Inherited geomagnetic signposts can maintain migratory detours in changing geomagnetic landscapes

James D. McLaren, Heiko Schmaljohann and Bernd Blasius

Abstract

For many migratory species, inexperienced (naïve) individuals reach remote non-breeding areas independently using inherited headings and geomagnetic compass cues. Naïve migrants are also proposed to detour regions with unfavourable habitat or currents using inherited geomagnetic signposts to trigger changes in migratory headings. However, it remains unexplored whether migration based on inherited geomagnetic traits (headings and/or signposts) is viable at population levels, particularly in regions with strong spatial geomagnetic gradients or long-term geomagnetic changes. To address this unknown, we developed a migration model incorporating spatiotemporal geomagnetic data (1900-2015) and an evolutionary algorithm, accounting for trans-generational changes in inherited geomagnetic traits through population mixing and natal dispersal. Using this model, we assessed songbird migration from a highly unstable geomagnetic region (East-arctic North America and Greenland) via Europe to Africa. Model-evolved geomagnetic-based migration was (i) consistently successful over the 116-year period, (ii) up to twice as successful when geomagnetic-signposted compared with non-signposted migration, and (iii) consistent with records of detoured trans-Atlantic songbird migration in the wild. Our study supports the long-term viability of geomagnetic migratory headings, the benefit of inherited geomagnetic signposts, and illustrates how migratory orientation programs can mediate evolution of routes, in response to global environmental change.

Keywords: animal migration, evolutionary algorithm, geomagnetic compass, *Zugknick*, northern wheatear, natal philopatry

Introduction

Myriads of migrating animals undertake seasonal journeys across regional to cross-continental-scales (1,2). Experienced migrants can make use of a developed map-sense based on experienced geophysical (solar, stellar and geomagnetic) and olfactory cues (3,4). In particular, both first-spring bird migrants (5,6) and subadult oceanic migrants (4) apparently identify natal locations using geomagnetic signatures imprinted at the natal site. Contrastingly, many inexperienced (naïve) migrants on their first journey are thought to reach remote destinations independently in migratory steps based on inherited headings, often termed clock-and-compass migration (3,7). In the simplest case of a single inherited migratory heading, this would result in a fixed-heading geographic (e.g., star) or geomagnetic compass course, or else a gradually-shifting sun compass course (8–11). Many airborne migration routes can be largely explained by one or more compass courses (9,10), contingent upon possessing sufficient compass precision (11–13) and ability to negotiate currents (14,15). However, many migration routes require distinct direction changes (often termed "*Zugknicks"* for bird migration), e.g., to avoid regions with unfavourable habitats (16–18), or to exploit favourable habitat (19,20) or supportive current systems (4,21). Mediating such direction changes solely according to a circannual clock is likely unreliable given unpredictable variation in migratory schedules (22,23).

It remains therefore unclear how naïve migrants reliably identify where to change directions along unfamiliar routes. One possibility is that migrants use the broad-scale latitudinal patterns in the geomagnetic field. Specifically, both geomagnetic inclination (the vertical tilt of the geomagnetic field) and the total field intensity (hereafter, intensity) decrease from high to low latitudes (24,25). Therefore, both inclination and intensity have been proposed to act as directional signposts between endogenous headings (3,4). For example, laboratory experiments with naïve oceanic migrants such as hatchling turtles and salmon fry, geomagnetic-induced shifts in headings seem to induce headings which would facilitate travel through supportive current systems (4), and there is evidence that

naïve migratory bird orientation sometimes co-varies with the geomagnetic field (25,26). However, the geomagnetic component or combination of components which naïve migrants are able to perceive and respond to remains unclear, and the efficacy of geomagnetic-signposted migration, while theoretically feasible (27,28), has not been assessed for actual migration systems. In particular, we currently lack any information about the necessary precision in inheritance of migratory traits, such as headings or geomagnetic signposts, to track geomagnetic drift, which can occur rapidly in some areas such as currently near the geomagnetic North Pole (29,30). In fact, for migratory birds, it is often thought that orientation or navigation through unpredictable geomagnetic fields is intractable without primary reliance on or regular calibration using non-geomagnetic cues (31–34). However, these studies did not consider the possibility of adaptive gradients in geomagnetic fields (35), nor plasticity in inheritance of orientation cues (36,37). In order to assess these possibilities, it is necessary to account for trans-generational changes in orientation at population levels through mixing of orientation traits (7,38,39) and natal dispersal (40,41). This is because increased natal dispersal will lead to increased variability in inherited migratory headings, which along a given route are thought to be highly constrained (11,13).

To assess the long-term viability of inherited geomagnetic-based migration at the population level, including the benefit of inherited geomagnetic signposts, we used an evolutionary model approach in a spatiotemporally-varying geomagnetic landscape. We assessed three inherited migratory orientation programs for naïve bird migrants: non-signposted migration, i.e., following a constant inherited geomagnetic heading, and two signposted migrations, based on either geomagnetic inclination or intensity. With an inherited signpost, modelled migrants shift to a second inherited heading once the perceived magnitude in inclination or intensity falls below an inherited threshold value. The model simulates individual migration routes for an entire population (N = 50,000) across many generations (N= 116), accounting for long-term spatiotemporal variation (1900-2105) in the Earth's geomagnetic field (42), as well as directional precision among flight-steps (11) and

migrants' ability to gauge magnitudes of signposts (43). For simplicity, we assumed that all successful fall migrants would return to the breeding areas, which is equivalent to assuming no carry-over effects from fall migration (44). We implemented an evolutionary programming algorithm (45,46) which mimics inheritance of migratory traits among successful migrants, accounting for natal dispersal and stochastic variation in inheritance (36,37).

We showcase the model to compare night-migratory songbird migration following inherited geomagnetic headings, for migratory orientation programs with or without geomagnetic signposts. Evolution of actual migratory routes depends on many extrinsic and intrinsic factors, often related to energetic considerations (2,17,19,21). Since this could complicate model implementation and interpretation for many known migratory populations, we chose a relatively basic modelled migratory system of a population of the northern wheatear (*Oenanthe oenanthe leucorhoa*, hereafter *leucorhoa* wheatear), a small songbird. *Leucorhoa* wheatears face a single overriding energetic bottleneck, the Atlantic Ocean (47–49), while negotiating a large-scale region with strong geomagnetic gradients (33) in a rapidly shifting geomagnetic landscape (30). We compared the model's predictions with real migratory data of wild, free-flying *leuorhoa* wheatears (48,50–52). Our study provides a general assessment whether inherited migratory programs based on geomagnetic as opposed to geographic headings can be viable across large-scale geomagnetically varying region (3,35) and whether migratory populations can adapt to global changes of a key migration cue in their environment.

Methods

Model overview:

We extended our spatially explicit migration framework (11) to account for entire populations, long-term changes (1900-2015) in the geomagnetic field (42). To determine viable inherited headings and signposts, we used an evolutionary programming algorithm (45). The migration model

component simulates compass courses based on imperfect flight-steps, as in (11), but also considers flight-energy constraints (potential flight hours), and variable flight hours, e.g., to stop at coastlines when over water (see Migration rules). Precision among circular data (headings and geomagnetic inclination) were calculated using von Mises distributions, the circular equivalent to a normal distribution with circular concentration κ (53), but are listed in degrees (σ) following (11) according to $\sigma = 180\sqrt{\kappa}/\pi$. We considered a 15° default precision among flight-steps (11,54,55), and conservative estimates of 5° for precision in gauging inclination (56) and 2% in gauging intensity, i.e., ca. 5000 nT at mid-latitudes (43,54). For sensitivity analysis, these parameters were varied to include 5°-45° directional precision among flight-steps, 1-25° precision in gauging inclination, and 1-10% in inclination.

