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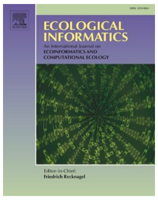

Simulating geomagnetic bird navigation using novel high-resolution geomagnetic data

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ABSTRACT

Birds rely on precise navigational mechanisms, especially for long-distance migrations. One debated mechanism is their use of the geomagnetic field. It is unclear if and how different species of birds are using intensity or inclination (or both) for navigation. Previous geomagnetic modelling research is based on static geomagnetic data despite a temporally and spatially varying geomagnetic field. Animals supposedly have a high sensitivity to those changes of the geomagnetic field. In order to understand how birds respond in real-time to its temporal variation, we need to use accurate geomagnetic information linked to the position of the bird through co-location in space and time.

We developed a data-driven approach to simulate geomagnetic migratory strategies, using, for the first time, accurate contemporaneous geomagnetic data obtained from Swarm satellites of the European Space Agency. We created biased correlated random walk models which were based on both GPS data from greater white-fronted geese (*Anser albifrons*) during fall migration between north-west Russia and central Europe and contemporaneous satellite geomagnetic data. Different strategies of geomagnetic navigation associated with different geomagnetic values were translated into probability surfaces, built from geomagnetic data, and included into the random walk models. To evaluate which strategy was most likely, we compared the measured GPS trajectories to the simulated trajectories using different trajectory similarity measurements. We propose this as an approach to track many bird species for future comparative studies.

We found that navigational strategies in these geese using magnetic intensity were closer to the observed data than those using inclination. This was the case in 80% of the best models and is an indication that it should be more beneficial for these geese to use intensity over inclination. Additionally, our results supported results from a previous study, that navigation based on taxis and compass mechanisms were more similar to the observed data than other mechanisms. We therefore suggest that these geese may use a combination of these strategies for navigation at a broad-scale. Overall, it seems likely that for successful navigation to the target location more than one mechanism is necessary; indicating a multifactorial navigation mechanism of these migratory geese in the study area. The satellite geomagnetic data are available at a higher temporal resolution and the use significantly improved the fit of the modelled simulations in comparison to the modelled geomagnetic data. Therefore, using annotated geomagnetic data could greatly improve the modelling of animal geomagnetic navigation in future research.

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1. Introduction

Birds rely on accurate and effective navigational mechanism especially for long-distance migration (Alerstam, 1987; Baker and Mather, 1982; Gwinner, 1977; Mouritsen, 2015; Thorup and Holland, 2009; Tryjanowski et al., 2002). It is widely believed that migratory birds use multifactorial navigation mechanisms which is defined as using several different cues for navigation (Holland et al., 2009; Mouritsen, 2015; Wiltschko and Wiltschko, 1996). These can be based on visual (Cochran et al., 2004; Emlen, 1975; Griffin, 1952; Holland, 2003; Kramer, 1953; Moore, 1987; Muheim, 2011; Sauer, 1957), olfactory (Bonadonna and Bretagnolle, 2002; Bonadonna and Gagliardo, 2021; Safi et al., 2016; Wikelski et al., 2015), pressure (O'Neill, 2013), auditory (Hagstrum, 2013; Hagstrum et al., 2000) or geomagnetic cues (Kramer, 1953; Phillips, 1996) but less is known how these mechanisms interact or function together. One of the most debated navigational mechanisms is based on the Earth's magnetic field. It is still unclear how much birds rely on the use of the geomagnetic field and how they navigate with it. However, it has been suggested in the past that birds can detect different values of the Earth's magnetic field, intensity, F (Holland, 2010; Winklhofer et al., 2013) or inclination, I (Muheim et al., 2002; Ritz et al., 2000). Different experiments indicate a potential for different navigational strategies based on those values.

There are two main navigational strategies, compass and map navigation. Compass navigation is defined as using a global geomagnetic extreme for navigation either along a gradient (Deutschlander and Beason, 2014; Mueller and Fagan, 2008) or to maintain a constant heading with the use of the global extreme (Cochran and Wikelski, 2005; Hore and Mouritsen, 2016; Mouritsen, 2015; Wiltschko and Wiltschko, 2015, 1972). In contrast, map navigation is based on a two-dimensional grid, within which the navigating animal can position itself relative to the value of the target location. These navigational mechanisms can either be used by the birds independently or in combination with other mechanisms (e.g. landmark-based-navigation). Research has mostly focused on how animals may use these mechanisms independently (Åkesson and Hedenström, 2007; Gagliardo, 2013; Moore, 1987; Wikelski et al., 2015), either focusing on a single navigational strategy (Hore and Mouritsen, 2016; Wiltschko and Wiltschko, 2015) or on one geomagnetic value (Muheim et al., 2002; Ritz et al., 2000; Schiffner and Wiltschko, 2011; Wiltschko and Wiltschko, 2013). Combinations of different navigational mechanisms have been addressed in several modelling studies (Åkesson and Bianco, 2015; Zein et al., 2021). To date, most studies have only used either a static representation of the geomagnetic field where field does not vary across time at all (Åkesson and Bianco, 2015), varies across time scales of decades, i.e. with secular variation (Putman, 2020), or in rare cases, varies spatially and temporally at coarse-scales, using modelled geomagnetic data (Zein et al., 2021). However, birds are navigating at a local scale and may be affected by sudden changes of the geomagnetic field, which are caused by the solar wind and range at temporal scales of seconds to hours. To understand their responses to these changes, we need to know the exact measurements of the geomagnetic field at the location and time of the birds' passage. Until recently, the only way to do so was to use geomagnetic data from magnetometers on animal-borne loggers, however at present, these magnetometers are very small and they create data that are very noisy and not accurate enough for study of geomagnetic navigation (Brum-Bastos et al., n.d., in preparation.).

Global real-time geomagnetic data are measured by satellites, such as the Swarm constellation of the European Space Agency (ESA). New developments that use geomagnetic data from these satellites in the study of animal navigation (Benitez-Paez et al., 2021) might help disentangle an ongoing debate about geomagnetic bird navigation. These data represent records of fast local changes of the geomagnetic field induced by solar storms and enable the use of fine-scale temporal data which can be linked to the precise spatial position of an animal. The use of these data might improve modelling approaches of geomagnetic bird navigation.

Data-driven approaches, like Agent Based Models (ABMs), can be used to study bird navigation and simultaneously incorporate interactions with the environment (Bousquet and Le Page, 2004; Grimm et al., 2005; Hogeweg and Hesper, 1990; Huston et al., 1988; Johnson et al., 1992; O'Sullivan and Perry, 2013; Siniff and Jessen, 1969; Tang and Bennett, 2010). Mathematically, the movement can be modelled as a random walk (Turchin, 1998) where the movement is simulated based on random decision of the simulated animal. The models are based on random changes of step length and turning angle but can be extended to include bias in movement direction based on previous steps (correlated random walks (CRW)) and/or a bias/drift component based on external factors (O'Sullivan and Perry, 2013). CRW models have been successfully used to study geomagnetic bird navigation in a previous publication by Zein et al. (Zein et al., 2021). This study utilised temporally coarse magnetic models and found that compass navigation based on taxis lead to the most similar simulations in comparison to empirically collected GPS trajectories. However, the magnitude of the effects of the different strategies and especially the effect of the different geomagnetic field values was low. One way to improve this methodology is to use fine resolution temporally varying geomagnetic data from satellites, which capture solar wind-induced short-term variation of the geomagnetic field.

