

Natal imprinting to the Earth's magnetic field in a pelagic seabird

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Summary

In migratory animals where post-natal care is limited, it is essential that there are inherited mechanisms whereby an individual can navigate - firstly, to the terminus of their migration and, secondly, back to a suitable breeding site. In birds, empirical evidence suggests that orientation on first migration is controlled by an inherited navigational vector; a direction and a distance in which to move (the 'clock and compass' model) [1-5]. The mechanism and information that underlies the return to the natal breeding site is, however, almost entirely unknown. A potential solution to this problem would be for an animal to learn the values for spatially and temporally stable gradient cues which specifically indicate the location of the natal site [6-16]. One potential cue for latitude is magnetic inclination. Here, we use ringing recoveries made over the last 80 years to investigate whether magnetic inclination might be used as a navigational cue to control the latitude of recruitment in a trans-global migrant, the Manx shearwater (*Puffinus puffinus*). We find that small changes in inclination between when a bird fledges and when it returns from first migration correlate with probabilistic changes in latitude at recruitment, in doing so quantitatively fulfilling *a priori* predictions as to the magnitude and direction of latitudinal shift. This, we believe, suggests that a) natal magnetic inclination is learnt prior to fledging and b) is used to provide latitudinal information when making the first return trip from the wintering grounds.

Results and Discussion

Natal philopatry is widespread across migratory vertebrate taxa, from reptiles and fish to marine mammals and birds including colonial seabirds [17]. The accurate return of species without post-natal care to breeding grounds after first migration, sometimes called “natal homing” [18], constitutes a remarkable behavioural phenomenon. It requires the learning of locale-specific information capable of guiding long-distance homeward movements, after perhaps years of elapsed time and based on very limited experience. Spatial familiarity acquired through exploratory movements and outbound migration may be an important component of natal homing in many species [19-20]. Nevertheless, imprinting by neonates prior to first migration on locale-specific values of a wide-ranging gradient cue could in principle provide a natal-site signature targetable over very long distances without requiring the exploratory experience needed to build some kind of navigational “map”. Suitable cues could be provided by components of the Earth’s magnetic field, such as magnetic inclination (the angle between the Earth’s magnetic field and the Earth’s surface) or magnetic intensity (the overall strength of the Earth’s magnetic field).

Here we used available ringing data from the British Trust for Ornithology to investigate the role of magnetic cues in the natal philopatry of Manx shearwaters (*Puffinus puffinus*), a small but long-lived pelagic Procellariiform seabird with a trans-equatorial, trans-Atlantic migration. Manx shearwaters breed on islands in the East Atlantic across a latitudinally diverse but longitudinally constrained range ($\sim -5^{\circ}\text{E}$ to -10°E , $\sim 45^{\circ}\text{N}$ to 65°N). From ringing recoveries [21] and geolocators [22], both adult and first year birds are known to spend the boreal winter on the Patagonian shelf, Argentina. Immatures return to European colonies for the first time from around 3 years post-fledging, with breeding commencing several years later [21, 23-24]. Since 1954, some 2996 Manx

52 shearwaters from colonies in Britain, Ireland and on the Isle of Man have been ringed as chicks
53 and later recovered as returners (>1 year later) at or close to a breeding colony, with around 4% of
54 these birds recovered at non-natal colonies indicating a high degree of natal philopatry.

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56 Secular variation, changes in the Earth's magnetic field caused by the movement of magnetic
57 material in the core, causes inclination and intensity at a given latitude to increase or decrease year-
58 on-year. This is associated with a corresponding northward or southward movement in the latitude
59 at which specific parameter values occur (see Figure 1 for magnetic shifts over the sampled
60 period). Thus, if Manx shearwaters make use of magnetic parameters during natal homing, such
61 changes might be reflected in the errors or biases associated with where they return to breed,
62 allowing for the following qualitative prediction: with decreased magnetic intensity/inclination
63 values, birds will be more likely to recruit to the north of their natal colony, whilst increases will
64 lead to a greater chance of recruiting to the south (see Figure 1). Further, if inclination/intensity
65 is being used to infer latitude, then we can make two further quantitative predictions. First, we
66 predict that the intercept of the linear regression of latitude against inclination/intensity should be
67 zero (i.e. when there is no change in inclination/intensity there is also no change in latitude).
68 Second, if inclination is used to infer latitude, the gradient of the inclination vs latitude linear
69 model should be approximately 1.34, the ratio of degrees inclination to degrees latitude in the UK.
70 By comparing the magnetic field at the point when a fledgling leaves its colony and the field at the
71 point it returns (3 years later [21, 23-24]) we can calculate a change in the magnetic field
72 parameters of interest. We can then assess how this change predicts the change in latitude at
73 recruitment.

