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RESEARCH ARTICLE

The Indo-European flyway: Opportunities and constraints reflected by Common Rosefinches breeding across Europe

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Abstract

Aim: The configuration of the earth's landmasses influences global weather systems and spatiotemporal resource availability, thereby shaping biogeographical patterns and migratory routes of animals. Here, we aim to identify potential migratory barriers and corridors, as well as general migration strategies within the understudied Indo-European flyway.

Location: Europe, Central Asia.

Major taxon studied: Common rosefinches.

Methods: We used a combination of theoretical optimization modelling and empirical tracking of Common Rosefinches (*Carpodacus erythrinus*) breeding across a large latitudinal gradient in Europe. First, we identified optimal migration routes driven by wind and resource availability along the Indo-European flyway. Second, we tracked rosefinches from five breeding populations using light-level geolocators. Finally, we compared to what extent empirical tracks overlapped with the modelled optimal routes.

Results: In autumn, theoretical wind driven migration routes formed a broad-front corridor connecting Europe and the Indian Subcontinent while the theoretical resource driven routes formed a distinct north-south divide. The latter pattern also reflected the rosefinch tracks with all but the most southerly breeding birds making a northern detour towards non-breeding sites in Pakistan and India. In spring, the resource availability model predicted a similar migratory divide, however, the southern route seemed relatively more favourable and closely matched with the optimal wind driven migration routes. Spring tracking data showed larger overlap with the modelled wind driven migration routes compared to the resource driven routes.

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Main conclusions: Optimal wind and resource driven migration routes along the Indo-European flyway are seasonally specific and to a large extend do not overlap with one another. Under these conditions, migratory birds adopt seasonally distinct migration strategies following energy minimization strategy in autumn, driven by resource availability, and time minimizing strategy in spring, driven by wind conditions. Our optimal migration models can be applied worldwide and used to validate against empirical data to explain large-scale biogeographic pattern of migratory animals.

KEYWORDS
Carpodacus erythrinus, ecological barriers, flyways, geolocation, India, long-distance migration, migration strategies, wind support

1 | INTRODUCTION

During their seasonal migration, birds typically travel between breeding and non-breeding grounds, which are connected by well-established migratory routes that are grouped into major flyways. For long-distance migrants, these routes can stretch for thousands of kilometres crossing vastly different habitats and linking ecological communities worldwide (Bauer & Hoye, 2014). Most migratory birds in Europe spend the non-breeding period south of their breeding sites with some species travelling as far as southern Africa (Briedis et al., 2020). Yet, a handful of species migrate southeast along the Indo-European flyway to non-breeding sites on the Indian subcontinent (Brlík et al., 2018; Lislevand et al., 2015; Stach et al., 2016). This flyway has so far received little attention in migration ecology research and the exact migration routes and schedules, key stopover areas, and precise non-breeding sites of the species and populations travelling along the Indo-European flyway remain poorly understood.

Similar to the relatively well-studied Afro-Palearctic, North American and Asian bird migration systems, the Indo-European flyway comprises several ecological barriers (Figure 1) – the Black and Caspian Seas, Dasht-e Lut, Karakum and Thar Deserts, and Caucasus, Zagros, Alborz and Hindu Kush mountain ranges. Major migratory corridors are established around ecological barriers and relatively few individuals cross them in long endurance (Klaassen et al., 2011, Battley et al., 2012; but see Adamík et al., 2016) or high altitude flights (Hawkes et al., 2011). Circumvention of barriers leads to an aggregation of large number of migrants at migratory hotspots forming so-called migratory bottlenecks, e.g. at the Strait of Gibraltar and Israel in the Afro-Palearctic migratory system (Phipps et al., 2019; Ditto, 1988), and the land bridge between North and South America, e.g. Panama, in the Nearctic-Neotropical migratory system (Bayly et al., 2018; La Sorte et al., 2016).

Migratory flyways and individual routes are not only shaped by geographic features, but also by biotic and abiotic factors such as suitable habitats with available food resources (La Sorte et al., 2014), and prevailing wind patterns at various geographic scales (Kranstauber et al., 2015). Furthermore, optimal migration routes and barriers en-route can be specific to species, populations and individuals depending on biological traits and ecological requirements, individual migration timing, as well as start and end points of migration (breeding and non-breeding site locations). For example, in the Afro-Palearctic migratory system, populations that breed further west tend to use more westerly migration routes and non-breeding areas compared to populations breeding further east (Briedis et al., 2020). On the contrary, in the Indo-European flyway the main migration displacement takes place across the longitudinal axis and therefore, populations of various breeding latitudes may be expected to differ regarding their optimal migration corridors. Unfortunately, recoveries of ringed birds have remained scarce and insufficient for describing the Indo-European flyway. Thus, we miss fundamental knowledge on the Indo-European flyway and the migration ecology of the species travelling within it.

Here, we used a modelling framework and individual tracking data, aiming at identifying potential migratory barriers and corridors as well as general migration strategies within the Indo-European flyway. First, we developed a trajectory-based migration model that optimizes routes based on wind (theoretical wind driven migration routes) or resources (theoretical resource driven migration routes) across the flyway. Second, we tracked five latitudinally distinct European breeding populations of a small passerine migrant, the Common Rosefinch (*Carpodacus erythrinus*, hereafter – rosefinch) with geolocators, to serve as an example for a general description of this flyway. By combining modelling output and tracking results, we identified the extent to which rosefinches followed wind driven or resource driven routes during their seasonal journeys. During the first half of the 20th century rosefinches expanded their range, colonizing new breeding areas in central and northern Europe (Bozhko, 1980, Stjernberg 1985) while still migrating to the species' traditional non-breeding areas on the Indian subcontinent (Stach et al., 2016). Because individual migration routes and timing result from a combination of endogenous and exogenous factors, we expected to find differences between breeding populations across Europe. In particular, we expect that latitudinal differences of populations during the breeding seasons is maintained during migration, leading to segregated migration routes and stopovers that may, however, converge at potential migratory bottlenecks.