Since we were specifically interested in the success of inexperienced migrants, modelled birds for each year were inherited from successfully arriving individuals at the wintering destination from the previous year (see Evolutionary programming algorithm). We did not account for how success or mortality affects population size or distribution, i.e., the model re-populated the same locations and number of individuals in each year based on natal dispersal. Each migratory orientation program was assessed by long-term geometric mean in arrival success over the 116-year simulated period (36; geometric means reflect heightened negative effects of infrequent low success). To achieve a stable population adapted to the geomagnetic field in the first modelled year (1900), we first ran a preliminary model "spin-up", analogous to in climate models (57) and to previous migration models incorporating evolved traits (16,58). We allowed the model to "spin up" for 150 years, for the first 75 years using geomagnetic data from a random year, and the last 75 years using geomagnetic data from the first year (1900).

The code was also optimized to compute several processes in parallel for the entire modelled population, e.g., the selection of closest locations on land using the Climate Data Toolbox for

MATLAB (59), the incident geomagnetic field for each flight-step using MATLAB package igrf (60), and to determine population (trait) mixing at each location among successfully arriving migrants for each year simulated.

Evolutionary programming algorithm:

Following each year of simulated migration, two successful "parent" individuals were randomly selected for each departure location (with replacement), with probabilities weighted by the distance between their natal location and the new breeding location, i.e., their natal dispersal distance (40). To promote population mixing, the same location was excluded if individuals from other candidate locations were available (i.e., had non-zero probabilities). A half-Gaussian probability with this distance (default mean displacement $R_N = 25$ km) was assumed, but this was varied between 50 m and 625 km as a sensitivity analysis (41,61). For the half-normal distribution, relative probabilities between two natal dispersal distances (i.e., among candidate "parents") can be assessed using the standard deviation, which can be derived from the mean as $\sigma_N = R_N \cdot \sqrt{\pi/2}$ (53). To accelerate convergence of adaptive headings and variability in headings during the model spin-up, selection of candidate pairs of "parental" migrants was further weighted by the relative proximity of their standard deviation in inheritance of headings (i.e., multiplied by a weight of zero when maximally different and a weight of one when identical). To allow evolution along any plausible route between the natal and wintering grounds, we populated the model for the first (spin-up) year with a broad range of headings and signposts. Specifically, inherited headings were set to a population mean value based on all departure locations and randomly sampled locations within the arrival area, plus a random offset to this mean. The offsets were determined using von Mises (random normal) headings within 180° of the mean heading, from a pool of headings with directional (von Mises) concentration based on the upper quartile of the difference between all rhumbline and great circle headings between the departure and sampled arrival locations (these arrival locations were only used to populate initial headings in the first year, i.e., were further not used during model

evolution). For signposted migration programs, second headings were distributed randomly from this pool among individuals. Initial population values for inherited signposts were selected as a random geomagnetic value between the departure and sampled location, plus a noise term calculated using, for inclination signposts, a von Mises distribution based on the default (5°) precision in gauging intensity signposts, or a normal distribution based on the default (2%) precision in gauging intensity signposts.

For the return at the breeding area, we assumed that parental migratory traits are passed on to the next generation as an average (7,39), together with stochastic variation (36,62). Since stochastic variability in inheritance of migratory orientation can be adaptive (36,37), we also included a standard deviation for both inheritance of headings and signposts as evolved traits. Standard deviations in inheritance of inherited headings were initially randomly populated between 0.5-5°. For inclination signposts, initial standard deviation in inheritance fell between 1-5° for inclination signposts and 0.2-1% for intensity signposts. This mixing of evolved "parental" traits mimics natural selection and can converge on adaptive values, but may not reflect the actual processes involved in inheritance of traits (e.g., stochastic variability in inheritance will presumably be constrained by molecular mechanisms, 63).

Modelled migration system

Juvenile *leucorhoa* wheatears migrate independently from high-latitude natal areas in North-East Canada, Greenland and Iceland (between 13°-80° W and 55°-84°N) to sub-Sahelian West Africa, often detouring via Europe (50–52). Initial departure locations were randomly-selected from within the natal region, based on interpolated landcover data within a 1° by 1° latitude (64). Locations were chosen with no more than 15% barren habitat and at least 10% low vegetation. This produced very similar range to that found in the literature (51,65). Migrants were considered successful if they arrived in Africa between 20°W - 5°E and 5°-15°N (48,49,65). For signposted migration,

successful arrival did not require signposted thresholds to be encountered, i.e., did not require a switch in heading *en route* (inherited signpost values were subsequently averaged among successful migrants regardless of use).

Migration rules

Long-distance bird migration usually requires extended periods of stopover to acquire needed energy reserves, typically following several consecutive (nightly) bouts of flight (66–69). Away from water, modelled migrants were assumed to fly between 90 minutes after civil dusk to 90 minutes before civil dawn (70,71), calculated using the algebraic formula for sunset in the Suppl. Material of (11), for minimally 6 hours and maximally 12 hours. *Leucorhoa* wheatears are further known to accumulate large energy reserves in fall to cross the Atlantic (50), to potentially even directly reach Africa in upwards of 72 hours of non-stop tailwind-assisted flight (49,51, and see Comparison with migration data). We here took a simple but conservative approach of initially providing migrants with enough energy to fly 48-72 hours (uniformly distributed, equivalent to 62-106% relative gain in body mass, 47,68). Flight ranges were refreshed in the model following any stopover whenever potential flight ranges fell below three times the nightly flight duration, or following flight-steps which were initiated over water. If found over water at dawn, modelled individuals stopped at the nearest viewable coastal point (on a ca. 20-km grid), which was identified at each of the last 3 deciles of the nightly flight, based on a detection probability which decreased linearly with increasing distance up to 300 km (i.e., land immediately on the coast was always detectable, to 50% of the time at 150 km, to never beyond 300 km). If no land was in sight, migrants flew until the next dusk, stopping at any viewable coastal point at each decile of flight, or flying until energy reserves were depleted (mortality).

Birds flew at constant ground speeds of 15 m/s (70,72) following a constant geographic compass-headings through the night, i.e., following a star compass. This is consistent with migrants not

updating their preferred heading relative to changing magnetic parameters while aloft (31,73,74). Using a geomagnetic rather than star compass in the model for nocturnal flights produced very similar results.

Comparison with migration data:

The exact routes of *leucoroha* wheatears are not well known, but ship and coastal observations (75,76), ring-recovery data (50–52) and a single geolocator track (48) indicate that they typically detour from Iqaluit to North-West Europe (via the UK, 48) or from SW Greenland to South-West Europe (mean departure and arrival latitude 64°-43°N, 50). The average latitude among European ringing stations where *leucorhoa* wheatears were recovered in fall was 53.9°N (52), which was very similar to the estimated arrival in Europe (ca. 54°N) for the Iqaluit individual tracked using geolocation (48). However, given extreme pre-migratory fattening by *leucoroha* wheatears in the Nearctic (50), a direct crossing to Africa from the Southern end of their range is feasible and possibly used, involving upwards of 72 hours non-stop flight (49,51). We assessed model-evolved individuals from SW Greenland (60°-70°N, 45°-55°W) and S Iqaluit (62.5°-66°N, 60°-72.5°W) according to arrival success (in 2015) and by comparing discrepancies between mean arrival latitudes of free-flying migrants to Europe, to latitudes where signposts were encountered among successful modelled migrants, or to the latitude of first arrival to Europe (excluding Iceland) among non-signposted modelled migrants. This comparison was made since it is likely both the possibility to recapture a tagged (ringed) migrant, and the possibility for a bird to update its preferred headings, are more likely to occur during extended stopover periods.