The range of movement affects the grain of environmental variables perceptible to and useful for navigation of wild animals (Meyer and Thuiller, 2006; Nams, 2005). Migratory birds are traveling up to thousands of kilometres, and it is unclear to what scale navigation is depending on local or global environmental conditions. Evidence for this can come from the sensitivity thresholds of birds to geomagnetic values and to the spatial and temporal scales of the change in the geomagnetic field. Previous research indicates that birds can detect changes in the magnitude of the geomagnetic intensity of 20–200 nanotesla (nT) (Beason and Semm, 1987; Schiffner and Wiltschko, 2011; Semm and Beason, 1990; Wiltschko and Wiltschko, 2013) and changes of the geomagnetic inclination of 1–5 degrees (Åkesson et al., 2001; Lefeldt et al., 2015; Sandberg et al., 1998). The geomagnetic field is spatially changing about 10nT and 0.009° per km but there is local temporal variation, induced by strong solar wind resulting from eruptions on the Sun, of magnitude of about 30-100nT in mid-latitudes and up to 1000nT in polar regions over a period of a few minutes to hours (Campbell, 2003). Based on these values a bird would need to fly for at least 2 km to detect changes in geomagnetic intensity and 112 km to detect changes in geomagnetic inclination. However, it is unknown to what extent birds are relying on the geomagnetic field and how large the area of the geomagnetic field is a bird can sense. Most research on modelling geomagnetic navigation is based on large-scale geomagnetic values and studying whole migration flights. Finer temporal and spatial resolutions of geomagnetic data could increase the understanding of local geomagnetic bird navigation. However, movement and behaviour is scale dependent and models need to be tested for the scale of their input variables to make reliable predictions with the results (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Nams, 2005; Pearson et al., 2004; Postlethwaite and Dennis, 2013).

This study takes an ABM approach to study geomagnetic bird navigation developed by Zein et al. (Zein et al., 2021). Here we use high-resolution GPS tracking data of greater white-fronted geese (Anser a. albifrons) as a model species and fine-scale contemporaneous satellite geomagnetic data along the entire migration of each individual. Correlated random walk models are modified to include an additional bias based on five different navigational strategies associated with dynamic geomagnetic field conditions, as captured by the satellite geomagnetic data. We address the following four questions: 1) which modelled navigational strategy most closely aligns with the real GPS tracking data 2); which geomagnetic components are associated with the best models; 3) what spatial scale is best for modelling bird navigation using geomagnetic cues; and 4) does the use of satellite geomagnetic data improve the fit of the modelled simulations.

2. Material and methods

2.1. Tracking data

We used high resolution GPS tracking data of adult greater white-fronted geese collected in an earlier study by Kölzsch et al. (Kölzsch et al., 2016). These geese travel between their breeding grounds in the Russian Arctic and their West-European wintering sites. For our study we selected migration flights in autumn (September–November) as the geese stop very little then (Kölzsch et al., 2016) and we only included migrations completed in 3 days. Greater white-fronted geese perform their autumn migration both at day and night-time which makes them a good study subject for geomagnetic navigation during migration (Kölzsch et al., 2016). We pre-processed the data to remove outliers due to GPS error and excluded GPS positions in the breeding/wintering areas (Fig. 1). Additionally, we selected GPS points in flight by excluding GPS points with ground speed of less than 6 km/h based on maximum running speed of bar-headed and barnacle geese 1.2 m/s = 4.2 km/h (Hawkes et al., 2014).

2.2. Geomagnetic data

There are two main sources of temporally varying geomagnetic data. One source is modelled data, which are created from terrestrial and satellite measurements of the field and are available at coarse temporal resolutions – an example are daily global magnetic models from the National Centres for Environmental Information (NCEI) of the National Oceanic and Atmospheric Administration (NOAA) which are based on the 12th Generation International Geomagnetic Reference Field released by the International Association of Geomagnetism and Aeronomy

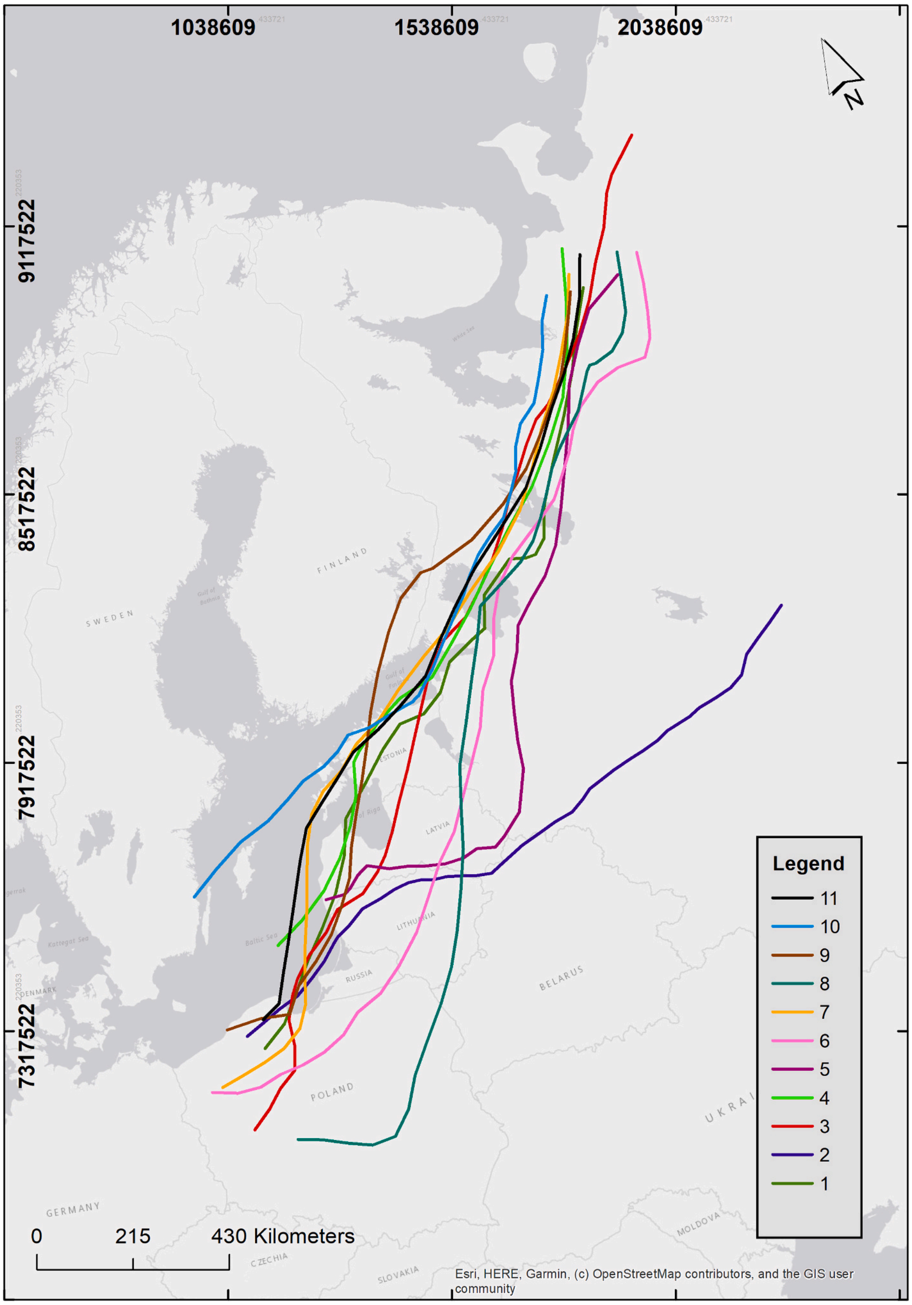

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Fig. 1. Migratory trajectories of individual greater white-fronted geese in autumn 2016–2019 in the lambert conformal conic projection.

(IAGA) (Thébault et al., 2015). These modelled data capture the slowly changing part of the geomagnetic field (core, crust and magnetosphere), but do not capture short-term variability induced by the solar wind. We used these modelled data in a previous study of geomagnetic navigation of geese (Zein et al., 2021).

The second source are satellite data, for example those from ESA's Swarm constellation (https://earth.esa.int/eogateway/missions/swarm), which provide exact measurements of the geomagnetic field, including the solar-induced variability, at the location of each satellite with a high temporal resolution (1 Hz). In this study, we used the MagGeo tool (Benitez-Paez et al., 2021) to accurately annotate our tracking data with Swarm measurements.