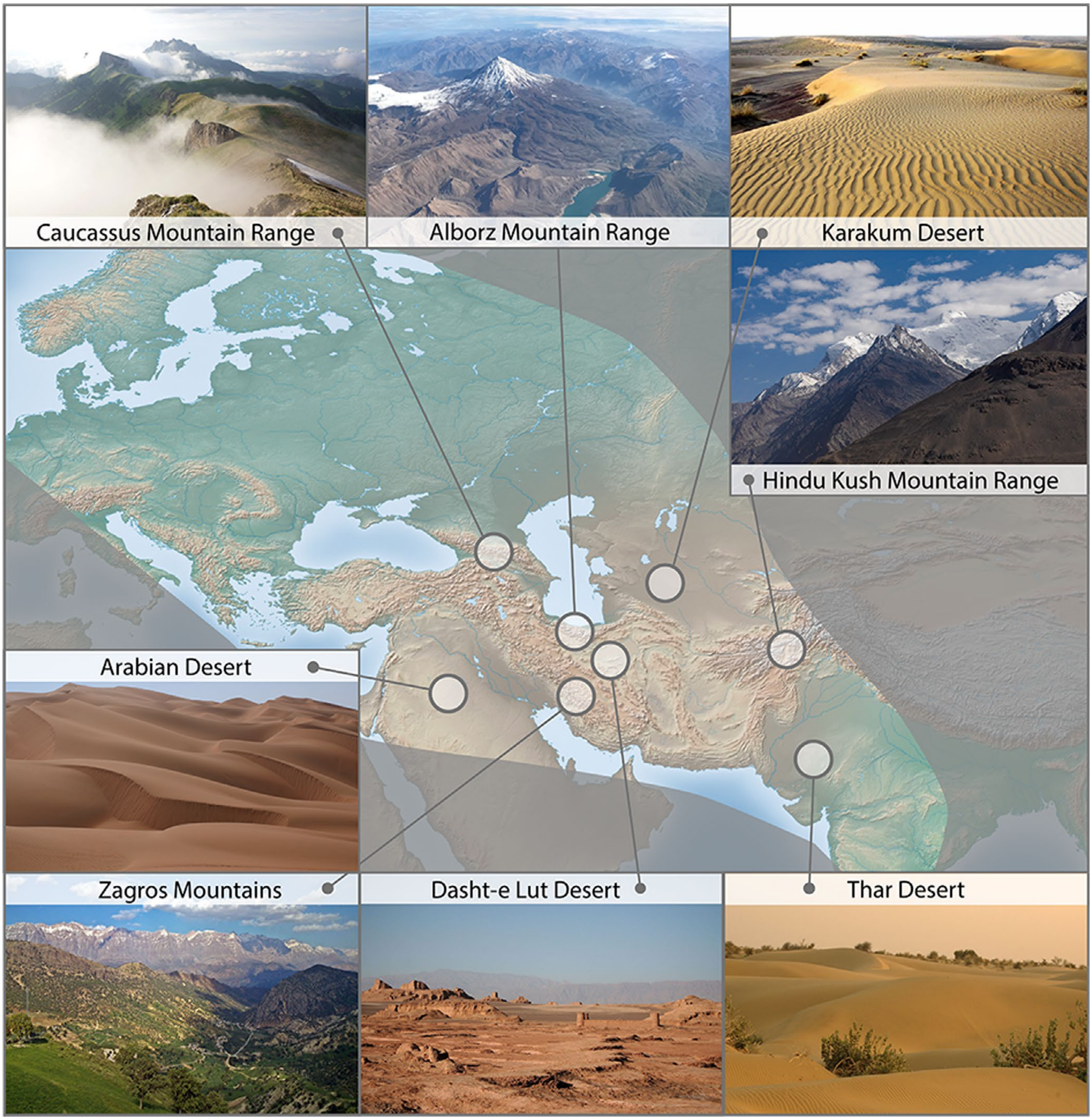


FIGURE 1 Indo-European Flyway and its major ecological barriers for migratory landbirds. (pictures credits: Caucassus MR: Vyacheslav Argenberg, Alborz MR: Greger Ravik, Karakum D: David Stanley, Hindu Kush MR: Ninara, Arabian D.: Nepenthes, Zargos M.: Vah.hem, Dasht-e Lut D.: Erik Albers, Thar D.: Honza Soukup. Pictures were downloaded from https://commons.wikimedia.org and www.flickr.com and used under Creative Commons CC BY 2.0)

2 | MATERIALS AND METHODS

We modelled the general optimal migratory routes with respect to wind and resources from the five major breeding sites of the tracking study (Finland, Sweden, Germany, Czechia and Bulgaria) to non-breeding sites in Pakistan and India and compared these optimal routes with the actual tracks of rosefinches.

2.1 | Wind simulations

To investigate routes optimized for wind support across all five rosefinch populations, we followed the approach from Kranstauber et al. (2015). In short, our model calculated the fastest route between five breeding locations (as identified in the tracking study) and five locations across the non-breeding range, travelling over a grid consisting of 2,955 nodes. We used a hexagonal grid such that cells were distributed equally across the area of interest (0.0°W–100.0°W, 5.0°S–72.0°N). Travel was allowed along straight connections to the six surrounding cells and the second-order neighbours, creating 12 travel connections about 30° apart. The distance to direct and second-order neighbouring cells was on average 150 and 300 km, respectively. Wind data were provided by the European Centre for Midrange Weather Forecast (ECMWF ERA-Interim; https://www.ecmwf.int/). For the interpolation of wind, we used three layers of the atmospheric pressure with 925, 850 and 700 millibar, corresponding to the median altitude of 779, 1,502 and 3,130 m above sea level. These altitudes cover the range where most migration is observed in radar and recent geolocator studies (Dhanjal-Adams et al., 2018; Kemp et al., 2013; Liechti et al., 2018). The model started at one breeding location and calculated travel times to all surrounding nodes. Travel time to the nodes depends on ground speed (v_g), which is a function of cross wind (w_c), wind support (w_s) and air speed (10 m/s; Bruderer & Boldt, 2001). For each time step of 3 hr, wind conditions from the altitude with the most supporting winds (or least crosswind) were chosen, assuming that birds can change altitude during flight (Liechti et al., 2018). By repeating this process, the algorithm finds the routes with most wind support and identifies the travel time needed to fly from the start to the defined destination. Note, that this approach (as described in Kranstauber et al., 2015) does not include any component of the species stopover ecology and individual birds were assumed to fly non-stop between breeding and non-breeding location. We calculated the fastest routes (routes with the highest wind support) from all five non-breeding locations to all five breeding locations, and vice-versa, starting every 2nd day during the entire migration seasons between 15 March and 31 May in spring and 15 July and 31 September in autumn from 2012 to 2017. This resulted in 40 routes per population and year. To weigh routes, we used the same approach as Kranstauber et al. (2015), that assumes travel time (t) has a sigmoidal relationship with mortality and calculates an average survival per year for each route using the travel time across all years:

$$\Phi_{\text{wind}} = 1 - \frac{t^2}{\lambda - t^2}$$

Where migration mortality λ is set to the mean travel time across all years squared for every location pair (combination) and starting date separately. This means, on an average migration between two locations half of the individuals would die. It is important to note that this measure of mortality does not reflect 'true' mortality but ranks the tracks within the continuum from optimal ($\Phi = 1$) to sub-optimal ($\Phi = 0$). To account for the differences in migration distance between populations, we calculated migration speed (km/day) based on flying duration (days) from the model output divided by the great circle distance (km) between start and end of each route.