Results

For wheatear migration to West Africa, migratory programs with inherited signposts were always successful (>50% arrival in each year), and were robust to 116-year changes in the geomagnetic field (<1% standard deviation in arrival success among years). Fig. 1 depicts sample trajectories of

from 2015 for each migratory program following the 116-year model evolution, based on default model parameters (see Model overview). With non-signposted migration (Fig. 1a), mortality was high over the Atlantic, especially from South-Eastern Canadian natal locations, except where trajectories came within sight of the Azores, permitting a stopover. This was also somewhat true for inclination-signposted migration (Fig. 1b), but intensity-signposted migration (Fig. 1c) evolved to consistently avoid the longest non-stop routes. Over the 116-year period, intensity-signposted migration was always the most successful (geometric mean and standard deviation among years 77.2±0.2%), with intensity-signposted program more successful (58.4±0.3%) compared with non-signposted migration (36.9±0.2%).

This long-term consistency and hierarchy in arrival success among the three migratory orientation programs was maintained across a broad range in mean natal dispersal (Fig. 1d-e, with the circle depicts the default scenario with population-mean natal dispersal of 25 km). Similarly, all three migratory programs were relatively robust to the degree of precision among flight-steps (Fig. 2a) or in gauging inclination and intensity to identify signposts (Fig. 2b). As precision among flight-steps decreased, so too did arrival success and also the differences in performance among migratory programs (Fig. 2a). Contrastingly, signposted migration was robust to a broad and conservative range in precision of gauging both inclination and intensity signposts (Fig. 2b). We also tested alternatives to the default inheritance of geomagnetic rather than geographic headings, and when nocturnal flights followed a geomagnetic rather than (default) star compass, keeping other parameters at default values. Intensity-signposted migration based on geographic inheritance was significantly less successful (62±0.3% compared with 77%±0.2%), but using a geomagnetic rather than star compass during flight had little effect on arrival success (79±0.3%).

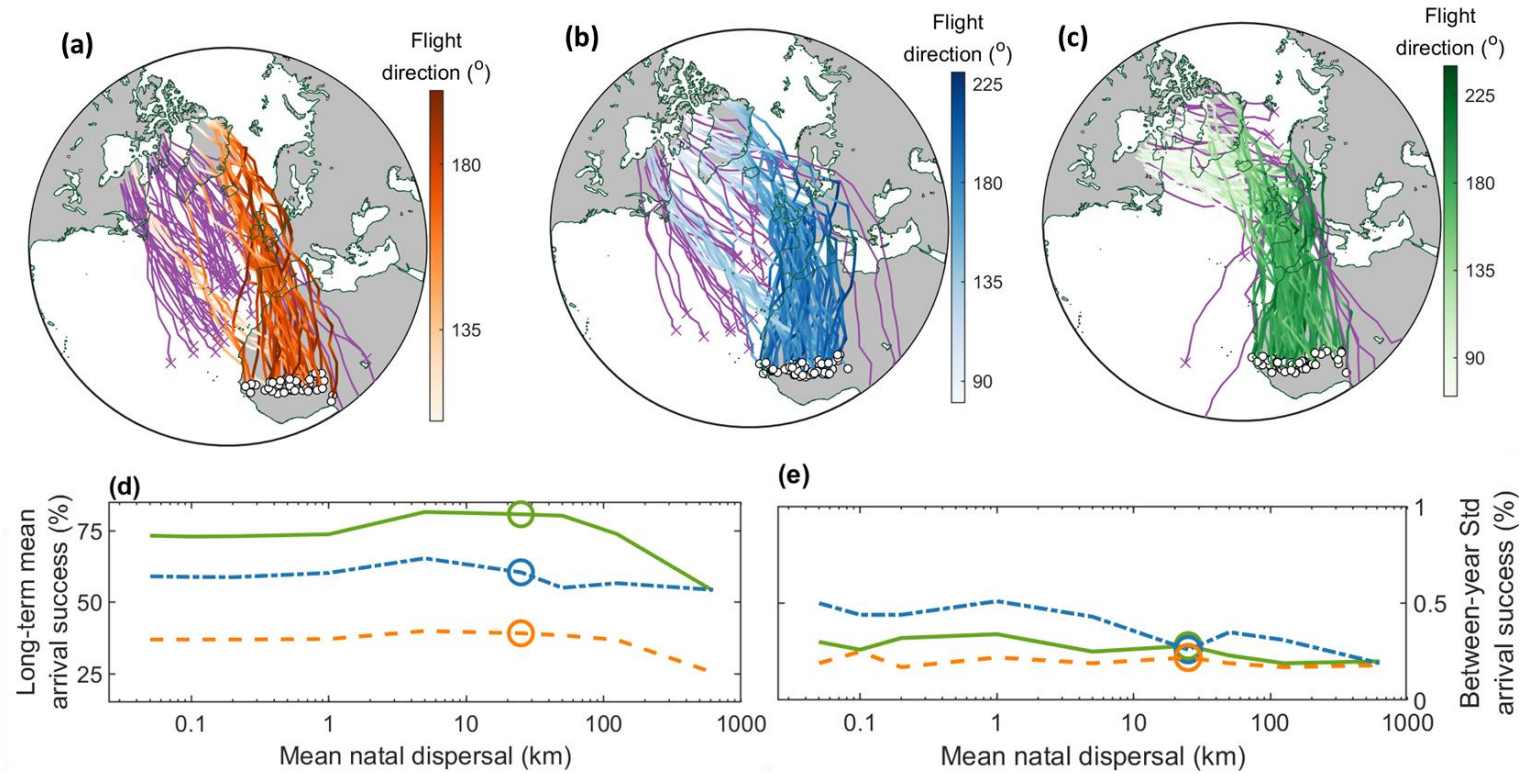

Figure 1: Predicted migratory flight trajectories and arrival success of juvenile (naïve) Atlantic-crossing northern wheatears (*Oenanthe oenanthe leucorhoa*) migrating from the breeding areas to the sub-Sahelian African wintering grounds. Randomly-sampled trajectories from 2015 are depicted, for model-evolved migration (1900-2015) based on (**a**) non-signposted migration, following a constant inherited geomagnetic heading (orange lines), (**b**) a geomagnetic signpost based on inclination (blue lines) and (**c**) a signpost based on geomagnetic intensity (green lines). The results in (a)-(c) are with default model parameters (see Methods). For (**b**) and (**c**), encountering a signpost (inherited threshold geomagnetic value) triggers a shift to a second model-evolved inherited heading. For successfully arriving individuals (white circles), flight directions (degrees clockwise from geographic North) are colour-coded (scales on right of each panel), with purple lines depicting unsuccessful migration and purple crosses mortality. (**d**) Long-term geometric mean arrival success (1900-2015) and (**e**) standard deviation in success among years are shown for each migratory orientation program, colour-coded as in (a)-(c), as a function of the mean dispersal radius (with results for the 25-km default mean circled. Note how, even without signposts (a), geographic flight directions for migrants departing close to magnetic North pole shift across the strong geomagnetic gradient (straight lines represent direction-changing great circle routes in the stereographic projection).