The MagGeo tool uses a spatio-temporal interpolation approach to assign a geomagnetic value from the satellite data to the GPS position of the tracked animal (Benitez-Paez et al., 2021).These data differ from modelled geomagnetic data because they measure the actual values of the geomagnetic field induced by particles from solar storms entering Earth's magnetosphere, rather than providing a general description of the field, such as geomagnetic models do. We used data for geomagnetic intensity (F, nT), horizontal intensity (H, nT) and magnetic inclination (I, degrees) derived from the satellite data in a grid with a spatial resolution of 5 km.

2.3. Modelling

To model navigation during long-term migration, we used correlated random walk models (CRW) (Kleyheeg et al., 2019; van Toor et al., 2018a, 2018b). These models simulate movement based on a pre-defined step length and turning angle distribution where the direction of the current step was correlated with the direction of the previous step (Turchin, 1998). We interpolated the GPS tracking data to one fix every hour. The distributions of step lengths and turning angles were derived from the interpolated GPS tracking data pooled for all individuals. With these distributions we calculated a two-dimensional probability distribution and a unidimensional distribution of the differences of step length and turning angles. To maintain autocorrelation for each term we included a lag of 1 for step length and turning angle. This ensured that the simulated trajectories were geometrically similar to the original GPS tracking data.

The movement parameters were used to derive probability surfaces that represent the probabilities of subsequent steps in the CRW models. For including the navigational strategies into our models, we conditioned the models with an additional probability surface. These rasters were based on the geomagnetic data provided by the satellite annotation tool and conditions defined by each strategy (Fig. 2). Based on literature we included five different strategies: no bias, geomagnetic taxis, constant heading, bi-gradient taxis and a combination of bi-gradient taxis

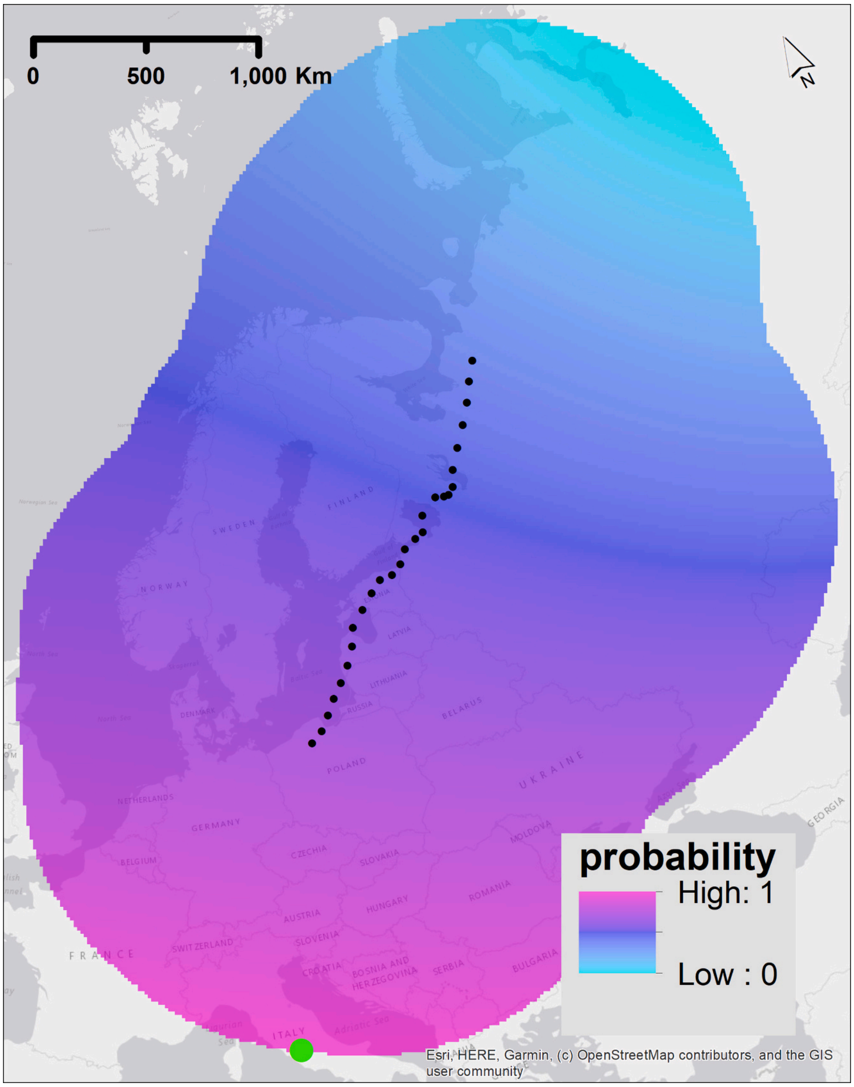

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Fig. 2. One example probability raster for the navigational strategy ‘geomagnetic taxis. These rasters were calculated before each movement decision of the simulated trajectory and are dependent on the position of the simulated bird and the geomagnetic conditions at the current location. The tracked GPS trajectory of the bird, interpolated to 1 h frequency (black dots), and the global geomagnetic extreme (green dot) are included for reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and constant heading navigation (Table 1). These were based on the approach in (Zein et al., 2021).

We simulated 100 trajectories for each of the four navigational strategies and the three associated different geomagnetic values (intensity F, inclination I and horizontal component H; Table 2) independently or in combination for each individual navigation flight. Therefore, for each of the 11 autumn migration flights we simulated and tested 19 different models, for a total of 1100 simulations per model and 20,900 simulations in total (Table 2).

All computation was done with the software R 3.6.3 using the following packages: move (Kranstauber et al., 2019) and adehabitatLT (Calenge, 2006) to analyse trajectories and lme4 (Bates et al., 2015) to fit the statistical models.

2.4. Statistical analysis

We compared the simulated trajectories to the empirical trajectories using three different similarity measurements (Ranacher and Tzavella, 2014): mean distance between trajectory points – a measure of geographical proximity (Ranacher and Tzavella, 2014), dynamic time warping (dtw) – a measure of spatial similarity (Cleasby et al., 2019) and a dynamic interaction index (DI) – a measure of coordination in movement direction of the step-length (Long and Nelson, 2013). The mean distance is calculated by taking the geographical distance between the observed tracking fix and the corresponding point in the simulated trajectory (in meters) and then taking the arithmetic mean of all of these values for each track and simulation pair. The mean distance measure is useful comparing the geographical proximity of the observed vs simulated routes, where lower values reflect a simulation that is more geographically close in comparison to the observed GPS tracking data. Dtw is a time series similarity measure that is sensitive to outliers and corrects for slight differences in the alignment of corresponding points along the trajectory (Cleasby et al., 2019). Lower dtw values reflect lower distances between simulated and real trajectories. The DI index evaluates the similarity in the distance (step length) and direction components of each movement step and it is a measure of coordination of the vectors between consecutive fixes along two trajectories (Long and Nelson, 2013). Coordination of the movement path between two tracks is expressed in the DI index with $+1$ representing movement that is perfectly coordinated in terms of the similarity of movement direction and speed, 0 no similarity in movement direction and speed, and -1 opposite movement directions and low similarity in movement speeds.

For each of the three-similarity measurements we calculated the relative average values of the modelled data vs the measured data for each migratory track to quantify the degree of improvement provided by using the measured geomagnetic data for each individual bird. We then perform separate linear mixed effect models to compare the simulated navigational strategies with geomagnetic navigational mechanisms with the navigation without geomagnetic navigation. We included a random intercept effect term for animal identity. To evaluate fit of the models we calculated marginal and conditional R^2 values.

Table 1
Overview of the four different navigational mechanisms including a geomagnetic bias.

Navigation strategy	Geomagnetic taxis	Constant heading	Bi-gradient taxis	Bi-gradient taxis & constant heading
Definition	Following a gradient towards a global geomagnetic extreme value	Keeping a constant angle to a global extreme value	Geomagnetic value at target location is used to maximise two different gradients	Combination of two previous strategies
Calibration	- not necessary	- daily	- not necessary	- as previous

Table 2
List of all combinations of strategies and associated geomagnetic values.