2.2 | Resource simulations

To investigate resource driven routes, we used a similar procedure as described above, using normalized differenced vegetation indices (NDVI) as the underlying environmental variable. Weekly noise reduced AVHRR NDVI products with a 4 × 4 km resolution were collected from NOAA Centre for Satellite Application and Research (SMN product from: ftp://ftp.star.nesdis.noaa.gov/pub/corp/scsb/wguo/data/Blend ed_VH_4 km/geo_TIFF/). NDVI values vary between 0 and 1 and indicate levels of photosynthetic activity. It has been shown that NDVI values correlate well with primary productivity and, to some extent, with productivity on higher trophic levels (Pettorelli et al., 2005).

Many migratory songbirds, including rosefinches, fly during the night and rest during the day (Dorka, 1966). Typically, they cannot cover the entire distance without refuelling, for which they need extended (>1 day) stopping periods at suitable locations. We here assumed that individual birds can fly approximately 10 hr per day with an average ground speed of 15 m/s (Pennycuick, 2008), i.e. up to 540 km per day. During the migration periods, simulation started on the same days as described in the wind simulation. For each non-breeding site in spring, breeding site in autumn and for all dates, a modelled individual started ($t = 0$) by assessing the survival reflecting the maximum use of resource availability along routes (not 'true' survival) for all sites within daily travel distance. Here, survival along routes is calculated from the NDVI value for the grid cell following a sigmoidal relation:

$$\Phi_{\text{NDVI}} = \frac{1}{1 + e^{-a(x-b)}}$$

with parameters $a = 20$ and $b = 0.3$ resulting in zero survival for NDVI = 0 and a survival of 0.5 for NDVI = 0.3 and survival of 1 for NDVI >0.5. We choose this low threshold for NDVI leading to high prospective survival to better reflect the ecology of rosefinches that are unlikely to strictly follow the 'green wave' of NDVI but may even feed on seeds left over from the non-productive season. Thus, we use NDVI as a proxy for the potential, rather than the direct availability of resources. In the next time step ($t = 1$), the individual started from the grid that provided the highest survival. Unlike in the previous step, only cells that are within reach but differ from those reached during the previous round are considered as potential destinations. The survival for these cells was again based on the NDVI for this time step, however, multiplied by the prospective survival of the cell in t–1. This process was repeated until all cells have been reached, allowing a path construction from all breeding sites (or non-breeding sites in autumn) to the starting point that indicates the paths with the highest possible prospective survival for this date. To weigh the paths, we also a normalized survival value that indicates routes with the highest survival ($\Phi = 1$), average routes ($\Phi = 0.5$) and non-optimal routes ($\Phi = 0$) (similar to above). Again, the term survival does not reflect 'true' survival but ranks the routes according to the maximum use of resource availability along routes. To illustrate the optimal routes for spring and autumn migration (Figure 2), we used all paths with a Φ higher than the 75 percentiles of each route and season.

2.3 | Empirical geolocator tracking data

Light-level geolocators were deployed on adult male rosefinches in Finland, Sweden, Germany, Czechia and Bulgaria (exact field sites are listed in Supplementary material S1). In Finland, geolocators were deployed at different field sites during 2015 (SOI GDL2 n = 49, Migrate Technology Intigeo P50B1-7-DIP n = 4 and MT Intigeo P50Z11-7-DIP n = 3) and 2016 (SOI GDL2 n = 64 and Migrate Technology Intigeo P30Z11-7-DIP n = 1). In Sweden, birds were captured and equipped with geolocators at two sites in 2011 (BAS Mk12S n = 10), 2012 (MT Intigeo P65 n = 6) and 2013 (MT Intigeo P65 n = 21). In Germany, fieldwork took place at one site during 2013 (SOI GDL2 n = 20). At two sites in Czechia, geolocators were put on rosefinches in 2012 (Migrate Technology Intigeo P55, n = 14) and 2013 (SOI GLD2 n = 20). At one site in Bulgaria, geolocators were put on eight individuals (Migrate Technology Intigeo P55) in 2012. At all sites, birds were caught at their breeding locations using mist nets and subsequently marked, measured and equipped with a geolocator using a leg-loop harness. Including the harness, Geolocators weighted between 0.7 and 0.9 g, which represents 2.5%–4.9% of the body mass of rosefinches. Thus, we expect no or very minor effects on the individuals behaviour and fitness due to the extra weight of the device (Brlík et al., 2019). Due to the patchy distribution of rosefinches and generally small population sizes, we could not establish standardized control groups to directly investigate tag effects on annual survival within the studied populations.