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To test whether changes in magnetic inclination predicted changes in recruitment latitude, we fitted a linear model between the changes in the inclination angle/magnetic intensity and the actual changes in latitude between ringing and recruitment. Because ringing effort at colonies of different latitudes has not remained constant, changes in the relative recovery effort in the north and south of the species range could result in apparent mean latitudinal changes even if birds were to disperse at random with respect to latitude. As such, we modelled out the bias in average latitudinal change caused by sampling latitude over time by first mechanistically modelling the expected latitudinal bias owing to sampling and then including it as a predictor in our linear model (see STAR methods for details). Additionally, we also tested for an effect of change in sea surface temperature (SST) on the change in latitude between bird fledging and recruitment as this variable is often assumed to play a key role in distribution changes in oceanic organisms [12].

We found that shifts in recruitment latitude are significantly predicted by shifts in inclination (LM; $F = 34.7935$, $p = 4.1 \times 10^{-10}$, Figure 2) and the change in the sampling latitude bias (see STAR methods for more information; LM; $F = 71.3764$, $p = 2.2 \times 10^{-16}$; total model $r^2 = 2.8\%$). In order to ensure that the statistically significant effect of inclination observed was not the product of zero-inflated distributions, we also tested for statistical significance using a rank order randomisation (see methods). This too suggested a significant effect of inclination shift on recruitment latitude ($p < 0.01$), further indicating that changes in inclination conformed to our *a priori* prediction. We also noted that the linear model intercept was close to the expected 0 value (-0.013 ± 0.020 [SE]) and that the estimated gradient of inclination change versus recruitment latitude change was, as with the intercept, close to our expected value of 1.34 (1.34 ± 0.23 degrees latitude per degree inclination). We found that intensity change is not a significant predictor of latitudinal change

during recruitment when considered either as part of a linear regression model (LM; $F = 0.001$, $p = 0.99$) or in a rank-order randomisation ($p > 0.05$). Similarly, the model was not changed significantly by the inclusion of changes in SST as a predictor (LM; $F = 2.44$; $p = 0.118$).

Within our ringing data we also have 1207 records of adult shearwaters (aged 3 years or greater) that were recaptured a second time. Of these between-year adult recoveries, we find only 6 individuals that change colony. Given that in this time 109 fledgling shearwaters changed colony we suggest that, unlike with naïve returners, non-magnetic cues may contribute to orientation in adult shearwaters or, alternatively, that adult shearwaters update their magnetic inclination target yearly and are thus more resilient to fluctuations in the Earth's magnetic inclination.

Our finding, that changes in latitude between fledging and recruitment are significantly predicted by changes in inclination over the same period, is consistent with magnetic inclination being used directly by shearwaters as a measure of latitude when returning to colonies for the first time. This is supported not only by the qualitative expectation that northwards and southwards shifts in inclination between the year of hatching and the probable year of recruitment predict northwards and southwards recruitment of birds, but by the quantitative predictions of an inclination-based measure of latitude. The linear model intercept value of 0 suggests that when inclination is constant there is no change in recruitment latitude. Furthermore, the gradient of the effect is remarkably close to the predicted 1.34 degree change in latitude per degree change in inclination. Conversely, despite being correlated with inclination (LM; $F = 77.708$, $p = 2.2 \times 10^{-16}$), total magnetic intensity did not predict latitude at recruitment. Given that this is a correlative study, it is possible that the results detailed above arise due to the confound of magnetic inclination with another variable.

121 However, we found no effect of changes in sea surface temperature on recruitment latitude, which
122 would probably be the most plausible non-navigational driver of post-natal dispersal in a pelagic
123 seabird. As such, given how precisely the data fit the magnitude and direction of our *a priori*
124 predictions, we believe that the most parsimonious explanation is the direct use of magnetic
125 inclination in seabird natal philopatry.