Strategy	Geomagnetic values used in models						Total number of simulations
1. No bias	none						1100
2. Geomagnetic taxis	F	H	I				3300
3. Constant heading	Max F	Max H	Max I	Min F	Min H	Min I	6600
4. Bi-gradient taxis	FH	FI	IH				3300
5. Combination Bi-gradient taxis-Constant heading	FH	FI	HF	HI	IF	IH	6600

To evaluate the navigational strategies related to the best performing simulations in our models, we evaluated the top 10% of our model simulations (following Oudman et al., 2020). However, we needed to correct for different numbers of simulations for each of the five different navigational strategies (Table 1.). Therefore, we used the results of the linear mixed effect models to choose the specific geomagnetic cue (i.e., F, I, or H) that represents each of the five navigational strategies best and used the selected results for the evaluation. The final sample of 5500 simulations were then used to acquire the best performing navigational strategies and geomagnetic characteristics, by counting the occurrence of the best performing geomagnetic navigational strategies for each similarity measurement. The proportion of the navigational mechanisms and geomagnetic values in the best 10% of our models is than used estimate which navigational mechanism is most similar to the true movement data.

2.5. Spatial resolution sensitivity test

Previous simulation studies on navigation during migration were based on a coarse spatial resolution (often hundreds of kilometres). Here we included sensitivity analysis, to help choose the optimal spatial resolution of the input raster for our analysis. We randomly sampled 3 birds and repeated the analysis at 5 different spatial resolutions (5, 10, 50, 100, 250 km). We averaged the model outputs for the three different similarity measurements and found best performance for a resolution of 5 km (supplement, Table S1), which was chosen for subsequent analysis.

2.6. Evaluation of real vs. modelled geomagnetic data

The current study is the first application of contemporaneous geomagnetic data acquired by satellite sensors to represent geomagnetic conditions as experienced by birds in real-time (Benitez-Paez et al., 2021). We explored if there is a difference in using modelled geomagnetic data (e.g., from NOAA) with the measured satellite data by comparing the results from this study to those in a similar previous study (Zein et al., 2021). To compare both studies, we took the average of all 19 simulations for each bird and for each of the two studies. We compared the results of the three trajectory similarity measurements for each bird using linear mixed effect model.

3. Results

3.1. Geomagnetic parameters

In our simulation experiment we used three different geomagnetic values. To measure the effect of those values on the simulated trajectories in relation to the real trajectories we looked at the proportion of the different geomagnetic values in the best 10% of our models. At least 80% of the best simulations were based on geomagnetic intensity and the horizontal component of the magnetic intensity, independently or in combination with each other. This result can be seen for all three different similarity measurements (Table 3). This indicates, that simulated trajectories based on navigation with geomagnetic intensity are most similar to the real trajectory of the migratory bird. In comparison, the navigation with no geomagnetic bias is represented in 14–25% of the best models in the similarity measurements and I is not represented in most similarity measurements in the best simulations.

3.2. Navigational strategies

Similarly, we estimated the effect of the different navigational strategies on our simulated trajectories. The four different navigation strategies in combination with the different geomagnetic values (19 different simulations) were used to model navigation for every individual bird (example Fig. 3, full output of all simulation in Supplement S1, Fig. S1–S11). The most represented strategy in the top 10% of our model was based on the combination of bi-gradient taxis and compass navigation and the two different compass navigations alone (Table 4). The count for the combination of bi-gradient taxis and compass navigation was in 29–30% of all models and the two compass navigations were represented in 22–27% of the best models. The least similar simulations are based on Bi-gradient taxis navigation and no magnetic bias (9–14%).

3.3. Evaluation of geomagnetic data

To evaluate if the outputs of our models have improved with the use of annotated geomagnetic satellite data, we compared the current study with a previous study based on modelled geomagnetic data (NOAA), which additionally differed in their temporal resolution. The modelled data can only be obtained daily whereas the geomagnetic satellite data are available at a much higher temporal resolution (1 Hz). We compared the averaged model outputs of both studies of the three different similarity measurements for all models combined (19 models with 100 simulations each) for each bird. The models based on the measured geomagnetic data perform better than those based on modelled geomagnetic data with every single animal track for all three measures of similarity. Improvement when measured by the mean distance ranging from 4 to 17%, dtw improvement ranged from 4 to 20%, and DI improvement ranged from 27 to 54% (Fig. 4). In all three cases of the similarity measurements (mean distance, dtw, DI), we found that the simulations based on the satellite annotated geomagnetic data were significantly better than the models based on modelled geomagnetic data (Fig. 4, statistical outputs in supplement Model 4–6). Additionally, the likelihood ratio test showed a significantly better fit ($p < 0.001$ for mean distance, dtw and DI) of the current models based on measured geomagnetic values in comparison to the previous models based on modelled geomagnetic data.

4. Discussion

Birds may potentially sense two main geomagnetic values (intensity - F and inclination - I) (Mouritsen, 2015) which they could potentially use for navigation. Our results show a strong indication that when using geomagnetic intensity (F) as the main geomagnetic cue, our simulations produced trajectories that were the most similar to the original paths of these migratory geese. Specifically, in our results, in 80% of the cases the best models were based on F. This is evidence that under given geomagnetic condition these birds may be using the geomagnetic intensity, F rather than inclination, I. This result is supported by comparing the scale of the spatial dynamics of the two different geomagnetic field values and the sensitivity threshold of birds for these two values (Åkesson et al., 2001; Beason and Semm, 1987; Lefeldt et al., 2015; Sandberg et al., 1998; Schiffner and Wiltschko, 2011; Semm and Beason, 1990; Wiltschko and Wiltschko, 2013). This comparison means that a bird needs to fly approximately 2 km to detect a change in F but about 112 km to detect a change in I. This would indicate that changes in F are sensed on finer spatial scale and therefore could be used for a finer scale mechanism for navigation.

These geomagnetic values could be used by animals in various ways. In literature, there are two main mechanisms suggesting either compass and/or map type navigation (Gould, 2011; Mouritsen, 2015). Our results, support previous findings by Zein et al. (Zein et al., 2021), indicating that simulations based on strategies using either a combination of constant heading and bi-gradient taxis or on taxis and constant heading produced the most similar trajectories when compared with the original trajectories. This indicates that several navigation types based on compass navigation could be used by these birds for navigation, a result that is in line with previous studies based on behaviour experiments (Wiltschko and Wiltschko, 2007). However, in our outputs the simulated trajectories rarely ended up directly near the final point of the original trajectories indicating that a multifactorial navigation mechanism is most likely necessary for precise navigation to specific locations. Additionally, this is supported by our results in that a combination of two navigational strategies, constant heading and bi-gradient taxis, allows a more precise navigation. Again, a multifactorial navigation system would be best suited to achieve such a task (Chernetsov, 2017; Schiffner et al., 2016) but it is unknown to what degree these birds switch between different strategies. They can make movement decisions on a very fine temporal scale and these decisions largely depend on the environmental conditions at the position of the animal. However, our model cannot account for a sudden change of navigational strategies of birds and can only look at a general movement pattern of the whole length of the trajectory.