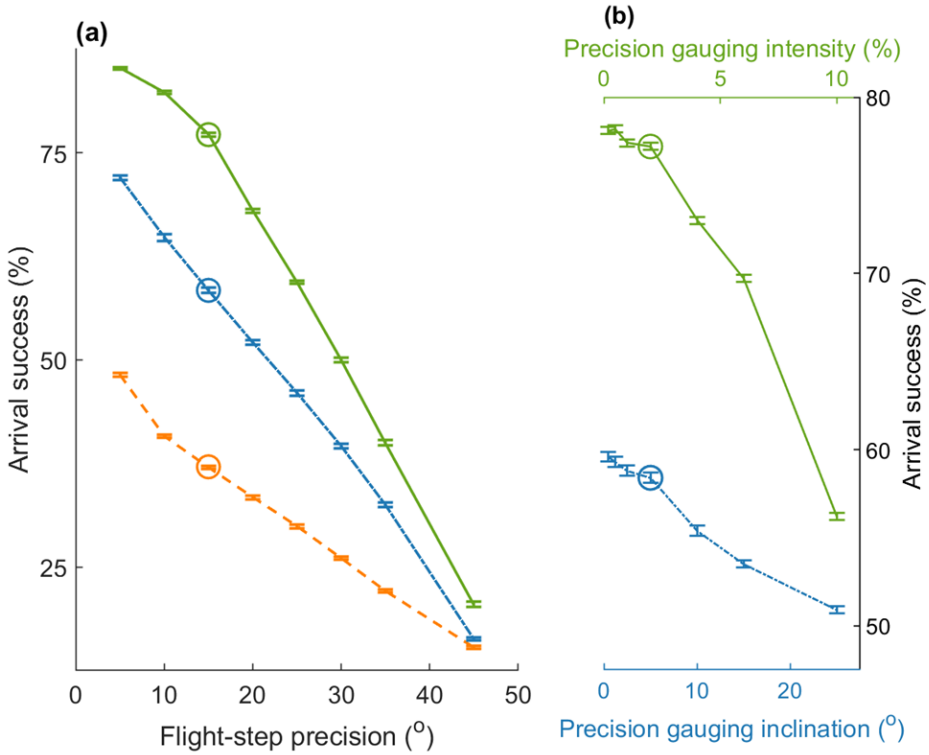

Figure 2. Robustness of modelled geomagnetic-based migration to precision among flight-steps and in gauging signposts. (**a**) Long-term mean arrival success, and standard deviation among years, for non-signposted migration (orange dashed line), and signposted migration based on inclination (dot-dashed blue line) and intensity (solid green line), versus precision among flight-steps (degrees), with the default (15º) depicted with circles. (**b**) For simulations with default precision among flight-steps, long-term mean and standard deviation in arrival success versus the precision in gauging signposts based on inclination (lower x-axis, in degrees, and dot-dashed blue line), and based on intensity (upper x-axis, in percent intensity, and solid green line). Here the circled values represent model default values (5º in inclination and 2% in intensity). For this sensitivity analysis, a mean natal dispersal of 100 km was used.

For migration commencing from the far Western natal regions (SW Greenland and S Iqaluit), the three migratory programs contrasted strongly regarding arrival success and consistency with migratory data from free-flying *leucorhoa* migrants (48,50,52). As shown in Fig. 3 and Table 1, non-signposted migration in 2015 from these two areas performed by far the most poorly in arriving to Africa (<25% arrival), yet best fit the data of Greenland-born migrants both regarding arrival latitude in Europe and initial flight headings (50). Latitudes of signpost locations fell generally to the North of the data, but inclination-signposted migration most closely fit the Iqaluit track (Bairlein) and ring-recovery stations (52). On the other hand, intensity-signposted locations were more tightly centred in North and Western Europe, similarly to known *leucorhoa* migration observations (52,65) . More generally, signpost locations for the entire modelled population remained consistent throughout the 116-year simulation (Suppl. Fig. 1), with intensity signpost locations centred around the North Sea area, and inclination signpost locations more widely spread between Britain and the Iberian Peninsula. Lastly, some signposted populations were not required to change their heading to reach the wintering grounds so that theoretically routes without a signpost could evolve (Suppl. Fig. 1). This was especially the case among inclination-signposted migrants for breeding locations both in the eastern (Iceland and East Greenland) and northern breeding limits (North Greenland and the Canadian high arctic).

