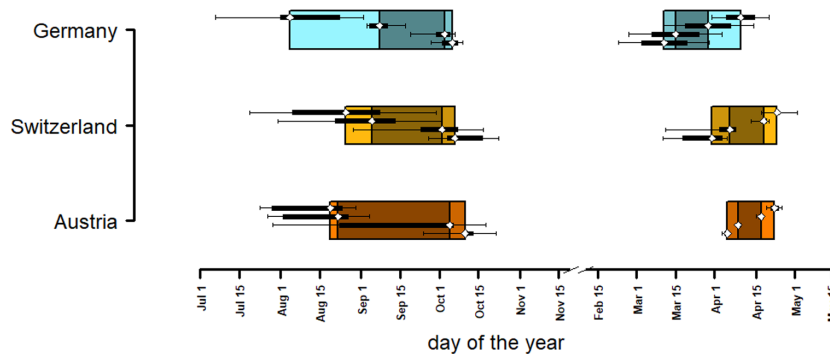
Figure 3. Comparisons of timing during autumn and subsequent spring migration in the three study populations (large squares by the colours: Switzerland, dark gold, Germany, turquoise, and Austria, brown). The colour shading within each square corresponds to three distinct "sub-periods" of each migration: 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.
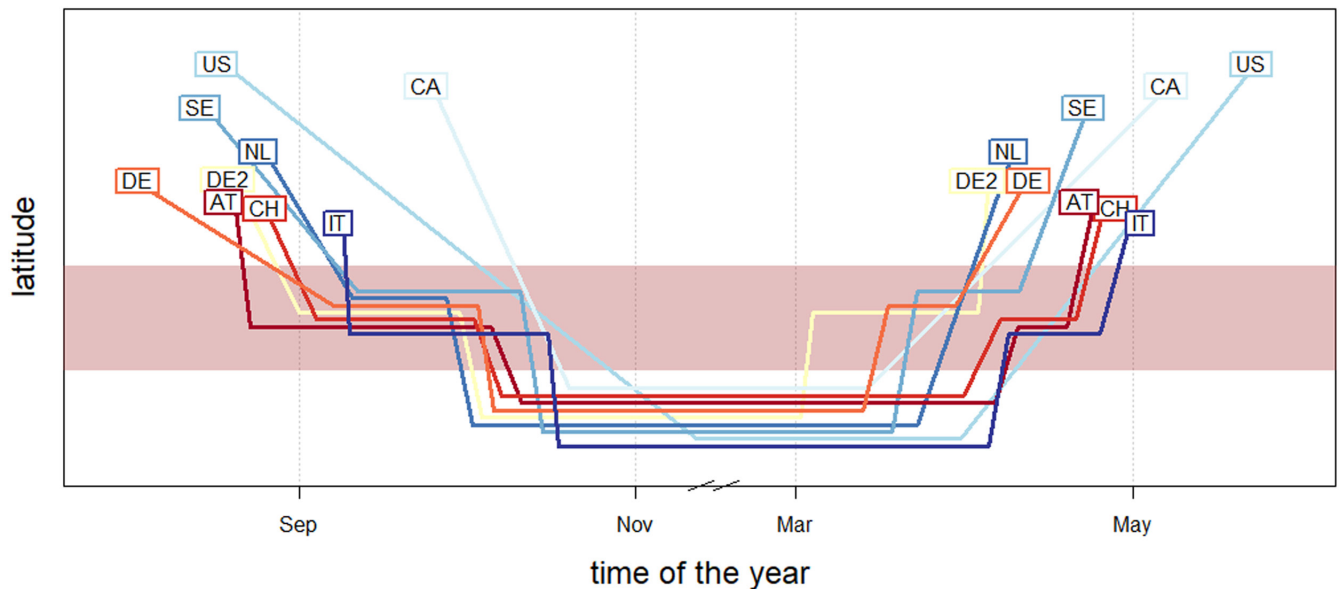
Figure 4. Comparison of the timing between all wheatear populations for which geolocator tracks exist. Lines show the median timing in each population along a proxy for latitude, indicating whether the birds were either north of the Mediterranean (>46°N), within the Mediterranean region between 46°N 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

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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).

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).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/jav.02932>.

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.

References

Alaei Kakhki, N., Aliabadian, M. and Schweizer, M. 2016. Out of Africa: biogeographic history of the open-habitat chats (Aves, Muscicapidae: Saxicolinae) across arid areas of the old world. – Zool. Scr. 45: 237–251.

Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. – In: Gwinner, E. (ed.), Bird migration: physiology and ecophysiology. Springer, pp. 331–351.

Arlt, D., Low, M. and Pärt, T. 2013. Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. – PLoS One 8: e82316.

Arlt, D., Olsson, P., Fox, J. W., Low, M. and Pärt, T. 2015. Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird. – Anim. Migr. 2: 379.

Aurbach, A., Schmid, B., Liechti, F., Chokani, N. and Abhari, R. 2018. Complex behaviour in complex terrain – modelling bird migration in a high resolution wind field across mountainous terrain to simulate observed patterns. – J. Theor. Biol. 454: 126–138.

Bairlein, F., Eikenaar, C. and Schmaljohann, H. 2015. Routes to genes: unravelling the control of avian migration – an integrated approach using northern wheatear *Oenanthe oenanthe* as model organism. – J. Ornithol. 156: 3–14.

Bairlein, F., Norris, D. R., Nagel, R., Bulte, M., Voigt, C. C., Fox, J. W., Hussell, D. J. T. and Schmaljohann, H. 2012. Cross-hemisphere migration of a 25 g songbird. – Biol. Lett. 8: 505–507.

Barras, A. G., Liechti, F. and Arlettaz, R. 2021. Seasonal and daily movement patterns of an alpine passerine suggest high flexibility in relation to environmental conditions. – J. Avian Biol. 52: 801.

Biebach, H., Biebach, I., Friedrich, W., Heine, G., Partecke, J. and Schmidl, D. 2000. Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert: a radar study. – Ibis 142: 623–634.

Briedis, M., Bauer, S., Adamík, P., Alves, J. A., Costa, J. S., Emmenegger, T., Gustafsson, L., Koleček, J., Krist, M., Liechti, F., Lisovski, S., Meier, C. M., Procházka, P., Hahn, S. and McGill, B. 2020. Broad-scale patterns of the Afro-Palaearctic landbird migration. – Global Ecol. Biogeogr. 29: 722–735.

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

Briedis, M., Kurlavičius, P., Mackevičienė, R., Vaišvilienė, R. and Hahn, S. 2018. Loop migration, induced by seasonally different flyway use, in northern European barn swallows. – J. Ornithol. 159: 885–891.

Bruderer, B. and Jenni, L. 1990. Migration across the Alps. – In: Gwinner, E. (ed.), Bird migration: physiology and ecophysiology. Springer, pp. 60–77.

Bruderer, B. and Liechti, F. 1990. Richtungsverhalten nachtziehender Vögel in Süddeutschland und der Schweiz unter besonderer Berücksichtigung des Windeinflusses. – Ornithol. Beob. 87: 271–293.

Bruderer, B., Peter, D. and Korner-Nievergelt, F. 2018. Vertical distribution of bird migration between the Baltic Sea and the Sahara. – J. Ornithol. 159: 315–336.

Buchan, C., Gilroy, J. J., Catry, I. and Franco, A. M. A. 2020. Fitness consequences of different migratory strategies in partially migratory populations: a multi-taxa meta-analysis. – J. Anim. Ecol. 89: 678–690.

Buchmann, M. 2001. Die Brutbiologie des Steinschmatzers *Oenanthe oenanthe* auf intensiv genutzten Flachen in Rheinland-Pfalz. – Vogelwarte 41: 1–17.

Buchmann, M., Helm, B., Rothery, P. and Flinks, H. 2009. Auswirkung von Spätbruten auf Mauser und Rückkehrrate bei einem Weitstreckenzieher, dem Steinschmätzer *Oenanthe oenanthe*. – Vogelwarte 47: 125–133.

Ćiković, D., Barišić, S., Hahn, S., Tutiš, V., Kralj, J. and Briedis, M. 2021. Tracking migration of black-headed buntings *Emberiza melanocephala* reveals the Iranian Plateau as an ecological barrier along the Indo-European flyway. – J. Avian Biol. 52: 335.

Conklin, J. R., Battley, P. F., Potter, M. A. and Fox, J. W. 2010. Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. – Nat. Commun. 1: 67.

Cox, G. W. 1968. The role of competition in the evolution of migration. – Evolution 22: 180–192.

Corman, A.-M., Bairlein, F. and Schmaljohann, H. 2014. The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. – Behav. Ecol. Sociobiol. 68: 391–402.

Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the new world. – Am. Nat. 126: 451–474.

Cramp, S. 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. – Oxford Univ. Press.

Ekström, P. A. 2004. An advance in geolocation by light. – Mem. Natl Inst. Polar Res. 58: 210–226.

Fortin, D., Liechti, F. and Bruderer, B. 1999. Variation in the nocturnal flight behaviour of migratory birds along the northwest coast of the Mediterranean Sea. – Ibis 141: 480–488.

Glutz von Blotzheim, U. N., Bauer, K. M. and Bezzel, E. 1988. Handbuch der Vögel Mitteleuropas: Teil I, Passeriformes (2. Teil): Turdidae. Schmätzer und Verwandte: Erithacinae. – Akademische Verlagsgesellschaft.

Gow, E. A., Burke, L., Winkler, D. W., Knight, S. M., Bradley, D. W., Clark, R. G., Bélisle, M., Berzins, L. L., Blake, T., Bridge, E. S., Dawson, R. D., Dunn, P. O., Garant, D., Holroyd, G., Horn, A. G., Hussell, D. J. T., Lansdorp, O., Laughlin, A. J.,

Leonard, M. L., Pelletier, F., Shutler, D., Siefferman, L., Taylor, C. M., Trefry, H., Vleck, C. M., Vleck, D., Whittingham, L. A. and Norris, D. R. 2019. A range-wide domino effect and resetting of the annual cycle in a migratory songbird. – Proc. R. Soc. B 286: 20181916.

Grattarola, A., Spina, F. and Pilastro, A. 1999. Spring migration of the garden warbler *Sylvia borin* across the Mediterranean Sea. – J. Ornithol. 140: 419–430.

Gwinner, E. 1986. Circannual rhythms: endogenous annual clocks in the organization of seasonal processes. – Springer.

Hahn, S., Emmenegger, T., Lisovski, S., Amrhein, V., Zehtindjiev, P. and Liechti, F. 2014. Detours in long-distance migration across ecological barriers are partly related to habitat availability at ground. – Ecol. Evol. doi:10.1002/ece3.1279.

Hedenström, A. 1993. Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. – Phil. Trans. R. Soc. B 342: 353–361.

Klein, G., Vitasse, Y., Rixen, C., Marty, C. and Rebetez, M. 2016. Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. – Clim. Change 139: 637–649.

Klvaňa, P., Cepák, J., Munclinger, P., Michálková, R., Tomášek, O. and Albrecht, T. 2018. Around the Mediterranean: an extreme example of loop migration in a long-distance migratory passerine. – J. Avian Biol. 49: jav-01595.

Kokko, H. 1999. Competition for early arrival in migratory birds. – J. Animal Ecol. 68: 940–950.

Kranstauber, B., Weinzierl, R., Wikelski, M. and Safi, K. 2015. Global aerial flyways allow efficient travelling. – Ecol. Lett. 18: 1338–1345.

Lack, D. 1950. The breeding season of European birds. – Ibis 92: 288–316.

Lack, D. 1968. Bird migration and natural selection. – Oikos 19: 1.

Lerche-Jørgensen, M., Korner-Nievergelt, F., Tøttrup, A. P., Willemoes, M. and Thorup, K. 2018. Early returning long-distance migrant males do pay a survival cost. – Ecol. Evol. 8: 11434–11449.

Lisovski, S. and Hahn, S. 2012. GeoLight-processing and analysing light-based geolocator data in R. – Methods Ecol. Evol. 3: 1055–1059.

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W. and Hahn, S. 2012. Geolocation by light: accuracy and precision affected by environmental factors. – Methods Ecol. Evol. 3: 603–612.

Lisovski, S., Neumann, R., Albrecht, T., Munclinger, P., Ahola, M. P., Bauer, S., Cepak, J., Fransson, T., Jakobsson, S., Jaakkonen, T., Klvana, P., Kullberg, C., Laaksonen, T., Metzger, B., Piha, M., Shurulinkov, P., Stach, R., Ström, K., Velmala, W. and Briedis, M. 2021. The Indo-European flyway: opportunities and constraints reflected by common rosefinches breeding across Europe. – J. Biogeogr. 48: 1255–1266.

Lisovski, S., Sumner, M. D. and Wotherspoon, S. J. 2015. TwGeos: basic data processing for light based geolocation archival tags. – <https://github.com/slisovski/TwGeos>.