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127 Baker [19] postulated that natal philopatry in migratory birds might be enabled by the learning of
128 locale-specific cues pertaining to the natal site, perhaps utilising exploratory movements [25] or
129 information gathered on the first outward migratory journey. The mechanisms involved have,
130 however, been seldom investigated. Unlike the learning of a detailed familiar area map, or a larger
131 scale extrapolated navigational map, around the home site, the specific task of first returning to
132 the natal site long after fledging (and a potentially rapid first autumn migration like that seen in
133 shearwaters [21]) may favour a targeting mechanism based on some form of imprinting which
134 requires no exploratory experience. Support for a “Geomagnetic Imprinting Hypothesis” [18] has
135 been found in sea turtles (Cheloniidae) and several teleost fish species (notably the
136 Salmoniformes), where natural variation in the Earth’s magnetic field and contrasts induced by
137 local topography suggest the use of magnetic cues specific to the natal site when navigating [6-7,
138 12, 15-16, 18]. Experimental sensory manipulations in loggerhead turtles, *Caretta caretta*, and
139 several fish species also suggest that map-like magnetic cues could play a role in neonatal
140 navigation [8-11, 13-14].

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142 Our results suggest that, as in sea turtles and teleost fish taxa, shearwaters might imprint onto the
143 magnetic inclination (but apparently not magnetic intensity) of their natal colony prior to or around

fledging to provide a potentially very long-distance targeting mechanism for natal homing three or more years later. Most likely, such a mechanism would provide only approximate position (latitude), with other cues focussing specific colony choice (whether similarly learnt location cues, or social and habitat attractors). Hence, and given the geographical spacing of active breeding colonies, small shifts in magnetic inclination at a given latitude should lead only to shifts in the probability of recruiting at the natal versus another colony (see Figure 2). Consequently, we see significant latitudinal shift with inclination shift on the population level, but with comparatively few individuals (109) exhibiting the precise expected shift.

The role of the earth's magnetic field in avian navigation has had a controversial history. Considerable evidence exists for the use of an inclination compass in night-migrating passerines [26-30], currently thought to be underpinned by the differential reactivity of quantum-entangled electrons [31-36]. The use of magnetic information for non-compass navigational cues has also been postulated in migratory birds such as reed warblers (*Acrocephalus scirpaceus*) [37-41] and Silvereyes (*Zosterops lateralis*) [42]. However, in the diurnal homing pigeon the consensus is that magnetic cues are at best of secondary importance in homeward navigation [43-44]. Interestingly, in procellariiforms, the taxon studied here, there is also as yet no empirical evidence for the use of magnetic cues when navigating either after experimental displacement or during natural foraging excursions [45-52]. The results presented here, then, provide the first evidence at least that young seabirds must have a sensitivity to magnetic inclination. Our finding that, unlike fledglings, adult birds are not sensitive to inclination shifts suggests that inclination is not the only indicator of latitudinal position in experienced returners which, in turn, is parsimonious with previous studies

suggesting that spatial position in adult procellariiforms is unlikely to be primarily ascertained using magnetic cues.

Additionally, even in fledglings inclination cannot be the only indicator of geographic position since it only provides a guide to latitude. Other cues, magnetic or otherwise, must be required to provide fledglings with longitudinal information. Further, inclination cannot be used to determine latitude if acted upon using a simple monotonic response since inclination forms an approximate mirror-image pattern across the equator. Consequently, trans-equatorial movement requires at least a reversal of response either side of the magnetic equator, a problem shared with the magnetic inclination compass [26, 28].

While our results constitute the first evidence for magnetoreception in a seabird as well as a mechanistic explanation of natal philopatry following first time migration, they also demonstrate the power of re-analysing historic ringing data when attempting to understand the mechanisms underpinning the migrations of millions of birds world-wide. While ultimately, as with any correlative study, experimental verification will be needed in future, these results nonetheless represent the first attempt to explain the sensory basis of avian natal philopatry, one of the great enigmas of animal behaviour.

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Author Contributions

The study was conceptualised by J.W. and the analysis designed by J.W. and O.P. Ringing data were analysed by J.W. with assistance from O.P. and input from T.G., H.M. and C.P. An initial manuscript was written by J.W. with assistance from O.P. and T.G., upon which all authors commented to produce the manuscript submitted for peer review.