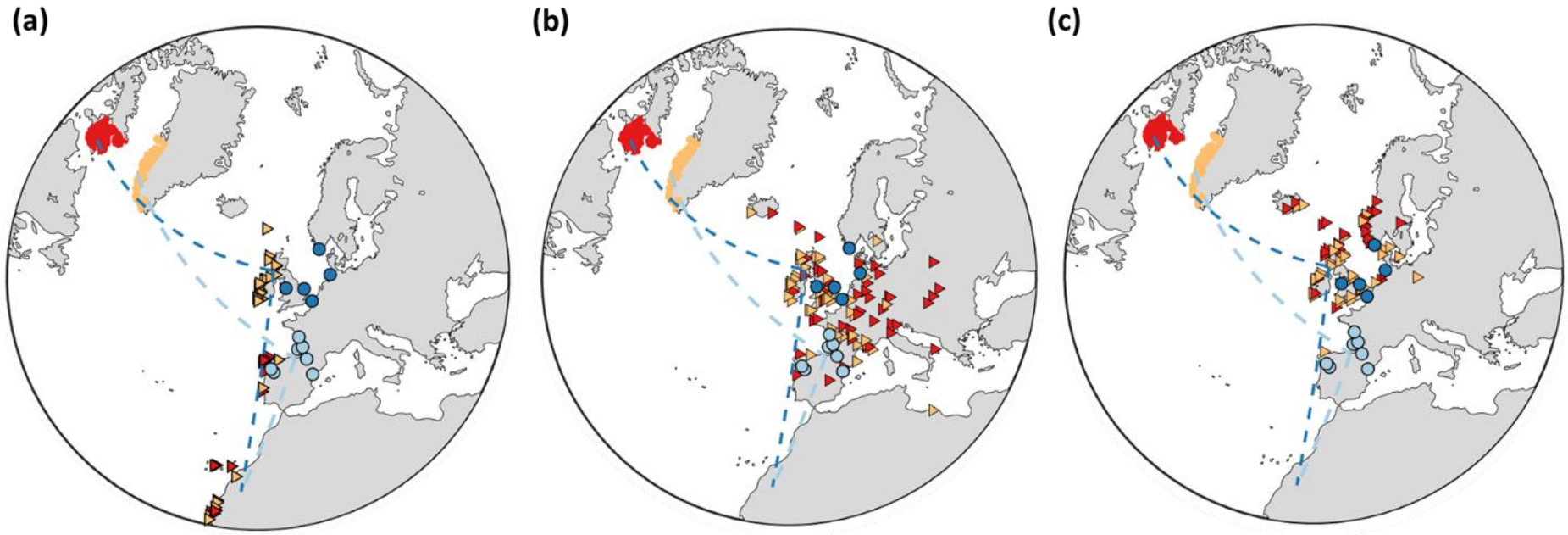

Figure 3: Predicted routes (in 2015) of migrating wheatears (*Oenanthe oenanthe leucorhoa*) from natal regions in SW Greenland (light-orange shaded area) and S Iqaluit (red-shaded region), with comparison of modelled stopover locations in Europe with observations and tracking, for (**a**) first arrival on land with in Europe for non-signposted migration, and signpost locations triggering switches in headings with migration based on (**b**) inherited geomagnetic intensity signposts and (**c**) inherited intensity signposts. Filled triangles represent randomly chosen locations of signposted switches in heading among successful modelled individuals (2015), colour-coded to natal location. Actual locations (bird-ringing stations) of recovered northern wheatears (*Oenanthe oenanthe leucorhoa*) originating from the North-West Atlantic are depicted with dark blue circles (52), and the dark-blue dashed line represents the most likely trajectory of a single wheatear tracked with geolocation from Iqaluit, Canada to West Africa (48). Recoveries of fledgling wheatears banded in SW Greenland (50) are depicted as light-blue circles, with the light-blue dashed line representing a constant-heading route between the centroid of the capture and recovery locations (N=7) and another constant-heading route to W Africa. See Table 1 for a comparison of arrival success and proximity of modelled to observed locations.

Table 1: Arrival success and proximity of geomagnetic-based migration vs. actual flown routes through Europe. For modelled departures from SW Greenland (60°-70°N, 45°-55°W) and S Iqaluit (62.5°-66°N, 60°-72.5°W), performance (% arrival success in 2015), estimated latitude in Europe (signposted locations, or first landing points for non-signposted migration) and, for migration from SW Greenland, initial (geographic) flight directions. For comparison with data of free-flying *leuco-roha* wheatears in Europe (48,50,52), discrepancies in arrival latitude and initial flight direction were scaled by the standard deviation in these quantities in the model among successful individuals. Highest performance and closest proximity among the three migratory programs are depicted in bold font, and lowest performance and least close proximity in italics. Positive discrepancies represent modelled stopovers to the North of the (inferred) actual routes, and positive headings are clockwise from observed orientation (circular mean 144° in 50).

	SW Greenland – Europe			**S Iqaluit – Europe**	
Migratory orientation program	Arrival success (%)	Arrival latitude to Europe (°) / Discrepancy (-)	Initial flight direction (°) / Discrepancy (-)	Arrival success (%)	Arrival latitude to Europe (°) / Discrepancy (-)
Non-signposted	*22*	**40°±15° / -0.2**	**122°±17° / -1.3**	*17*	*28°±11° / -2.4*
Inclination-signposted	83	56°±4° / 3.1	108°±22° / -1.6	68	**56°±5° / 0.5**
Intensity-signposted	**92**	*58°±4° / 3.8*	*97°±23° / -2.0*	**84**	59°±4° / 1.2

The adaptive benefit of stochastic variability in inheritance of headings (36) is supported by the model-evolved standard deviation (variability) in inheritance of both flight headings (Fig. 4a) and signposts (Fig. 4b). The population-mean variability in both headings and signposts (left y-axes and solid lines) remained fairly constant across the tested range in mean natal dispersal (50 m – 625 km). Contrastingly, the standard deviation within the population of this variability in inheritance (right axes and dashed lines) decreased as the natal dispersal increased, reflecting population mixing affecting local variability in inheritance. This was especially true for signposts (right y-axes in Fig. 4b), suggesting that population mixing in inherited headings is more locally constrained than for signposts in this model migration system.

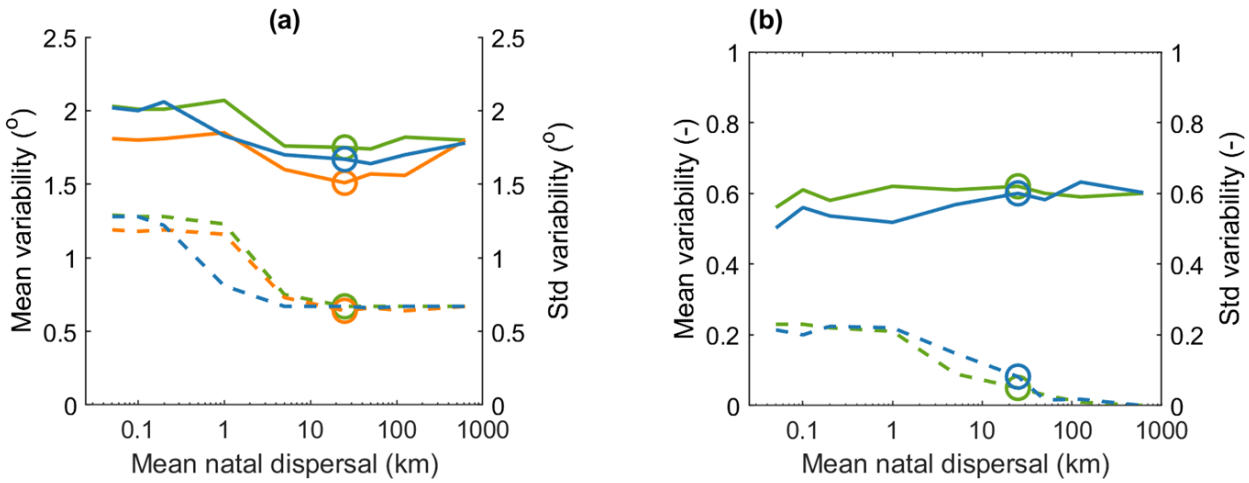

Figure 4.

Population mixing in evolved variability (i.e., standard deviation) in inheritance of migratory headings and signposts, versus population-mean natal dispersal (x-axis, in km). (**a**) Model-evolved population-mean (left y-axis and solid lines) and within-population standard deviation (right y-axis and dashed lines) in (stochastic) variability in inheritance of headings, for non-signposted migration (orange lines), inclination-signposted migration (blue lines) and intensity-signposted migration (green lines). The circled values represent model defaults of 25-km mean dispersal. (**b**) as in (a), but for model-evolved variability in inheritance of inclination signposts (blue lines) and intensity signposts (green lines). Here both y-axes have been scaled to the maximum allowable modelled variability (here for the model default of 5° for inclination and 1% for intensity).

Discussion

This study represents a first spatiotemporal analysis of how detours in migratory trajectories can evolve based on inherited geomagnetic signposts and adapt to a dynamic geomagnetic landscape. This supports the idea that proximate magnetic cues can provide a spatiotemporally robust cue, not only to calibrate nightly headings, but also as signposts to guide inexperienced migrants along detoured, compass-shifting routes. This may be important to migratory populations where naïve migrants travel independently, since it offers the possibility to combine headings between historic and novel routes, for example shaped by shifting habitat suitability and climate refugia (20,77). We also note that the geomagnetic field can therefore also play an important role in the evolution of migration routes even when these are based on a primary celestial compass, such as a sunset compass or star compass (the former likely being particularly advantageous over long-distance and high-latitude routes, 10,11).