There is a debate if birds are using compass and/or map navigation which is additionally suffering from a lack of clear methodological explanations of the different strategies. For example, in our study the constant heading navigation could represent a form of compass or map navigation depending on how the birds acquire the knowledge of its final migratory destination. If the bird uses knowledge of the angle of the final location to the geomagnetic extreme from a previous migratory flight, then the navigation could be entirely classified as compass type navigation. This is supported by previous research on juvenile birds, indicating that they are able, without prior knowledge, to navigate into

Table 3
Counts and probability proportions in the best 550 models for the similarity measurements (mean distance, dtw, similarity) evaluating the use of the different geomagnetic values (F, I, H).

	mean distance		dtw		DI	
Strategy	Count [#]	Proportion [%]	Count [#]	Proportion [%]	Count [#]	Proportion [%]
No additional bias	104	19	140	25	78	14
F	114	21	103	19	121	22
I	0	0	0	0	0	0
H	125	23	116	21	142	26
FH	207	38	191	35	48	9
FI	0	0	0	0	161	29
IH	0	0	0	0	0	0

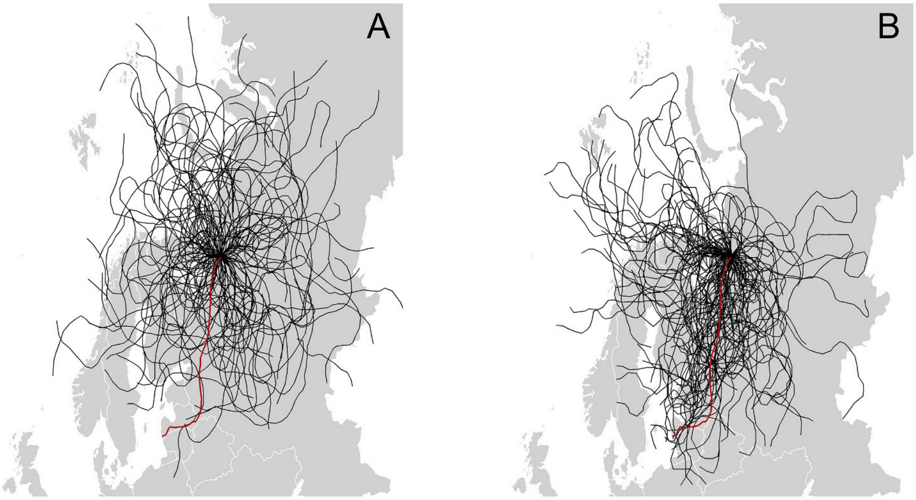

Fig. 3. Example of the correlated random walk simulations of geomagnetic navigation for one animal. Panel A shows the GPS trajectory of one animal in red and 100 black simulations without geomagnetic bias. Equally, panel B shows geomagnetic navigation with constant heading navigation based on the minimum magnetic intensity F. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Counts and probability proportion of the best 550 simulations for the similarity measurements (mean distance, dtw, DI) evaluating the 5 different navigational strategies.

	mean distance		dtw		DI	
Strategy	Count [#]	Proportion [%]	Count [#]	Proportion [%]	Count [#]	Proportion [%]
No additional bias	54	10	55	10	78	14
Geomagnetic taxis	137	25	127	23	121	22
Constant heading	138	25	150	27	142	26
Bi-gradient taxis navigation	59	11	51	9	48	9
Combination Bi-gradient taxis-Constant heading	162	29	167	30	161	29

the right direction even after displacement (Perdeck, 1958; Thorup et al., 2020, but also check Piersma et al., 2020). A system based on the magnetic angle would indicate that birds have a general sense of direction even without previous information and would indicate that in our navigational strategy constant heading can be classified as compass navigation. However, to maintain a constant heading towards the final point the simulated bird needs knowledge where, or in what relation this point is to its actual position. In migratory birds an element of map navigation is involved, if the birds are using a map-based mechanism to position themselves frequently in relation to a target (Kramer, 1953). Therefore, it is also possible that the bird has a map sense which could be used for constant heading navigation. It is difficult to simulate how the bird actually acquired this information for constant heading navigation. However, independent of these contrasting definitions, we can show that taxis and compass navigation can be used to simulate migratory trajectories of our study species and might be used by these birds at a large scale.

There are different models estimating the geomagnetic field which are based on the field generated by the core of the Earth (Barrois et al., 2018; Finlay et al., 2020; Olsen, 2002; Thébault et al., 2015). These models can vary from the real geomagnetic field by at least 3.4nT-5.4nT (Olsen, 2002) which would not largely affect the simulation of bird navigation as the sensitivity of birds is around 20–200 nT (Beason and Semm, 1987; Schiffner and Wiltschko, 2011; Semm and Beason, 1990; Wiltschko and Wiltschko, 2013). However, these models are based on the conditions of the geomagnetic field without incorporating large changes of the geomagnetic storms generated by the sun which have been suggested to affect bird navigation (Chernetsov, 2017; Emlen and Emlen, 1966; Kishkinev et al., 2015; von Middendorff, 1855). Our study is the first application of real geomagnetic satellite data to the study of migratory navigation and uses a precise estimate of the experienced geomagnetic values at the positions of the bird along a trajectory. We compared simulations with modelled geomagnetic data from NOAA (Thébault et al., 2015) and measured satellite geomagnetic values (Zein et al., 2021) to estimate the effect on the outputs of our simulations. In our results we found a highly significant difference between these two studies when comparing the outputs of the 3 similarity measurements. We could model more similar trajectories in comparison to the measured GPS trajectories of the birds when using the satellite geomagnetic data. This shows that satellite geomagnetic data from the MagGeo annotation tool allowed us to create more realistic simulations than modelled geomagnetic data. These fine-scale satellite data, by incorporating temporal changes of the geomagnetic field, can greatly improve the modelling of animal geomagnetic navigation in the future.

It is a common procedure to use environmental raster data in movement models, however how the spatial resolution of the raster data affects simulations is rarely studied. Ecological processes work at varying scales and therefore it is important to identify the right resolution for each process studied (Boyce, 2006; Levin, 1992; Meyer and Thuiller, 2006; Nams, 2005; Pearson et al., 2004). To optimise the method in this paper we compared different spatial resolutions of the geomagnetic rasters used in the biased correlated random walk models and explored the effects of the different resolutions on the model outputs. We found that if a lower resolution of the raster, in this case 5 km, was used the average outputs of the similarity measurements over all birds were lowest. This might also indicate that the optimum resolution might also be at lower than 5 km resolution. The range of the outputs greatly varied depending on the resolution of the input rasters and indicates that optimising this parameter in a movement model should become standard practice (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Nams, 2005; Pearson et al., 2004; Postlethwaite and Dennis, 2013; Wiens, 1989).