We used a threshold approach (Lisovski et al., 2020) to estimate locations from the light-level data using the R packages *TwGeos* (Lisovski et al., 2015), *GeoLight* v2.01 (Lisovski & Hahn, 2012) and *SGAT* (Wotherspoon et al., 2013). First, sunrise and sunset events were identified using a light intensity threshold of 0.8 arbitrary values for the SOI GDL2 and 0.5 lux for MT Intigeo as well as for BAS Mk models. Calibration was conducted for each tag separately using the maximum number of days recorded at the breeding sites after logger

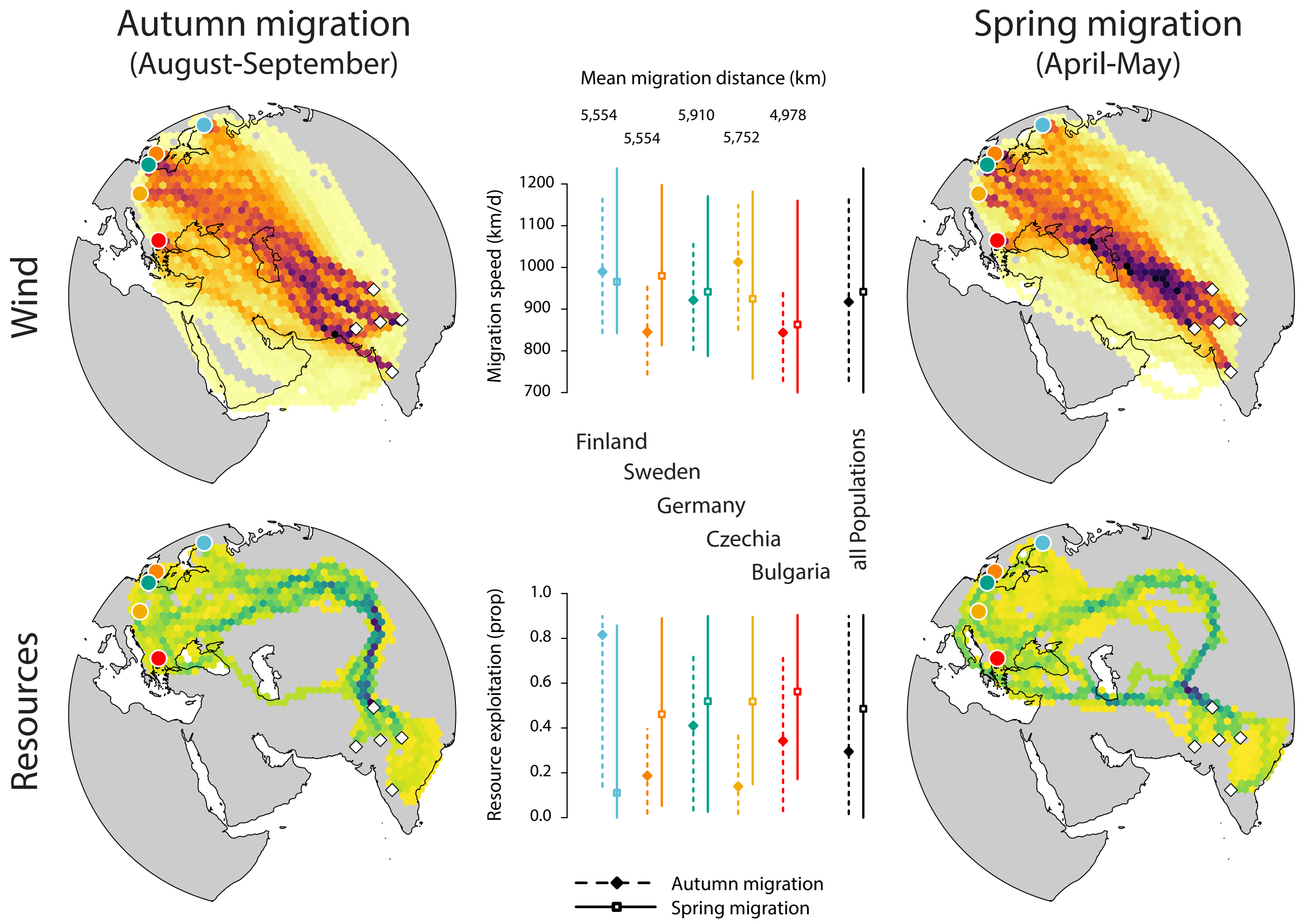


FIGURE 2 Simulated optimal routes for autumn (left) and spring (right) migration along the Indo-European Flyway; theoretical wind driven routes (upper panel) and theoretical resource (NDVI) driven routes (lower panel). Darker colours in the maps represent grid cells with a higher number of transient migrants predicted by the model. Both maps include the optimal 25% (Φ > 75) of simulated tracks (for each population and season). The middle panels show the median and the range of values for the same subset of tracks. Dashed lines for autumn migration and solid lines for spring migration

deployments. Next, we applied the *invChanges* function from *GeoLight* to identify changes in sunrise and sunset times and distinguish between movement and stationary periods. Based on this analysis, we assigned twilight events to either a stationary period (only for periods that were found to include at least 3 days) or to movement. We used the group method in SGAT to estimate geographical locations and their uncertainties. SGAT uses a Bayesian framework to incorporate prior information including the assigned stopover periods, twilight error distribution (parameters from the calibration), speed distribution (gamma distribution with shape = 2.2 and scale = 0.08) and a land mask (so that stopover locations are less likely to occur in the sea). During a Markov Chain Monte Carlo (MCMC) simulation, the geographical probability distribution was calculated for each twilight time during movement and for each stationary period. Providing stationary periods and thereby grouping twilight times and estimate a single location from all sunrise and sunset events that belong to the same stationary period helps finding the best possible fit to the data during this period, and importantly, increasing the precision of the estimated location. We fixed the first and, if the tag was still recording when the bird returned in spring, the last location to the known capture and recapture locations where appropriate. We first ran a *modified Gamma* model (relaxed assumptions) for 1,000 iterations to initiate the model, before tuning the model with final assumptions/priors (three runs with 300 iterations). Finally, the model was run for 2,000 iterations to ensure convergence. We repeated the MCMC simulation using the results from the first to further tune the proposals. From the resulting 2,000 chains, we extracted median location estimates for each twilight during movement and for each stationary period including the 95% credibility interval.

To investigate the overlap of the estimated tracks based on empirical data, and the simulated optimal routes for speed and resources (Figure 4), we first created a path along the shortest great circle route between the start and the end of each track (spring and autumn migration separately). We then created a perpendicular line through each longitudinal degree along the great circle route. For each of the last 500 MCMC chains of the track estimates as well as the simulated fastest and safest routes (one for each day of migration), the intersection of the track and each perpendicular spatial line was defined and the distance to the great circle route calculated (negative distance if the track intersected the perpendicular line south of the great circle route).