For *leucorhoa* wheatears in particular, geomagnetic signposts would clearly be of adaptive benefit, given the significant hazard involved in direct flights to Africa (49). Nonetheless, the robustness of modelled migration based on geomagnetic headings across the rapidly-shifting geographic North pole region is somewhat remarkable. The fact that geographic inheritance of headings resulted in lower arrival success suggests that the strong spatial gradients in this region can actually be adaptive (cf. 35) rather than a hazard (cf. 33). The robustness of arrival success to the precision in gauging signposts (Fig. 2b) may also reflect the broad migration route and (modelled) flexibility of this generalist migrant. While no one migratory orientation program reproduced the known location and orientation data of migrating *leucorhoa* wheatears from both Greenland and Iqaluit, this is not unexpected given the simple model approach used. The degree to which migration would actually favour longer ocean crossings (e.g., to the Iberian Peninsula rather than the North Sea) will be contingent on reliability of winds, sufficient fuel reserves and avoidance of hazards further North (colder weather, longer migration and exposure to predation).

The exact nature of the geomagnetic compass mechanism, in particular how the perceived magnetic signal varies with configurations of the geomagnetic field and migrant's body orientation (78,79), remain uncertain. However, geomagnetic intensity and inclination seem the most likely components, since intensity will amplify the received signal (80) and a discernible (though not necessarily precisely measurable) inclination angle is required to break the N-S symmetry of the geomagnetic axes (3,25). Geomagnetic declination, which quantifies the discrepancy between the local geomagnetic and geographic axes, cannot be counted out as a cue among experienced migrants (81), but would require an ability to precisely distinguish between geographic and geomagnetic poles. Doing so may be problematic if naïve migrants need to compare magnetic fields close to dark (80,82) with celestial cues while on the move (11,83). Hence, it is more reasonable to conjecture that inexperienced migrants use inclination or intensity, both readily available whenever the magnetic compass is useable.

While the evidence is strong that naïve migrants do adjust their orientation to the Earth's magnetic field, it is important to consider why inexperienced migrants might use a geomagnetic signpost to mediate detours, rather than rely on other ecologically-relevant environmental cues such as habitat quality (19) or topography (16,84). While these are clearly important underlying factors, they may not always be reliable or unambiguous in negotiating long-distance routes. For example, given the prevalence of *leucoroha* wheatears to stop in Iceland and Northern Europe (73,74,83), reorientation to the South or following an ocean crossing could lead to frequent misorientation (e.g., heading directly South or following coastlines might be adaptive after reaching France or Spain, but not Iceland or Sweden). Certainly, coastal, habitat and olfactory cues are adaptive during the narrowing-in or homing phase of migration (3), but could also strengthen or modulate an inherited migratory orientation program during the long-distance phase (16,85).

As an alternative to a clock-and-compass migratory orientation program, it has been proposed that naïve migrants might be able to perform navigation by following gradients in the geomagnetic field (4,28). However, this would result either tend to produce nearly N-S routes following large-scale inclination or intensity gradients, or else involve interpolation between often nearly-parallel inclination and intensity gradients (27,86). The simpler possibility considered in our current study may, when compared with such naïve navigational abilities, be less robust to errors in some cases for individual migrants, but may also be more flexible from a sensory perspective, as well as easier to evolve and maintain through natural selection.

Little is known regarding the population consequences of how migratory headings are transmitted across generations (13,63,87). Our methods open new doors for analysing and interpreting migratory orientation data, exploring evolution of historic and novel migration routes, migratory connectivity between non-breeding and breeding areas (88–90), and how spatial sensitivity or robustness to endogenous headings could affect resilience to climate change. Our methods can also be extended to include and assess other geophysical cues (e.g., sun azimuth) and flexible reaction to other environmental factors (21,69,70,91). In this way, the geomagnetic field may possibly play a vital role in the evolution of migration routes, as mediator between proximate environmental cues and ultimate drivers of population fitness through migratory success.

1. Dingle H, Drake VA. What Is Migration? BioScience. 2007 Feb 1;57(2):113–21.

2. Alerstam T, Hedenström A, Åkesson S. Long-distance migration: evolution and determinants. Oikos. 2003;103(2):247–60.

3. Mouritsen H. Long-distance navigation and magnetoreception in migratory animals. Nature. 2018 Jun;558(7708):50–9.

4. Lohmann KJ, Goforth KM, Mackiewicz AG, Lim DS, Lohmann CMF. Magnetic maps in animal navigation. J Comp Physiol A. 2022 Jan 1;208(1):41–67.

5. Wynn J, Padget O, Mouritsen H, Perrins C, Guilford T. Natal imprinting to the Earth's magnetic field in a pelagic seabird. Current Biology. 2020 Jul;30(14):2869-2873.e2.

6. Wynn J, Padget O, Mouritsen H, Morford J, Jaggers P, Guilford T. Magnetic stop signs signal a European songbird's arrival at the breeding site after migration. Science. 2022 Jan 28;375(6579):446–9.

7. Berthold P. Control of Bird Migration. Springer Science & Business Media; 1996. 370 p.

8. Alerstam T, Pettersson SG. Orientation along great circles by migrating birds using a sun compass. Journal of Theoretical Biology. 1991 Sep;152(2):191–202.

9. Åkesson S, Bianco G. Route simulations, compass mechanisms and long-distance migration flights in birds. J Comp Physiol A. 2017 Jul;203(6–7):475–90.

10. Muheim R, Schmaljohann H, Alerstam T. Feasibility of sun and magnetic compass mechanisms in avian long-distance migration. Mov Ecol. 2018 Dec;6(1):8.

11. McLaren JD, Schmaljohann H, Blasius B. Self-correcting Sun Compass, Spherical Geometry and Cue-transfers Predict Naïve Migratory Performance [Internet]. 2021 [cited 2022 Jun 30]. Available from: https://www.researchsquare.com

12. Mouritsen H, Mouritsen O. A Mathematical Expectation Model for Bird Navigation based on the Clock-and-Compass Strategy. Journal of Theoretical Biology. 2000 Nov;207(2):283–91.

13. Thorup K, Rabøl J, Erni B. Estimating variation among individuals in migration direction. Journal of Avian Biology. 2007 Mar;38(2):182–9.

14. McLaren JD, Shamoun-Baranes J, Dokter AM, Klaassen RHG, Bouten W. Optimal orientation in flows: providing a benchmark for animal movement strategies. J R Soc Interface. 2014 Oct 6;11(99):20140588.

15. Sergio F, Barbosa JM, Tanferna A, Silva R, Blas J, Hiraldo F. Compensation for wind drift during raptor migration improves with age through mortality selection. Nat Ecol Evol. 2022 Jun 9;1–9.

16. Erni B, Liechti F, Bruderer B. How Does a First Year Passerine Migrant Find Its Way? Simulating Migration Mechanisms and Behavioural Adaptations. Oikos. 2003;103(2):333–40.

17. Alerstam T. Detours in Bird Migration. Journal of Theoretical Biology. 2001 Apr 7;209(3):319–31.

18. Cohen EB, Barrow WC, Buler JJ, Deppe JL, Farnsworth A, Marra PP, et al. How do en route events around the Gulf of Mexico influence migratory landbird populations? cond. 2017 May;119(2):327–43.

19. Thorup K, Tøttrup AP, Willemoes M, Klaassen RHG, Strandberg R, Vega ML, et al. Resource tracking within and across continents in long-distance bird migrants. Science Advances. 2017 Jan 4;3(1):e1601360.

20. Thorup K, Pedersen L, da Fonseca RR, Naimi B, Nogués-Bravo D, Krapp M, et al. Response of an Afro-Palearctic bird migrant to glaciation cycles. Proc Natl Acad Sci USA. 2021 Dec 28;118(52):e2023836118.