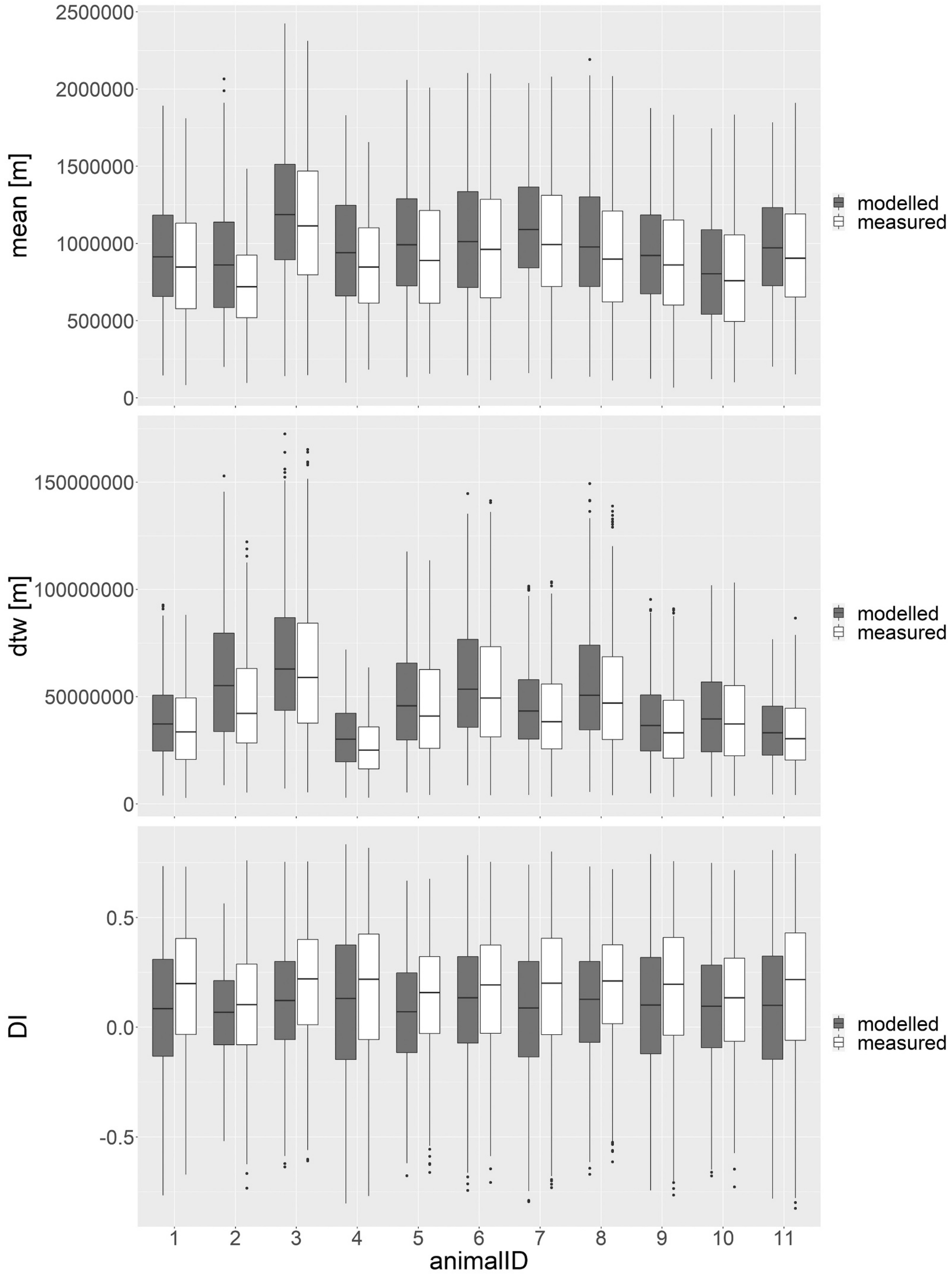

Fig. 4. Comparison between two different types of geomagnetic data for navigational studies. Dark grey box plots represent the average results for the simulation results with geomagnetic models from NOAA and white box plots represent the average results from the navigational study which used fine-scale satellite geomagnetic data. The comparison is made based on the three different similarity measurements (mean distance; dynamic time warping, dtw; and the dynamic interaction index, DI). Better modelling performance for mean distance and dtw is represented by lower values and values closer to 1 in the dynamic interaction index.

One limitation of applying this method to migration flights is the relatively large temporal scale of the trajectories required for running the models. Migration flight trajectories are geometrically straight lines and have a low variability in the distribution of turning angles. One solution to increase the variability of the turning angle distribution, is to create a pool of all animals within a population to draw the empirical values of step length and turning angles for the simulations of random walk models of migratory birds.

Research shows that birds likely rely on multiple mechanisms for navigation (Holland et al., 2009; Mouritsen, 2015; Wiltschko and Wiltschko, 1996) and yet studies addressing combinations of navigational strategies or the switch between these are rare. Our current models focus on a single navigation mechanism, and we are able to demonstrate that geomagnetic navigation can be used for broad-scale navigation (based on observed movements and the structure of the geomagnetic field). However, while these results are in line with existing literature, they raise further questions about the integration of multiple mechanisms during navigation, which remain difficult to study. The approach we have presented here could be used to address the interaction of geomagnetic strategies with those based on other senses (e.g. visual or auditory cues) or to study whether navigation mechanisms change during different stages of the migration. On the other hand, environmental factors, like the wind (Amélineau et al., 2014; Liechti, 2006) or thermals (Sapir et al., 2010), can largely impact flight energetics and could therefore influence individual navigation (Amélineau et al., 2014; Liechti, 2006; Sapir et al., 2010). Previous studies have shown that wind and geography can shape the routes birds are flying (Mitchell et al., 2015; Nourani et al., 2021, 2018). Therefore, future studies should investigate methods of combining navigational mechanisms and environmental factors affecting the flight trajectory of birds. This could improve the similarities of the modelled trajectories in comparison to the measured GPS trajectories further. However, since we did not include any environmental factors in our study design, we cannot validate geomagnetic navigation under near natural local conditions. Including environmental factors might alter the output of our models. Especially local and temporal variations of environmental factors like the wind are considered very important for migration. However, even with a large uncertainty of local environmental factors in our models we can show that that geomagnetic navigation can be used for broad-scale navigation in the study area.

5. Conclusion

In this study, we presented a data-driven approach to study the potential geomagnetic migratory navigational mechanism of Greater white-fronted geese during fall migration from Russia to central Europe. Based on our simulations, there is evidence that these geese could rely more heavily on navigation based on geomagnetic intensity F than inclination I. Additionally, we show that compass and taxis navigation could be used by these birds for broad-scale navigation. However, our results support the findings of previous studies indicating that birds most likely rely on a multifactorial navigation mechanism for fine scale movements towards the final location. This study is the first application of using fine-scale satellite geomagnetic data associated directly with the animal's position in space and time. Our results show that the use of satellite geomagnetic data significantly improves model fit over modelled geomagnetic data. Therefore, fine-scale satellite data incorporates temporal changes of the geomagnetic field which can greatly improve the modelling of animal geomagnetic navigation in the future. Nevertheless, we highlight that these results are so far only applicable to the geese migrating along the observed route and thus more studies using this approach are necessary to generalize across populations, species and migration systems.

Ethics approval and consent to participate

Secondary data use and as such does not require ethics approval.

Consent for publication

Not applicable.

Availability of data and materials

The datasets analysed during the current study are available in the Movebank Data Repository: Kölzsch, A. et al. 2016. Data from: Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. Movebank Data Repository. DOI: https://doi.org/10.5441/001/1.31c2v92f.

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Authors' contributions

BZ designed the methodology and performed the analysis with contributions from JAL, KS, AK and UD. BZ also led the writing, drafted the manuscript and coordinated revisions from all co-authors. UD, JAL and KS contributed to the development of statistical methodology. AK and HK provided geese tracking data and, together with MW, contributed to biological interpretation of results. FBP helped providing the geomagnetic data. UD conceived the study and led the Leverhulme project. All authors contributed to writing and critically revised the manuscript.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2022.101689.

References

Åkesson, S., Bianco, G., 2015. Assessing vector navigation in long-distance migrating birds. Behav. Ecol. 27, 865–875.

Åkesson, S., Hedenström, A., 2007. How migrants get there: migratory performance and orientation. Bioscience 57, 123–133.

Åkesson, S., Morin, J., Muheim, R., Ottosson, U., 2001. Avian orientation at steep angles of inclination: experiments with migratory white-crowned sparrows at the magnetic north pole. Proc. R. Soc. B Biol. Sci. 268, 1907–1913.

Alerstam, B.Y.T., 1987. Bird migration across a strong magnetic anomaly. J. Exp. Biol. 130, 63–86.

Amélineau, F., Péron, C., Lescroël, A., Authier, M., Provost, P., Grémillet, D., 2014. Windscape and tortuosity shape the flight costs of northern gannets. J. Exp. Biol. 217, 876–885.

Baker, R.R., Mather, J.G., 1982. A Comparative Approach to Bird Navigation: Implications of Parallel Studies on Mammals, pp. 308–312.

Barrois, O., Hammer, M.D., Finlay, C.C., Martin, Y., Gillet, N., 2018. Assimilation of ground and satellite magnetic measurements: inference of core surface magnetic and velocity field changes. Geophys. J. Int. 215, 695–712.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Beason, R.C., Semm, P., 1987. Magnetic responses of the trigeminal nerve system of the bobolink (Dolichonyx oryzivorus). Neurosci. Lett. 80, 229–234.

Benitez-Paez, F., Brum-Bastos, V.da S., Beggan, C.D., Long, J.A., Demšar, U., 2021. Fusion of wildlife tracking and satellite geomagnetic data for the study of animal migration. Mov. Ecol. 9, 31.

Bonadonna, F., Bretagnolle, V., 2002. Smelling home: a good solution for burrow-finding in nocturnal petrels? J. Exp. Biol. 205, 2519–2523.

Bonadonna, F., Gagliardo, A., 2021. Not only pigeons: avian olfactory navigation studied by satellite telemetry. Ethol. Ecol. Evol. 33, 273–289.

Bousquet, F., Le Page, C., 2004. Multi-agent simulations and ecosystem management: a review. Ecol. Model. 176, 313–332.