3 | RESULTS

3.1 | Wind simulations

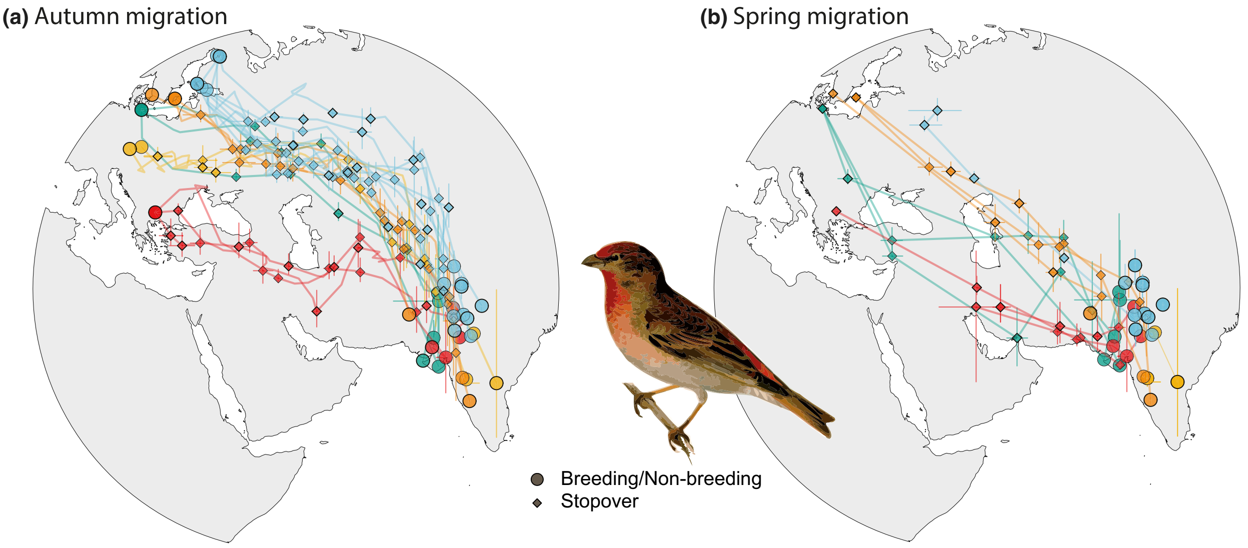
Based on wind conditions (2012–2017), simulated nocturnal migrants flying on the routes with the highest wind support (Φ > 75 percentile) were able to cover a median distance of 917 (727–1,164) km per day during autumn migration and slightly longer 941 (700–1,237) km distances per day during spring migration (Figure 2, top panels). During spring migration, the maximum as well as the median distances per day, were shorter the more south the breeding latitude was. This pattern across populations was, however, more heterogeneous during autumn migration. Simulated birds breeding in Finland attained the highest wind support and could travel with the highest top speeds (autumn/spring 1,164/1,237 km/day) whereas the top speeds of the Bulgarian birds were lowest among the five populations (951/1,159 km/day). The largest differences in median speeds between the seasons were found in the Swedish and the Czech simulations; however, while the median speed of the Swedish simulations was higher during spring (979 compared to 845 km/day), the simulated Czech birds could achieve faster speeds in autumn (1,012 compared to 924 km/day). Spatially, the optimal routes were less funnelled during autumn migration, compared to spring, where most routes converged after departure over northern Pakistan heading northwest towards the Caspian Sea. Thereafter, the routes diverged towards the breeding sites. Interestingly, some of the optimal routes in the south circumvented the Arabian Peninsula over the Indian Ocean, indicating high wind support for a large detour south.

3.2 | Resource simulations

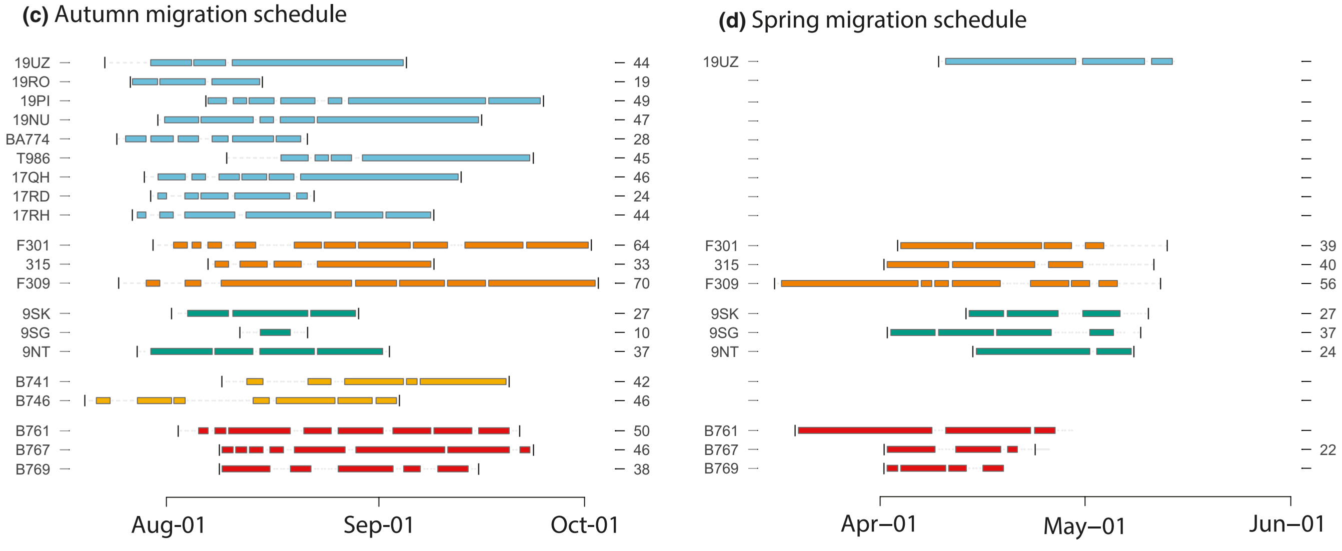
In this simulation, birds chose routes that allow them to stop in places with some signal of vegetation growth indicating water availability, shade and possibly food (Figure 2, bottom panels). Routes with higher Φ values followed resource availability, or avoided sites that could be detrimental, to a higher degree. Overall, birds achieved higher Φ values during spring migration (0.48; 0–0.90) compared to autumn migration (0.29; 0.01–0.89). During autumn migration, the simulated Finish routes achieved the highest Φ values (0.89). However, during spring migration this pattern was reversed with the Finish birds having the lowest median Φ values (0.11). The simulated Swedish and the Czech birds had exceptionally low median Φ values (0.18, 0.13) during autumn migration. Spatially, the simulated birds avoided the dry areas of south-western Russia, Kazakhstan, Uzbekistan and Turkmenistan during both autumn and spring migration. This led to a divide in optimal migratory corridors from northern Pakistan onward with routes leading either to the north of the Caspian Sea or due west south of the Caspian Sea.