Declaration of Interests

The authors declare no competing interests.

Figure Captions

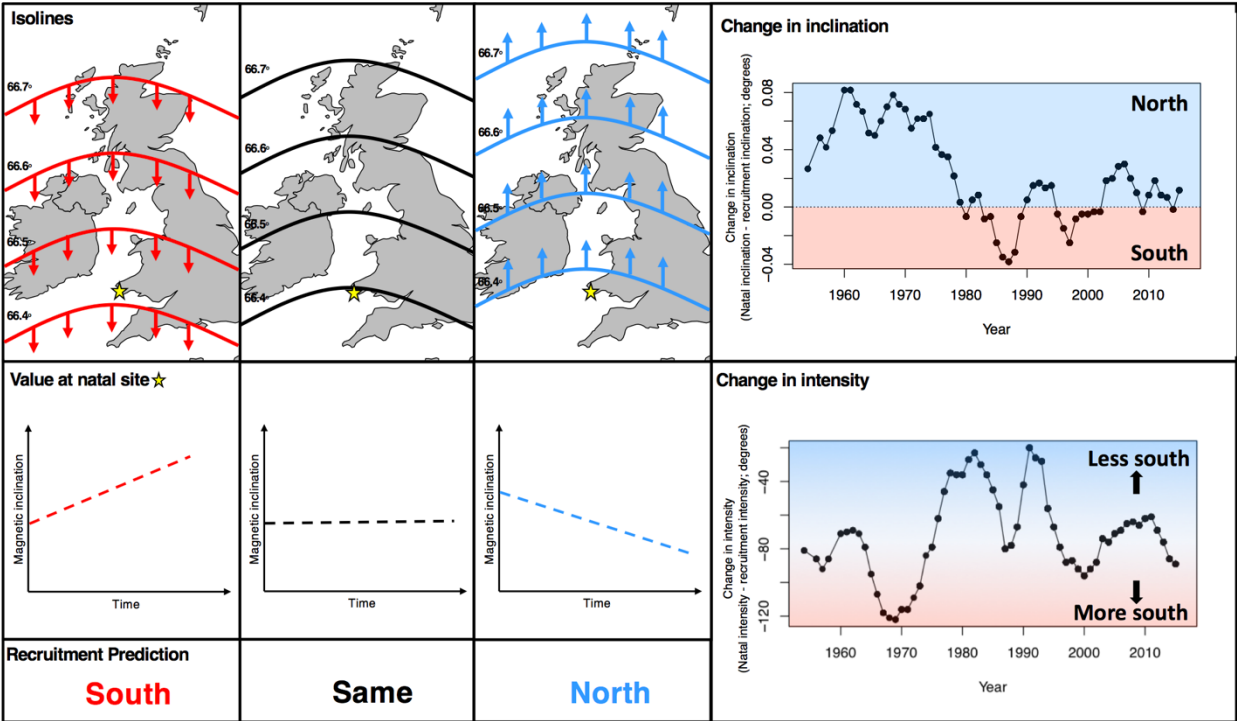
Figure 1: Changes in magnetic field parameters and their predicted effects. (left) The effects of changes in inclination on (top) isolines, (middle) recorded inclination at a given site and (bottom) predicted shifts in recruitment. (right) the changes in magnetic inclination (top) and intensity (bottom) in the British Isles 1954-2019.

Figure 2: The recruitment of Manx shearwaters with magnetic inclination. (left) The expectation of homing biases based on changes in inclination. We expect that small shifts in the Earth's magnetic field will interact with an existing probability of changing colonies (due to, for example, imprecisely imprinting onto magnetic field values) causing very few individuals to exhibit a shift in colony but that the proportion of the population that changes colony will be related to shifts in the Earth's magnetic field. (right) A) Changes in inclination plotted against changes in latitude for all birds ($n = 2996$), B) changes in inclination plotted against changes in latitude for birds that changed colony ($n = 109$).