Boyce, M.S., 2006. Scale for resource selection functions. Divers. Distrib. 12, 269–276.

Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197 (3), 516–519.

Campbell, W.H., 2003. Introduction to Geomagnetic Fields, Physics Today. Cambridge University Press, Cambridge, UK.

Chernetsov, N., 2017. Compass systems. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 203, 447–453.

Cleasby, I.R., Wakefield, E.D., Morrissey, B.J., Bodey, T.W., Votier, S.C., Bearhop, S., Hamer, K.C., 2019. Using time-series similarity measures to compare animal movement trajectories in ecology. Behav. Ecol. Sociobiol. 73.

Cochran, W.W., Wikelski, M., 2005. Individual migratory tactics of New World Catharus thrushes: Current knowledge and future tracking options from space. In: Greenberg, R., Marra, P.P. (Eds.), Birds of Two Worlds: The Ecology and Evolution of Migration. Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 274–289.

Cochran, W.W., Mouritsen, H., Wikelski, M., 2004. Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science (80-.) 304, 405–408.

Brum-Bastos, V.da S., Wild, T., Zein, B., Beggan, C.D., Long, J.A., Demsar, U., n.d. Using data from MEMs Magnetometers on Tracking Tags to Study Wildlife Movement: A Geophysical and Mathematical Calibration Procedure.

Deutschlander, M.E., Beason, R.C., 2014. Avian navigation and geographic positioning. J. F. Ornithol. 85, 111–133.

Emlen, S.T., 1975. The stellar-orientation system of a migratory bird. Sci. Am. 233, 102–111.

Emlen, S.T., Emlen, J.T., 1966. A technique for recording migratory orientation of captive birds. Auk 83, 361–367.

Finlay, C.C., Kloss, C., Olsen, N., Hammer, M.D., Tøffner-Clausen, L., Grayver, A., Kuvshinov, A., 2020. The CHAOS-7 geomagnetic field model and observed changes in the South Atlantic Anomaly. Earth, Planets Sp 72.

Gagliardo, A., 2013. Forty years of olfactory navigation in birds. J. Exp. Biol. 216, 2165–2171.

Gould, J.L., 2011. Animal navigation: Longitude at last. Curr. Biol. 21, R225–R227.

Griffin, D.R., 1952. Bird navigation. Biol. Rev. Camb. Philos. Soc. 27, 359–400.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science (80-.). 310, 987–991.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.

Gwinner, E., 1977. Circannual rhythms in bird migration. Annu. Rev. Ecol. Syst. 8, 381–405.

Hagstrum, J.T., 2013. Atmospheric propagation modeling indicates homing pigeons use loft-specific infrasonic "map" cues. J. Exp. Biol. 216, 687–699.

Hagstrum, J.T., Survey, U.S.G., Park, M., Road, M., 2000. Perspective infrasound and the avian navigational map. J. Exp. Biol. 203, 1103–1111.

Hawkes, L.A., Butler, P.J., Frappell, P.B., Meir, J.U., Milsom, W.K., Scott, G.R., Bishop, C. M., 2014. Maximum running speed of captive bar-headed geese is unaffected by severe hypoxia. PLoS One 9.

Hogeweg, P., Hesper, B., 1990. Individual-oriented modelling in ecology. Math. Comput. Model. 13, 83–90.

Holland, R.A., 2003. The role of visual landmarks in the avian familiar area map. J. Exp. Biol. 206, 1773–1778.

Holland, R.A., 2010. Differential effects of magnetic pulses on the orientation of naturally migrating birds. J. R. Soc. Interface 7, 1617–1625.

Holland, R.A., Thorup, K., Gagliardo, A., Bisson, I.A., Knecht, E., Mizrahi, D., Wikelski, M., 2009. Testing the role of sensory systems in the migratory heading of a songbird. J. Exp. Biol. 212, 4065–4071.

Hore, P.J., Mouritsen, H., 2016. The radical-pair mechanism of Magnetoreception. Annu. Rev. Biophys. 299–344.

Huston, M., DeAngelis, D., Post, W., 1988. New models unify computer be explained by interactions among individual organisms. Bioscience 38, 682–691.

Johnson, A.R., Wiens, J.A., Milne, B.T., Crist, T.O., 1992. Animal movements and population dynamics in heterogeneous landscapes. Landsc. Ecol. 7, 63–75.

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., Mouritsen, H., 2015. Eurasian reed warblers compensate for virtual magnetic displacement. Curr. Biol. 25, R822–R824.

Kleyheeg, E., Fiedler, W., Safi, K., Waldenström, J., Wikelski, M., van Toor, M.L., 2019. A comprehensive model for the quantitative estimation of seed dispersal by migratory mallards. Front. Ecol. Evol. 7, 1–14.

Kölzsch, A., Müskens, G.J.D.M., Kruckenberg, H., Glazov, P., Weinzierl, R., Nolet, B.A., Wikelski, M., 2016. Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. Oikos 125, 1496–1507.

Kramer, G., 1953. Wird die Sonnehöhe bei der Heimfindeorientierung verwertet? J. Ornithol. 94, 201–2019.

Kranstauber, B., Smolla, M., Scharf, A.K., 2019. move: Visualizing and Analyzing Animal Track Data. R package version 3.2.2. https://CRAN.R-project.org/package=move.

Lefeldt, N., Dreyer, D., Schneider, N.-L., Steenken, F., Mouritsen, H., 2015. Migratory blackcaps tested in Emlen funnels can orient at 85 degrees but not at 88 degrees magnetic inclination. J. Exp. Biol. 218, 206–211.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.

Liechti, F., 2006. Birds: Blowin' by the wind? J. Ornithol. 147, 202–211.

Long, J.A., Nelson, T.A., 2013. Measuring dynamic interaction in movement data. Trans. GIS 17, 62–77.

Meyer, C.B., Thuiller, W., 2006. Accuracy of resource selection functions across spatial scales. Divers. Distrib. 12, 288–297.

Mitchell, G.W., Woodworth, B.K., Taylor, P.D., Norris, D.R., 2015. Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Mov. Ecol. 3, 1–13.

Moore, F.R., 1987. Sunset and the orientation behaviour of migrating birds. Biol. Rev. Camb. Philos. Soc. 62, 65–86.

Mouritsen, H., 2015. Magnetoreception in birds and its use for long- distance migration. In: Sturkie's Avian Physiology, pp. 113–133.

Mueller, T., Fagan, W.F., 2008. Search and navgation in dynamic environments - from individual behaviours to population distributions. Oikos 117, 654–664.

Muheim, R., 2011. Behavioural and physiological mechanisms of polarized light sensitivity in birds. Philos. Trans. R. Soc. B Biol. Sci. 366, 763–771.

Muheim, R., Bäckman, J., Åkesson, S., 2002. Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. J. Exp. Biol. 205, 3845–3856.

Nams, V.O., 2005. Using animal movement paths to measure response to spatial scale. Oecologia 143, 179–188.

Nourani, E., Safi, K., Yamaguchi, N.M., Higuchi, H., 2018. Raptor migration in an oceanic flyway: wind and geography shape the migratory route of grey-faced buzzards in East Asia. R. Soc. Open Sci. 5, 0–5.

Nourani, E., Bohrer, G., Becciu, P., Bierregaard, R.O., Duriez, O., Figuerola, J., Gangoso, L., Giokas, S., Higuchi, H., Kassara, C., Kulikova, O., Lecomte, N., Monti, F., Pokrovsky, I., Sforzi, A., Therrien, J.F., Tsiopelas, N., Vansteelant, W.M.G., Viana, D. S., Yamaguchi, N.M., Wikelski, M., Safi, K., 2021. The interplay of wind and uplift facilitates over-water flight in facultative soaring birds. Proc. R. Soc. B Biol. Sci. 288.

Olsen, N., 2002. A model of the geomagnetic field and its secular variation for epoch 2000 estimated from Ørsted data. Geophys. J. Int. 149, 454–462.

O'Neill, P., 2013. Magnetoreception and baroreception in birds. Develop. Growth Differ. 55, 188–197.