3.3 | Empirical geolocator tracking data

A total of 23 geolocators were retrieved in the year after deployment (Finland = 10 [8.2%], Sweden = 3 [8.1%], Germany = 4 [20%], Czechia = 3 [8.8%], Bulgaria = 3 [37.5%]) (Figure 3). From these loggers, one (FIN) failed due to a technical hardware problem, one (GER) stopped recording after a couple of days, and one (CZ) contained false measurements that could not be used to estimate locations. The remaining 20 loggers recorded light at least until the rosefinches reached their major non-breeding sites. Seven loggers were still recording when the logger was retrieved at the breeding site (SWE = 3, GER = 3, BUL = 1), and three stopped recording during spring migration (FIN = 1, BUL = 2). Focusing on the general migration pattern, all individuals migrated towards Pakistan and western India. Non-breeding sites were mainly located between the Indian Ocean (north of 21°S) and the southern edge of the Himalayas. Three non-breeding sites were likely located in eastern Pakistan along the Indus River. Four individuals wintered further south in central southern India. Individual non-breeding sites showed no clear separation between breeding populations, except for the Finish birds that were exclusively located in the northern part of the non-breeding range. Five individuals had two well-separated non-breeding sites with a first long stop in the north before moving further south (17RD from Finland, 9 NT and 9SK from Germany, B746 from Czechia and B767 from Bulgaria). Other individuals might have changed non-breeding locations too (as suggested for the Swedish birds in Stach et al., 2016), but our analysis was not conclusive in this respect, and for many individuals, recordings stopped during the non-breeding period. Autumn migration commenced between July 20 and August 10, with no apparent difference between populations. Arrival at the first non-breeding site was more variable between individuals (August 15 to October 4), owing to high variation in the migration duration (10–70 days). Stopover periods tended to become longer towards the end of migration and before reaching the non-breeding sites (Figure 3c). Autumn migration routes of all but the Bulgarian population converged in the broader Moscow area in Russia before continuing into central Kazakhstan towards the non-breeding sites (Figure 3a). The three Bulgarian birds migrated south of the Black Sea and the Caspian Sea before they took a northern detour, potentially avoiding the central Iranian Dasht-e Lut desert.


(a) Autumn migration

(b) Spring migration


(c) Autumn migration schedule

(d) Spring migration schedule

FIGURE 3 Southward (a) and northward (b) migration routes of Common Rosefinches (*Carpodacus erythrinus*) breeding in Finland (blue), Sweden (orange), Germany(green), Czechia (yellow) and Bulgaria (red). Tracks are based in on light-level geolocator estimates and a movement analysis to extract stopover sites (diamonds) and major wintering sites (circles). Sites are shown with their 95% credibility interval. The lower panel shows the timing of migration, with the individual specific (ID's on the left) departure and arrival dates and the time spent on stopover sites (thick coloured lines). Migration duration in days is shown on the right. Common Rosefinch drawing by Magnus von Wright (1805–1868)

Compared to autumn migration, the few tracks for spring migration suggest a straighter journey to the breeding sites, with the northern breeders (SWE, FIN) travelling north of the Caspian Sea, and the Bulgarian birds, as well as one German bird flying a southerly route with potential stopover sites in Turkey. Departure dates from the non-breeding sites (March 26 to April 24, *N* = 10) suggest a trend with breeding latitude: southern breeders left earlier than northern breeders. Duration of migration varied between 22 and 56 days (*N* = 7; Figure 3d).