21. Shamoun-Baranes J, Liechti F, Vansteelant WMG. Atmospheric conditions create freeways, detours and tailbacks for migrating birds. J Comp Physiol A. 2017 Jul;203(6–7):509–29.

22. Gill JA, Alves JA, Gunnarsson TG. Mechanisms driving phenological and range change in migratory species. Phil Trans R Soc B. 2019 Sep 16;374(1781):20180047.

23. Gwinner E, Wiltschko W. Endogenously controlled changes in migratory direction of the garden warbler,Sylvia borin. J Comp Physiol. 1978 Sep 1;125(3):267–73.

24. Laundal KM, Richmond AD. Magnetic Coordinate Systems. Space Sci Rev. 2017 Mar;206(1–4):27–59.

25. Wiltschko R, Wiltschko W. Avian Navigation: A Combination of Innate and Learned Mechanisms. In: Advances in the Study of Behavior [Internet]. Elsevier; 2015 [cited 2021 Feb 5]. p. 229–310. Available from: https://linkinghub.elsevier.com/retrieve/pii/S0065345414000047

26. Rakhimberdiev E, Karagicheva J, Jaatinen K, Winkler DW, Phillips JB, Piersma T. Naïve migrants and the use of magnetic cues: temporal fluctuations in the geomagnetic field differentially affect male and female Ruff *Philomachus pugnax* during their first migration. Bauer S, editor. Ibis. 2014 Oct;156(4):864–9.

27. Nichols S, Havens L, Taylor B. Sensation to navigation: a computational neuroscience approach to magnetic field navigation. J Comp Physiol A Neuroethol Sens Neural Behav Physiol. 2022 Jan;208(1):167–76.

28. Taylor BK, Corbin S. Bioinspired magnetoreception and navigation in nonorthogonal environments using magnetic signatures. Bioinspir Biomim. 2019 Sep 24;14(6):066009.

29. Witze A. Earth's magnetic field is acting up and geologists don't know why. Nature. 2019 Jan 9;565(7738):143–4.

30. Livermore PW, Finlay CC, Bayliff M. Recent north magnetic pole acceleration towards Siberia caused by flux lobe elongation. Nat Geosci. 2020 May;13(5):387–91.

31. Cochran WW. Migrating Songbirds Recalibrate Their Magnetic Compass Daily from Twilight Cues. Science. 2004 Apr 16;304(5669):405–8.

32. Sjöberg S, Muheim R. A New View on an Old Debate: Type of Cue-Conflict Manipulation and Availability of Stars Can Explain the Discrepancies between Cue-Calibration Experiments with Migratory Songbirds. Front Behav Neurosci [Internet]. 2016 Feb 23 [cited 2021 Feb 5];10. Available from: http://journal.frontiersin.org/Article/10.3389/fnbeh.2016.00029/abstract

33. Kok EMA, Tibbitts TL, Douglas DC, Howey PW, Dekinga A, Gnep B, et al. A red knot as a black swan: how a single bird shows navigational abilities during repeat crossings of the Greenland Icecap. Journal of Avian Biology [Internet]. 2020 [cited 2022 Jun 30];51(8). Available from: https://onlinelibrary.wiley.com/doi/abs/10.1111/jav.02464

34. Zein B, Long JA, Safi K, Kölzsch A, Wikelski M, Kruckenberg H, et al. Simulation experiment to test strategies of geomagnetic navigation during long-distance bird migration. Movement Ecology. 2021 Sep 15;9(1):46.

35. Alerstam T. Evaluation of Long-Distance Orientation in Birds on the Basis of Migration Routes Recorded by Radar and Satellite Tracking. J Navigation. 2001 Sep;54(3):393–403.

36. Reilly JR, Reilly RJ. Bet-hedging and the orientation of juvenile passerines in fall migration: Bet-hedging in passerine migration. Journal of Animal Ecology. 2009 Jul 29;78(5):990–1001.

37. Wagner GP, Altenberg L. Perspective: Complex Adaptations and the Evolution of Evolvability. Evolution. 1996;50(3):967–76.

38. Delmore K, Illera JC, Pérez-Tris J, Segelbacher G, Lugo Ramos JS, Durieux G, et al. The evolutionary history and genomics of European blackcap migration. Scordato E, Wittkopp PJ, editors. eLife. 2020 Apr 21;9:e54462.

39. Delmore KE, Fox JW, Irwin DE. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society B: Biological Sciences. 2012 Nov 22;279(1747):4582–9.

40. Weatherhead PJ, Forbes MRL. Natal philopatry in passerine birds: genetic or ecological influences? Behavioral Ecology. 1994 Dec 1;5(4):426–33.

41. Claramunt S. Flight efficiency explains differences in natal dispersal distances in birds. Ecology. 2021;102(9):e03442.

42. Thébault E, Finlay CC, Beggan CD, Alken P, Aubert J, Barrois O, et al. International Geomagnetic Reference Field: the 12th generation. Earth Planet Sp. 2015 Dec;67(1):79.

43. Komolkin AV, Kupriyanov P, Chudin A, Bojarinova J, Kavokin K, Chernetsov N. Theoretically possible spatial accuracy of geomagnetic maps used by migrating animals. J R Soc Interface. 2017 Mar;14(128):20161002.

44. Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology. 2011;80(1):4–18.

45. Boone RB. Evolutionary computation in zoology and ecology. Current Zoology. 2017 Dec 1;63(6):675–86.

46. Eiben AE, Smith JE. Introduction to Evolutionary Computing. Berlin: Springer; 2010. 315 p.

47. Delingat J, Bairlein F, Hedenström A. Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (Oenanthe oenanthe). Behav Ecol Sociobiol. 2008 May;62(7):1069–78.

48. Bairlein F, Norris DR, Nagel R, Bulte M, Voigt CC, Fox JW, et al. Cross-hemisphere migration of a 25 g songbird. Biol Lett. 2012 Aug 23;8(4):505–7.

49. Bulte M, McLaren JD, Bairlein F, Bouten W, Schmaljohann H, Shamoun-Baranes J. Can wheatears weather the Atlantic? Modeling nonstop trans-Atlantic flights of a small migratory songbird. The Auk. 2014 Jul;131(3):363–70.

50. Ottosson U, Sandberg R, Pettersson J. Orientation Cage and Release Experiments with Migratory Wheatears (Oenanthe oenanthe) in Scandinavia and Greenland: The Importance of Visual Cues. Ethology. 1990;86(1):57–70.

51. Thorup K, Ortvad TE, Rabøl J. DO NEARCTIC NORTHERN WHEATEARS (OENANTHE OENANTHE LEUCORHOA) MIGRATE NONSTOP TO AFRICA? :6.

52. Schmaljohann H, Meier C, Arlt D, Bairlein F, van Oosten H, Morbey YE, et al. Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. Behavioral Ecology. 2016 Jan 1;27(1):321–31.

53. Mardia KV. Statistics of Directional Data. Journal of the Royal Statistical Society Series B (Methodological). 1975;37(3):349–93.

54. Chernetsov N. Compass systems. J Comp Physiol A. 2017 Jul;203(6–7):447–53.

55. McLaren JD, Shamoun-Baranes J, Bouten W. Wind selectivity and partial compensation for wind drift among nocturnally migrating passerines. Behavioral Ecology. 2012;23(5):1089–101.

56. Lefeldt N, Dreyer D, Schneider NL, Steenken F, Mouritsen H. Migratory blackcaps tested in Emlen funnels can orient at 85 degrees but not at 88 degrees magnetic inclination. Journal of Experimental Biology. 2015 Jan 15;218(2):206–11.