O'Sullivan, D., Perry, G.L.W., 2013. Spatial Simulation: Exploring Pattern and Process. John Wiley & Sons, Ltd, Chichester, UK.

Oudman, T., Laland, K., Ruxton, G., Tombre, I., Shimmings, P., Prop, J., 2020. Young birds switch but old birds lead: how barnacle geese adjust migratory habits to environmental change. Front. Ecol. Evol. 7, 1–15.

Pearson, R.G., Dawson, T.P., Liu, C., 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography (Cop.). 27, 285–298.

Perdeck, A.C., 1958. Two Types of Orientation in Migrating Starlings, Sturnus yulgaris L., and Chaffinches, Fringilla coelebs L., as Revealed by Displacement Experiments. Ardea, 46, pp. 1–37.

Phillips, J.B., 1996. Magnetic navigation. J. Theor. Biol. 180, 309–319.

Piersma, T., Loonstra, A.H.J., Verhoeven, M.A., Oudman, T., 2020. Rethinking classic starling displacement experiments: evidence for innate or for learned migratory directions? J. Avian Biol. 51, 1–7.

Postlethwaite, C.M., Dennis, T.E., 2013. Effects of temporal resolution on an inferential model of animal movement. PLoS One 8, 1–11.

Putman, N.F., 2020. Animal navigation: seabirds home to a moving magnetic target. Curr. Biol. 30, R802–R804.

Ranacher, P., Tzavella, K., 2014. How to compare movement? A review of physical movement similarity measures in geographic information science and beyond. Cartogr. Geogr. Inf. Sci. 41, 286–307.

Ritz, T., Adem, S., Schulten, K., 2000. A model for photoreceptor-based magnetoreception in birds. Biophys. J. 78, 707–718.

Safi, K., Gagliardo, A., Wikelski, M., Kranstauber, B., 2016. How displaced migratory birds could use volatile atmospheric compounds to find their migratory corridor: a test using a particle dispersion model. Front. Behav. Neurosci. 10, 1–9.

Sandberg, R., Bäckman, J., Ottosson, U., 1998. Orientation of snow buntings (Plectrophenax nivalis) close to the magnetic north pole. J. Exp. Biol. 201 (Pt 12), 1859–1870.

Sapir, N., Wikelski, M., Mccue, M.D., Pinshow, B., Nathan, R., 2010. Flight modes in migrating European bee-eaters: heart rate may indicate low metabolic rate during soaring and gliding. PLoS One 5, 1–13.

Sauer, E.G.F., 1957. Die Sternenorientierung nchtlich ziehender Grasmcken (Sylvia atricapilla, borin und curruca). Z. Tierpsychol. 14, 29–70.

Schiffner, I., Wiltschko, R., 2011. Temporal fluctuations of the geomagnetic field affect pigeons' entire homing flight. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 197, 765–772.

Schiffner, I., Denzau, S., Gehring, D., Wiltschko, R., 2016. Mathematical analysis of the homing flights of pigeons based on GPS tracks. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 202, 869–877.

Semm, P., Beason, R.C., 1990. Responses to small magnetic variations by the trigeminal system of the bobolink. Brain Res. Bull. 25, 735–740.

Siniff, D.B., Jessen, C.R., 1969. A simulation model of animal movement patterns. Adv. Ecol. Res. 6, 185–219.

Tang, W., Bennett, D.A., 2010. Agent-based modeling of animal movement: a review. Geogr. Compass 4, 682–700.

Thébault, E., Finlay, C.C., Beggan, C.D., Alken, P., Aubert, J., Barrois, O., Bertrand, F., Bondar, T., Boness, A., Brocco, L., Canet, E., Chambodut, A., Chulliat, A., Coïsson, P., Civet, F., Du, A., Fournier, A., Fratter, I., Gillet, N., Hamilton, B., Hamoudi, M., Hulot, G., Jager, T., Korte, M., Kuang, W., Lalanne, X., Langlais, B., Léger, J.-M., Lesur, V., Lowes, F.J., Macmillan, S., Mandea, M., Manoj, C., Maus, S., Olsen, N., Petrov, V., Ridley, V., Rother, M., Sabaka, T.J., Saturnino, D., Schachtschneider, R., Sirol, O., Tangborn, A., Thomson, A., Tøffner-Clausen, L., Vigneron, P., Wardinski, I., Zvereva, T., 2015. International geomagnetic reference field: the 12th generation. Earth, Planets Sp. 67, 79.

Thorup, K., Holland, R.A., 2009. The bird GPS - long-range navigation in migrants. J. Exp. Biol. 212, 3597–3604.

Thorup, K., Vega, M.L., Snell, K.R.S., Lubkovskaia, R., Willemoes, M., Sjöberg, S., Sokolov, L.V., Bulyuk, V., 2020. Flying on their own wings: young and adult cuckoos respond similarly to long-distance displacement during migration. Sci. Rep. 10, 1–8.

Tryjanowski, P., Sparks, T.H., Kuźniak, S., 2002. Earlier arrival date of some farm land migrants in western Poland. Ibis (Lond. 1859). 144, 62–68.

Turchin, P., 1998. Quantitative Analysis of Movement: Measuring and Modeling Population Redis- Tribution in Animals and Plants. Sinauer Associates, Sunderland, MA.

van Toor, M.L., Avril, A., Wu, G., Holan, S.H., Waldenström, J., 2018a. As the duck flies-estimating the dispersal of low-pathogenic avian influenza viruses by migrating mallards. Front. Ecol. Evol. 6, 1–15.

van Toor, M.L., Kranstauber, B., Newman, S.H., Prosser, D.J., Takekawa, J.Y., Technitis, G., Weibel, R., Wikelski, M., Safi, K., 2018b. Integrating animal movement with habitat suitability for estimating dynamic migratory connectivity. Landsc. Ecol. 33, 879–893.

von Middendorff, A., 1855. Die Isopiptesen Russlands. Grundlagen zur Erforschung der Zugzeiten und Zugrichtungen der Vögel Russlands. St Petersbg. Mem. Acad. Sci. St. Petersbg. Sci. Nat. 8.

Wiens, J.A., 1989. Spatial scaling in ecology published by : British Ecological Society stable URL : https://www.jstor.org/stable/2389612 spatial scaling in ecology1. Funct. Ecol. 3, 385–397.

Wikelski, M., Arriero, E., Gagliardo, A., Holland, R.A., Huttunen, M.J., Juvaste, R., Mueller, I., Tertitski, G., Thorup, K., Wild, M., Alanko, M., Bairlein, F., Cherenkov, A., Cameron, A., Flatz, R., Hannila, J., Hüppop, O., Kangasniemi, M., Kranstauber, B., Penttinen, M.L., Safi, K., Semashko, V., Schmid, H., Wistbacka, R., 2015. True navigation in migrating gulls requires intact olfactory nerves. Sci. Rep. 5, 1–11.

Wiltschko, W., Wiltschko, R., 1972. Magnetic compass of European robins. Am. Assoc. Adv. Sci. 315, 1709–1712.

Wiltschko, W., Wiltschko, R., 1996. Magnetic orientation in birds. J. Exp. Biol. 199, 29–38.

Wiltschko, W., Wiltschko, R., 2007. Magnetoreception in birds: two receptors for two different tasks. J. Ornithol. 148.

Wiltschko, R., Wiltschko, W., 2013. The magnetite-based receptors in the beak of birds and their role in avian navigation. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 199, 89–98.

Wiltschko, R., Wiltschko, W., 2015. Avian navigation: A combination of innate and learned mechanisms. In: Advances in the Study of Behavior. Elsevier Ltd, pp. 229–310.

Winklhofer, M., Dylda, E., Thalau, P., Wiltschko, W., Wiltschko, R., 2013. Avian magnetic compass can be tuned to anomalously low magnetic intensities. Proc. R. Soc. B Biol. Sci. 280.

Zein, B., Long, J.A., Safi, K., Kölzsch, A., Wikelski, M., Kruckenberg, H., 2021. Simulation experiment to test strategies of geomagnetic navigation during long - distance bird migration. Mov. Ecol. 1–15.