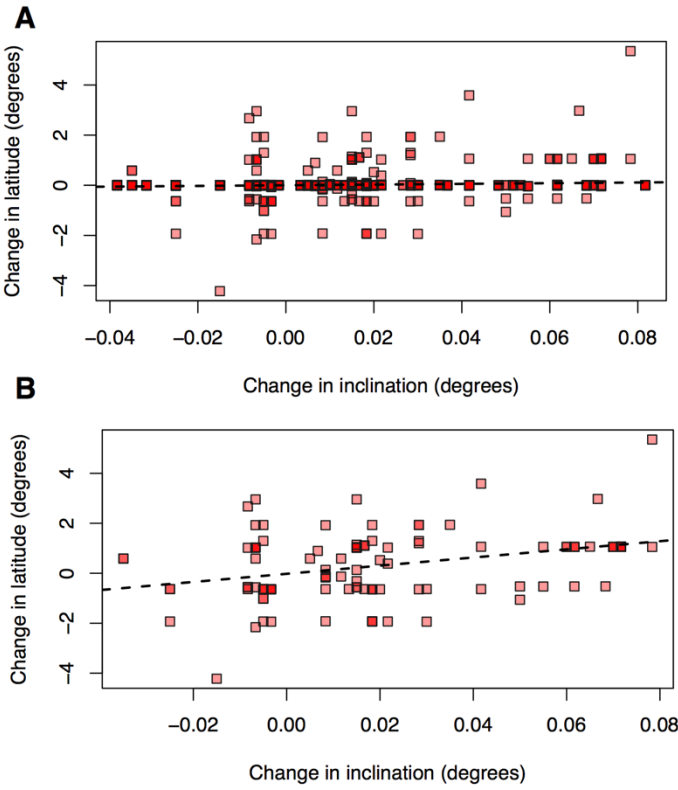
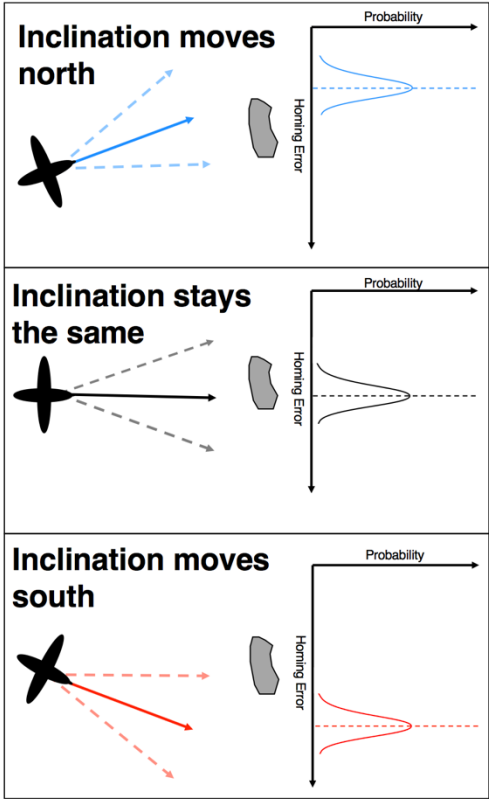
Supplemental data legend

Data S1. Full ringing dataset used in the final analysis presented here. Related to STAR methods.

233 Figure 1
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235 **Figure 2**
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STAR Methods

Resource availability

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Joe Wynn (joseph.wynn@zoo.ox.ac.uk).

Materials availability

This study did not generate or use any novel reagents.

Data and code availability

Data are available through the BTO at bto.org or in the supplemental information (Data S1). The R script used in this analysis is available from the authors upon request.

Experimental model and subject details

The data used in this study were provided by the British Trust for Ornithology (BTO) based on a search query for all Manx shearwaters that were ringed as pulli and subsequently recovered as adults. Manx shearwaters are procellariiform seabirds with a distribution centred around the west coast of the British Isles.