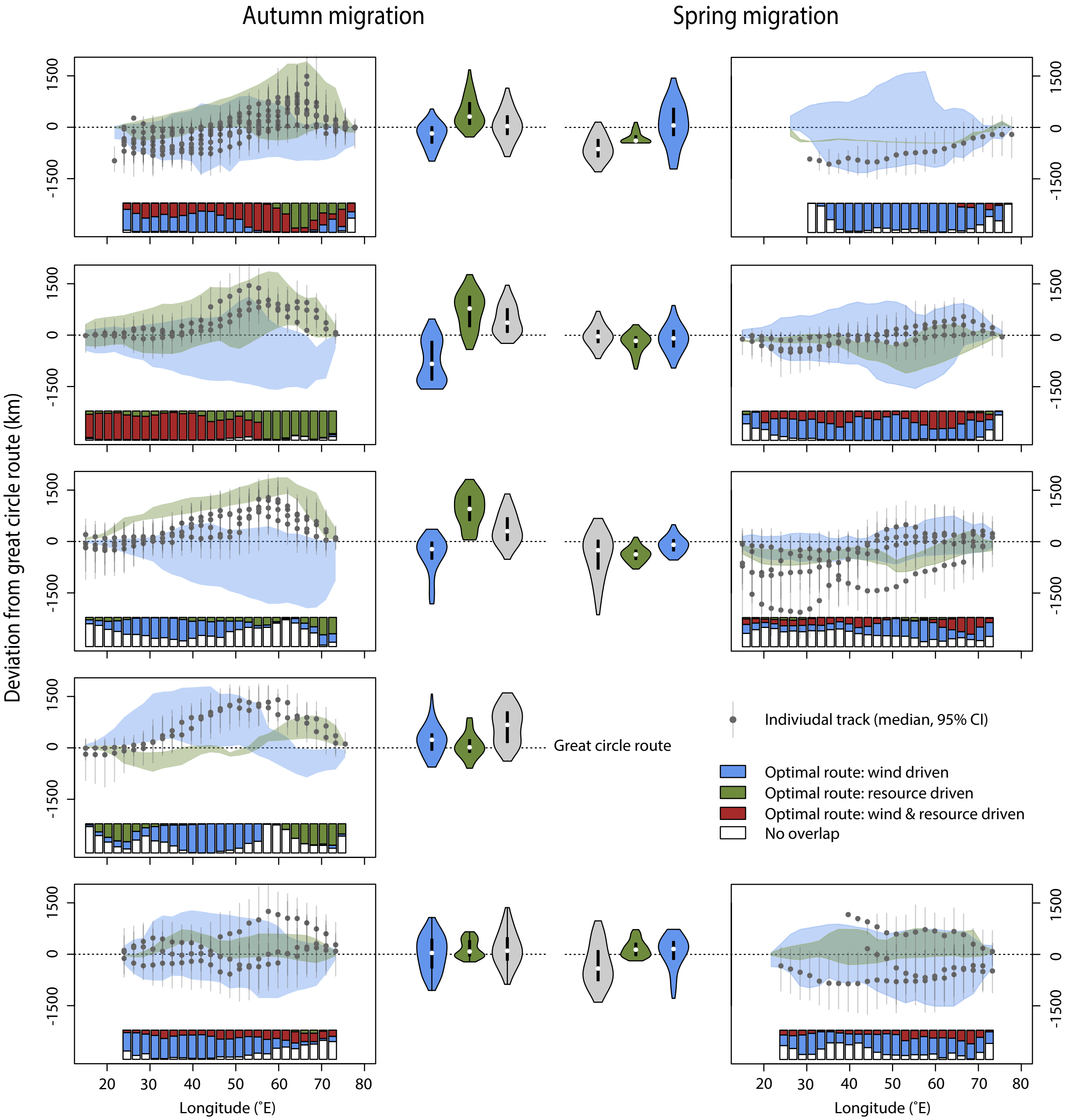


FIGURE 4 The deviations of the individual Common rosefinche geolocator track estimates (grey dots with 95% CI) from theoretical wind driven routes (blue area) and theoretical resource driven routes (green area). Left panels for autumn migration and right panels for spring migration. Each row represents the results for one population, from Finland (top), Sweden, Germany, Czechia (no spring tracks) and Bulgaria (bottom). The bar charts at the bottom of the plots indicate the relative overlap of the track estimates with the optimal migration routes (blue for wind, green for resources, red for both and white for no overlap). The violin plots in the centre provide the median (white dot) with the 20th to 80th IQR (black line) as well as the distribution of the 95% CI (violin plot) of the geolocator track deviation from the great circle route. Negative values indicate deviations to the south of the great circle route

3.4 | Empirical tracking versus simulated optimal routes

Deviations from the great circle route towards the north illustrate a detour for all but the Bulgarian birds during the second half of autumn migration (latitude >50°E: FIN = mean 240 ± SD 360 km; SWE = 706 ± 345 km; GER = 599 ± 412 km; CZ = 878 ± 283 km; BUL = 262 ± 550 km) (Figure 4). On this detour, the tracks overlap mainly with the optimal routes of resources, notably for the two northern populations from Finland and Sweden (FIN: wind = 14 ± 15%, resources = 52 ± 29%, both = 28 ± 30%; SWE: 1 ± 1%, 73 ± 29%, 18 ± 29%; GER: 17 ± 10%, 24 ± 18%, 0%; CZ: 19 ± 31%, 32 ± 32%, 0%; BUL: 32 ± 22%, 2 ± 4%, 28 ± 5%). In northern and central Europe, the optimal wind driven routes during the first half of autumn migration (<50°E) occurred close and around the great circle route allowing individuals to head straight towards their non-breeding sites (FIN = −177 ± 326 km, SWE = −602 ± 498 km, GER = −291 ± 390 km, CZ = 402 ± 283 km, BUL = 87 ± 477 km), before deviating towards the north of the great circle route. The Finnish and to a lesser extent the Swedish birds were following the optimal wind driven routes that deviated to the south from the great circle route during the first half of their migration (overlap with of routes: FIN wind = 58 ± 9%, resources = 0 ± 0%, both = 38 ± 9%; SWE 1 ± 1%, 14 ± 9%, 82 ± 10%), whereas the Czech birds went north to potentially benefit from supporting wind conditions (CZ 1 ± 1%, 14 ± 9%, 82 ± 10%). The optimal routes – wind and resources – for the Bulgarian rosefinches largely coincided with the great circle route and showed no particular pattern of detours (entire autumn migration: BUL = wind 22 ± 506 km, resources 167 ± 261 km). However, the tracks overlapped to a greater extent with the theoretical wind driven routes (wind = 22 ± 20%, resources = 1 ± 3%, both = 53 ± 25%).

The general trend of northern tracked birds to deviate from the great circle route towards the optimal resource driven routes during autumn migration was reversed during spring, indicating a loop migration system (deviation of tracks from great circle route: FIN = −602 ± 339 km, SWE = −27 ± 287 km, GER = −404 ± 626 km, BUL = −314 ± 583 km). Although the sample size for spring migration is limited, the tracks showed a larger overlap with the theoretical wind driven routes (FIN wind = 70 ± 23%, resources = 0 ± 0%, both = 2 ± 5%; SWE wind = 55 ± 18%, resources = 1 ± 2%, both = 30 ± 16%; GER wind = 33 ± 17%, resources = 3 ± 3%, both = 20 ± 13%; BUL wind = 52 ± 12%, resources = 0 ± 0%, both = 18 ± 10%) as compared the overlap with the theoretical resource driven routes during autumn migration.

4 | DISCUSSION

Configuration of the earth`s landmasses exerts profound impacts on migration routes of animals (Dingle, 2014). Deserts, oceans and mountains influence weather systems and resource availability and create corridors or barriers for moving animals. So far, based on observations, ringing and tracking, biogeographic patterns in migration routes have been identified within the major terrestrial flyways (e.g. Briedis et al., 2020; La Sorte & Fink, 2017; La Sorte, Fink, Hochachka, Farnsworth, et al., 2014). In the Afro-Palearctic migratory system, major flyways arch around the Mediterranean Sea and the Sahara Desert; while the Himalayas are arguably a major hurdle for migrations from the Asian continent (Irwin & Irwin, 2005). Such geographic barriers can lead to migratory divides with populations circumventing the barrier on either side (Briedis et al., 2020), which may separate populations and eventually result in speciation (Willow warbler; Bensch et al., 1999; Bensch et al., 2009; Greenish warbler; Irwin, 2002; Swainson's thrush; Ruegg, 2007). Here, we used a novel modelling approach and tracking data of Common Rosefinches breeding across Europe to reveal migration patterns and spatial configurations within the hitherto understudied Indo-European flyway.