Low, M., Arlt, D., Pärt, T. and Öberg, M. 2015. Delayed timing of breeding as a cost of reproduction. – J. Avian Biol. 46: 325–331.

Marra, P. P., Francis, C. M., Mulvihill, R. S. and Moore, F. R. 2005. The influence of climate on the timing and rate of spring bird migration. – Oecologia 142: 307–315.

Maggini, I. and Bairlein, F. 2010. Endogenous Rhythms of Seasonal Migratory Body Mass Changes and Nocturnal Restlessness in Different Populations of Northern Wheatear Oenanthe oenanthe. – J Biol Rhythms 25: 268–276.

McNamara, J. M., Barta, Z., Klaassen, M. and Bauer, S. 2011. Cues and the optimal timing of activities under environmental changes. – Ecol. Lett. 14: 1183–1190.

Meier, C. M., Karaardıç, H., Aymí, R., Peev, S. G., Bächler, E., Weber, R., Witvliet, W. and Liechti, F. 2018. What makes Alpine swift ascend at twilight? Novel geolocators reveal year-round flight behaviour. – Behav. Ecol. Sociobiol. 72: 45.

Meier, C. M., Karaardıç, H., Aymí, R., Peev, S. G., Witvliet, W. and Liechti, F. 2020. Population-specific adjustment of the annual cycle in a super-swift trans-Saharan migrant. – J. Avian Biol. 51: 258.

Meier, C. M., Buchmann, M., Liechti, F. 2022. Data from: Locally adapted migration strategies: Comparing routes and timing of northern wheatears from alpine and lowland European populations [Austria]. – Movebank Data Repository. doi:10.5441/001/1.tn4h3kt0

Meier, C. M., Buchmann, M., Liechti, F. 2022. Data from: Locally adapted migration strategies: Comparing routes and timing of northern wheatears from alpine and lowland European populations [Germany]. – Movebank Data Repository. doi:10.5441/001/1.b285q8gh

Meier, C. M., Rime, Y., Liechti, F. 2022. Data from: Locally adapted migration strategies: Comparing routes and timing of northern wheatears from alpine and lowland European populations [Switzerland]. – Movebank Data Repository. doi:10.5441/001/1.vp61g6gd

Moreau, R. E. 1972. Palaearctic-African bird migration systems. – Academic Press.

Morrison, C. A., Alves, J. A., Gunnarsson, T. G., Þórisson, B. and Gill, J. A. 2019. Why do earlier-arriving migratory birds have better breeding success? – Ecol. Evol. 9: 8856–8864.

Newton, I. 2008. The migration ecology of birds. – Elsevier/Academic Press.

Nicholson, S. E. 2013. The West African Sahel: a review of recent studies on the rainfall regime and its interannual variability. – ISRN Meteorol. 2013: 1–32.

Panov, E. N. 2005. Wheatears of Palearctic: ecology, behaviour and evolution of the genus *Oenanthe*. – Pensoft Publ.

Pedersen, L., Onrubia, A., Vardanis, Y., Barboutis, C., Waasdorp, S., van Helvert, M., Geertsma, M., Ekberg, P., Willemoes, M., Strandberg, R., Matsyna, E., Matsyna, A., Klaassen, R. H. G., Alerstam, T., Thorup, K. and Tøttrup, A. P. 2020. Remarkably similar migration patterns between different red-backed shrike populations suggest that migration rather than breeding area phenology determines the annual cycle. – J. Avian Biol. 51: 722.

Pomeroy, A. C., Butler, R. W. and Ydenberg, R. C. 2006. Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. – Behav. Ecol. 17: 1041–1045.

Pons, J.-M., Thibault, J.-C., Aymí, R., Grussu, M., Muntaner, J., Olioso, G., Sunyer, J. R., Touihri, M. and Fuchs, J. 2016. The role of western Mediterranean islands in the evolutionary diversification of the spotted flycatcher *Muscicapa striata*, a long-distance migratory passerine species. – J. Avian Biol. 47: 386–398.

Rappole, J. H. and Tipton, A. R. 1991. New harness design for attachment of radio transmitters to small passerines. – J. Field Ornithol. 62: 335–337.

Rodriguez-Galiano, V., Dash, J. and Atkinson, P. 2015. Characterising the land surface phenology of europe using decadal MERIS data. – Remote Sens. 7: 9390–9409.