57. Thornton PE, Rosenbloom NA. Ecosystem model spin-up: Estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. Ecological Modelling. 2005 Nov 25;189(1):25–48.

58. Erni B, Liechti F, Bruderer B. The role of wind in passerine autumn migration between Europe and Africa. Behavioral Ecology. 2005 Jul 1;16(4):732–40.

59. Greene CA, Thirumalai K, Kearney KA, Delgado JM, Schwanghart W, Wolfenbarger NS, et al. The Climate Data Toolbox for MATLAB. Geochemistry, Geophysics, Geosystems. 2019;20(7):3774–81.

60. Compston D. International Geomagnetic Reference Field (IGRF) Model [Internet]. Available from: https://www.mathworks.com/matlabcentral/fileexchange/34388-international-geomagnetic-reference-field-igrf-model

61. Ceresa F, Belda EJ, Monrós JS. Similar dispersal patterns between two closely related birds with contrasting migration strategies. Population Ecology. 2016;58(3):421–7.

62. Hu T, Banzhaf W. Evolvability and Speed of Evolutionary Algorithms in Light of Recent Developments in Biology. Journal of Artificial Evolution and Applications. 2010 Jun 2;2010:e568375.

63. Liedvogel M. Genetics of Animal and Bird Migration. In: Encyclopedia of Animal Behavior [Internet]. Elsevier; 2019 [cited 2021 Aug 5]. p. 323–30. Available from: https://linkinghub.elsevier.com/retrieve/pii/B9780128096338900621

64. Tuanmu MN, Jetz W. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Global Ecology and Biogeography. 2014;23(9):1031–45.

65. Cramp S (chief ed). Handbook of Europe the Middle East and North Africa, Volume 5: Tyrant Flycatchers to Thrushes [Internet]. Oxford: Oxford University Press; 1988 [cited 2022 Jun 30]. Available from: https://www.biblio.com/book/handbook-europe-middle-east-north-africa/d/1336501969

66. Hedenström A, Alerstam T. Optimum Fuel Loads in Migratory Birds: Distinguishing Between Time and Energy Minimization. Journal of Theoretical Biology. 1997 Dec 7;189(3):227–34.

67. Schmaljohann H, Eikenaar C, Sapir N. Understanding the ecological and evolutionary function of stopover in migrating birds. Biological Reviews [Internet]. [cited 2022 Jun 30];n/a(n/a). Available from: https://onlinelibrary.wiley.com/doi/abs/10.1111/brv.12839

68. McLaren JD, Shamoun-Baranes J, Bouten W. Stop early to travel fast: modelling risk-averse scheduling among nocturnally migrating birds. Journal of Theoretical Biology. 2013 Jan;316:90–8.

69. Cohen EB, Horton KG, Marra PP, Clipp HL, Farnsworth A, Smolinsky JA, et al. A place to land: spatiotemporal drivers of stopover habitat use by migrating birds. Ecology Letters. 2021;24(1):38–49.

70. Schmaljohann H, Naef-Daenzer B. Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird: Departure behaviour of free-flying birds. Journal of Animal Ecology. 2011 Nov;80(6):1115–22.

71. Müller F, Taylor PD, Sjöberg S, Muheim R, Tsvey A, Mackenzie SA, et al. Towards a conceptual framework for explaining variation in nocturnal departure time of songbird migrants. Mov Ecol. 2016 Dec;4(1):24.

72. Bruderer B, Boldt A. Flight characteristics of birds: Ibis. 2001;143(2):178–204.

73. Horton KG, Van Doren BM, Stepanian PM, Hochachka WM, Farnsworth A, Kelly JF. Nocturnally migrating songbirds drift when they can and compensate when they must. Sci Rep. 2016 Aug;6(1):21249.

74. ALERSTAM T. Bird Migration Across a Strong Magnetic Anomaly. Journal of Experimental Biology. 1987 Jul 1;130(1):63–86.

75. Snow D. The migration of the Greenland wheatear. Ibis. 1953;95:376–8.

76. Williamson K. Bergmann's rule and obligatory overseas migration. British Birds. 1958;51.

77. Zink RM, Gardner AS. Glaciation as a migratory switch. Science Advances. 2017 Sep 20;3(9):e1603133.

78. Worster S, Mouritsen H, Hore PJ. A light-dependent magnetoreception mechanism insensitive to light intensity and polarization. J R Soc Interface. 2017 Sep;14(134):20170405.

79. Mouritsen H, Feenders G, Liedvogel M, Kropp W. Migratory Birds Use Head Scans to Detect the Direction of the Earth's Magnetic Field. Current Biology. 2004 Nov 9;14(21):1946–9.

80. Xu J, Jarocha LE, Zollitsch T, Konowalczyk M, Henbest KB, Richert S, et al. Magnetic sensitivity of cryptochrome 4 from a migratory songbird. Nature. 2021 Jun;594(7864):535–40.

81. Kishkinev D, Packmor F, Zechmeister T, Winkler HC, Chernetsov N, Mouritsen H, et al. Navigation by extrapolation of geomagnetic cues in a migratory songbird. Current Biology. 2021 Apr;31(7):1563-1569.e4.

82. Hore PJ, Mouritsen H. The Radical-Pair Mechanism of Magnetoreception. Annu Rev Biophys. 2016 Jul 5;45:299–344.

83. Muheim R, Philips JB, Åkesson S. Polarized Light Cues Underlie Compass Calibration in Migratory Songbirds. Science. 2006 Aug 11;313(5788):837–9.

84. Aurbach A, Schmid B, Liechti F, Chokani N, Abhari R. Complex behaviour in complex terrain - Modelling bird migration in a high resolution wind field across mountainous terrain to simulate observed patterns. Journal of Theoretical Biology. 2018 Oct;454:126–38.

85. Wallraff HG. Conceptual Approaches to Avian Navigation Systems. In: Berthold P, editor. Orientation in Birds [Internet]. Basel: Birkhäuser; 1991 [cited 2022 Jun 30]. p. 128–65. (Experientia Supplementum). Available from: https://doi.org/10.1007/978-3-0348-7208-9_7

86. Boström JE, Åkesson S, Alerstam T. Where on earth can animals use a geomagnetic bi-coordinate map for navigation? Ecography. 2012 Nov;35(11):1039–47.

87. Piersma T, Loonstra AHJ, Verhoeven MA, Oudman T. Rethinking classic starling displacement experiments: evidence for innate or for learned migratory directions? Journal of Avian Biology [Internet]. 2020 [cited 2022 Apr 24];51(5). Available from: https://onlinelibrary.wiley.com/doi/abs/10.1111/jav.02337

88. Kölzsch A, Kleyheeg E, Kruckenberg H, Kaatz M, Blasius B. A periodic Markov model to formalize animal migration on a network. R Soc open sci. 2018 Jun;5(6):180438.

89. Taylor CM, Stutchbury BJM. Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. Ecol Appl. 2016 Mar;26(2):424–37.

90. Somveille M, Bay RA, Smith TB, Marra PP, Ruegg KC. A general theory of avian migratory connectivity. Ecology Letters. 2021;24(9):1848–58.

91. McLaren JD, Buler JJ, Schreckengost T, Smolinsky JA, Boone M, Emiel van Loon E, et al. Artificial light at night confounds broad-scale habitat use by migrating birds. Ecology Letters. 2018;21(3):356–64.