The migratory distances that birds cover along the Indo-European flyway are similar to those within the Afro-Palearctic and Nearctic-Neotropical migratory systems. However, apart from a few recent tracking studies (Lislevand *et al*., 2015; Stach et al., 2016; Brlík et al., 2018), migratory routes that link Europe and India remain largely unmapped. Our modelling results predicted two distinct migration routes circumventing the Black and the Caspian Seas as well as the desert in and around Uzbekistan (e.g. Karkum desert) – areas that could be identified as ecological barriers for common rosefinches and probably other migratory songbirds in this flyway. This pattern was more pronounced during autumn migration when rosefinches breeding in central and northern Europe migrate towards the east with a northward deviation from the great circle route, where the simulated birds experienced more optimal resource conditions. From the Bulgarian breeding sites, rosefinches took the route south of the Caspian Sea almost straight on the great circle route before navigating north to circumvent the deserts of northern Iran and Afghanistan – a detour that would again lead to a more optimal resource exploitation and avoidance of potentially detrimental areas. Although the resource driven model predicted a similar divide for the spring migration routes, the route south of the Caspian Sea seemed to provide better opportunities during spring compared to autumn. Tracking data showed that rosefinches flying towards their breeding site indeed took a detour south of the great circle route. This seems to make sense as the onset of spring is later in the north with conditions still harsh in northern Kazakhstan and Russia during April and early May. However, the loop migration with a more southerly route during spring, that is also a straighter route towards the breeding sites, may allow birds to also take advantage of stronger wind support. In general, rosefinch tracks during spring largely overlapped with the optimal wind driven routes (i.e. those with higher wind support) that were more funnelled and had higher potential for attaining high travel speeds for all populations from India towards the Caspian Sea. While rosefinches may follow these optimal routes, migration speed was not higher during spring and highly variable across individuals, which may indicate potential trade-offs between wind support during the movement phase and resource availability on stopover sites.

Although speculative, the observed migratory divide between the southern (Bulgarian) and other populations could lead to or reflect speciation in this species. It has recently been suggested that rosefinches in the southern part of the distribution range belong to a Caucasian subspecies, *C. e. kubanensis* (Hung et al., 2013; Pavlova et al., 2005). These southern European breeding sites might have been colonized by individuals with Turkish origin, while breeding areas further north, were likely colonized from the east by individuals with Russian origin (Bozhko, 1980). Thus, the population specific routes and the migratory divide between the Bulgarian and more northern populations may also reflect historic species colonization routes (Hahn et al., 2019). The larger northward detour of the Czech birds that cannot be explained by optimal routes might still be a remnant of historic routes and not yet adapted to the local conditions. After all, the Czech sites were colonized by rosefinches rather recently in the 1960 s and 70 s (Albrecht, 1996). Similarly, the only known migration track of the paddyfield warbler *Acrocephalus agricola* from a breeding site in Bulgaria to a non-breeding site in India contrasts Bulgarian rosefinches and follows the route along the northern edge of the Black and the Caspian Seas (Brlík et al., 2018). This migration pattern in the paddyfield warbler retraces of the recent range expansion further imposing that historic species colonization routes may play a major role in forming present day migratory routes.

Migratory birds have developed a number of adaptive behaviours that facilitate navigation across or around ecological barriers. The safest option might be to fully circumvent large barriers (Alerstam, 2001) as this avoids potentially hostile conditions, saves energy via reduced transport costs of carrying extra fuel and possibly reduces predation risk associated with reduced manoeuvrability when carrying fat stores (Kullberg et al., 1996) (but see: Witter & Cuthill, 1993). Thus, circumventing barriers could be considered a consequence of following an energy minimization strategy (Hedenstrom & Alerstam, 1997). Overall, tracked rosefinches seem to follow such energy minimization strategy with detours during autumn migration, following resource availability and circumventing the Central Asian deserts and Seas.

Alternatively, birds may choose to cross barriers (Adamík et al., 2016; Åkesson et al., 2016; Ouwehand & Both, 2016; Schmaljohann et al., 2007). This strategy may save time but involves a higher mortality risk (but see Gill et al., 2009). Therefore, birds may attempt the crossing only with sufficient body energy stores and in favourable environmental conditions (i.e. tailwinds) that favour a rapid traverse (Loonstra et al., 2019). Because crossing barriers may be less time consuming, if resources prior to the barrier allow fast fuelling, it could be considered a time minimization strategy (Hedenström & Alerstam, 1997). In accordance with this, and although our sample size for spring migration tracks is limited, rosefinches flying towards their breeding sites seem to have traversed some of the barriers they circumvented during autumn migration. Both wind conditions and resource availability may allow them to use this strategy during spring when timely arrival at the breeding sites increases individual fitness (Hasselquist, 1998; Møller, 1994; Velmala et al., 2015).

By combining multi-population tracking data with a modelling approaches we have identified the main migratory corridors along the Indo-European flyway. Optimal resource driven migratory routes create a clear north-south migratory divide around the deserts of central Asia and the Caspian Sea. Successfully tracked rosefinches were also found to exhibit a migratory divide during autumn migration when northern populations flew northerly detours while the Bulgarian birds used a straighter southern route. This divide seems less pronounced during spring when birds did not perform the northern detour but potentially made use of the better conditions south and the funnelled wind support over the central Asian deserts. We thus found a north-south loop migration, partly predicted by our model and performed in almost all individuals that were tracked during both seasons. Understanding how environmental variables influence migratory strategies of animals is one of the major challenges in migration ecology (Bauer et al., 2019). Our model can identify migration routes that are optimal in terms in resource availability (energy minimization) or wind support (time minimization), and by comparing these model predictions to empirical data, it can show adaptations and constraints in employed migratory strategies on animals across major flyways.

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DATA AVAILABILITY STATEMENT

Raw light recordings from geolocators, annotated twilight tables, location estimates and R code are available from the Movebank Data Repositories (Lisovski et al., 2021). Simulation code for optimal migration routes has been deposited with Zenodo (https://zenodo.org/record/4314725).

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BIOSKETCH

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Author contributions: SL, RN and TA initiated the study. SL, TA, PM, SB and MB conceptualized the study. SL, RN, TA, PM, MPA, JC, TF, SJ, TJ, PK, CK, TL, BM, MP, PS, RS, KS, WV collected the data. SL performed simulations and analysed all tracking data. SL and MB wrote the manuscript with important contributions from TA, PM and SB. All authors approved the final version.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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