Sander, M. M., Chamberlain, D., Mermillon, C., Alba, R., Jaehnig, S., Rossell, D., Meier, C. M. and Lisovski, S. 2021. Early breeding conditions followed by reduced breeding success despite timely arrival in an alpine migratory songbird. – Front. Ecol. Evol. 9: 676506.

Schano, C., Niffenegger, C., Jonas, T. and Korner-Nievergelt, F. 2021. Hatching phenology is lagging behind an advancing snowmelt pattern in a high-alpine bird. – Sci. Rep. 11: 20130016.

Schmaljohann, H. 2019. The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. – Mov. Ecol. 7: S169.

Schmaljohann, H., Buchmann, M., Fox, J. W. and Bairlein, F. 2012a. Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. – Behav. Ecol. Sociobiol. 66: 915–922.

Schmaljohann, H., Fox, J. W. and Bairlein, F. 2012b. Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. – Anim. Behav. 84: 623–640.

Schmaljohann, H., Meier, C., Arlt, D., Bairlein, F., van Oosten, H. H., Morbey, Y. E., Åkesson, S., Buchmann, M., Chernetsov, N., Desaever, R., Elliott, J., Hellström, M., Liechti, F., López, A., Middleton, J., Ottosson, U., Pärt, T., Spina, F. and Eikenaar, C. 2016. Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. – Behav. Ecol. 27: 321–331.

Schmidt, N. M., Reneerkens, J., Christensen, J. H., Olesen, M. and Roslin, T. 2019. An ecosystem-wide reproductive failure with more snow in the Arctic. – PLoS Biol. 17: e3000392.

Shamoun-Baranes, J., Liechti, F. and Vansteelant, W. M. G. 2017. Atmospheric conditions create freeways, detours and tailbacks for migrating birds. – J. Comp. Physiol. A 203: 509–529.

Sjöberg, S., Pedersen, L., Malmiga, G., Alerstam, T., Hansson, B., Hasselquist, D., Thorup, K., Tøttrup, A. P., Andersson, A. and Bäckman, J. 2018. Barometer logging reveals new dimensions of individual songbird migration. – J. Avian Biol. 49: e01821.

Thorup, K., Tøttrup, A. P., Willemoes, M., Klaassen, R. H. G., Strandberg, R., Vega, M. L., Dasari, H. P., Araújo, M. B., Wikelski, M. and Rahbek, C. 2017. Resource tracking within and across continents in long-distance bird migrants. – Sci. Adv. 3: 567.

Tøttrup, A. P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C. and Thorup, K. 2010. Local temperature fine-tunes the timing of spring migration in birds. – Integr. Comp. Biol. 50: 293–304.

van Loon, A., Ray, J. D., Savage, A., Mejeur, J., Moscar, L., Pearson, M., Pearman, M., Hvenegaard, G. T., Mickle, N., Applegate, K. and Fraser, K. C. 2017. Migratory stopover timing is predicted by breeding latitude, not habitat quality, in a long-distance migratory songbird. – J. Ornithol. 158: 745–752.

van Oosten, H. H., Mueller, J. C., Ottenburghs, J., Both, C., Kempenaers, B. and Voelker, G. 2016. Genetic structure among remnant populations of a migratory passerine, the northern wheatear *Oenanthe oenanthe*. – Ibis 158: 857–867.

van Oosten, H. H., Versluijs, R. and van Wijk, R. E. 2014. Migration routes and wintering areas of two Dutch northern wheatears *Oenanthe oenanthe* in the Sahel. – Limosa 87: 168–173.

Wang, E., Zhang, D., Braun, M. S., Hotz-Wagenblatt, A., Pärt, T., Arlt, D., Schmaljohann, H., Bairlein, F., Lei, F. and Wink, M. 2020. Can mitogenomes of the northern wheatear *Oenanthe oenanthe* reconstruct its phylogeography and reveal the origin of migrant birds? – Sci. Rep. 10: 9290.

Wartmann, B. A. 1985. Vergleichende Untersuchungen zur Populations-, Brut-und Nahrungsökologie von Wasserpieper und Steinschmätzer im Dischmatal GR. – Thesis, Univ. Zürich.

Wotherspoon, S. J., Sumner, M. D. and Lisovski, S. 2013. R package SGAT: solar/satellite geolocation for animal tracking. – <https://github.com/SWotherspoon/SGAT>.