Method details

5988 ringing recoveries were obtained from the BTO, representing 3336 unique individuals (see Data S1). Recoveries made within half a year of ringing were excluded as birds were unlikely to have left on first migration. Birds were also excluded if they were not recovered at, or within 10km of, a known breeding colony. 10 km was chosen so as to remove records of birds that plausibly could have died whilst foraging away from the breeding colony. Where the date of recovery was clearly many years after the bird made its return from first migration it was assumed that the bird did not switch colony in the interim. For each bird a change in latitude was calculated based on the latitude at which it fledged and the latitude at which it was subsequently recovered. In total, 2996 ringing recoveries were used in the final analysis of fledgling recruitment and 1207 recoveries were used in the analysis of adult colony shift. Of the 2996 fledglings recovered 109 had changed colony, moving a mean distance of 134km (\pm 90km; see Figure S2). Recovered birds that had changed colonies were recorded between 1962 and 2015, and were ringed on Skomer Island (n = 26; 51.74°N, -5.30°W), Skokholm Island, (n = 25; 51.70°N, -5.30°W), the Isle of Rum (n = 1; 56.98°N, -6.29°W), Lundy Island (n = 1; 51.17°N, -4.67°W), the Copeland Archipelago (n = 36; 54.70°N, -5.52°W), Bardsey Island (n = 14; 52.76 °N, -4.79°W), Sanda Island (n = 1; 55.27°N, -5.59°W) and Ramsey Island (n = 5; 51.86°N, -5.34°W). This represents recoveries from all colonies on which ringing occurred aside the Calf of Man (which has recently been the subject of rat eradication).

Magnetic data were derived from the British Geological Survey stations at Lerwick (60.14°N -1.18° W), Eskdalemuir (55.314°N -3.21°W) and Hartland (51.0°N -4.49°W). For each bird a natal intensity and inclination was assigned based on the year of fledging. To establish the magnetic parameters at the point of homing we estimated, based on ringing recoveries (Brooke,

1990), that birds first home around 3 years after fledging. Between these 2 dates we calculated an overall change in magnetic inclination and intensity.

Sea surface temperature data were derived from the European Environment Agency.

Quantification and Statistical Analysis

All statistical analyses were performed in R [53]. Linear models of changes in latitude included as predictors only magnetic inclination, magnetic intensity, sea surface temperature and the predicted shift in latitude due to sampling biases (see supplementary material). All linear models were fitted using least squares. Rank-order randomisations were carried out by assigning qualitative directions to both latitudinal shift and inclination/intensity shift (i.e. ‘north’, ‘south’ or ‘same’, the latter denoting no change in colony or a change in inclination of $< 0.02^\circ$). Shifts in latitude were sampled randomly (with replacement) and paired with shifts in magnetic parameters (also sampled randomly with replacement). In each iteration of the randomisation, a point was ascribed to each pairing if the values within the pairings matched (e.g. both magnetic shift and latitudinal shift were to the north). The randomisation was repeated 500,000 times, with the total ‘score’ for each iteration noted. This was treated as the null distribution, as if magnetic shifts had no bearing on changes in latitude. This null distribution was then compared to the score of the true magnetic shift/latitudinal shift to assess significance, with the final calculated p-value taking into account the 2-tailed nature of the test.

In addition to the magnetic and environmental variables of interest, we also attempted to account for biases in the latitude of sampling in our multi-variate models. In this study, we aimed to find a

signal in a large dataset that might suggest that changes in latitude between fledging and recruitment of shearwaters are driven by corresponding changes in inclination of earth's magnetic field. Key, therefore, is to setup a model where, without the inclination parameter, the remaining model is a reasonable null expectation. If our null expectation is that when shearwaters change colony they do so at random weighted by distance then then we might expect the slope of the resulting relationship between inclination and delta latitude to be 0 if the null hypothesis is true. However, this is unlikely to be what we would see since, under the null hypothesis changes in sampling effort across the latitudinal range of Manx shearwaters would mean that there would be an apparent non 0 change in latitude. If, for example, in 1960, there was equal ringing effort across all latitudes but then in 1963 90% of ringing activity took place in Scotland, at the north of the species' range, then only birds that moved north between ringing and recovery would be able to appear in our dataset. Within our sample this is most noticeable in 1975, where ringing effort in South Wales lessened and effort in North Wales and Northern Ireland increased (see Figure S1).

Hence, such that the null hypothesis does indeed account for the variation in response owing to parameters other than inclination, we have modelled how this sampling, would, on average, influence the apparent change in latitude of birds over time. Without doing this, if the general trend of increasing ringing effort in the north or south correlated with the general trend of increasing latitudinal inclination over time then we might erroneously find an effect of inclination on latitudinal change. Even if there is no overall correlation between these two parameters, apparent changes in latitude owing to sampling effort would still introduce noise reducing our ability to correctly estimate the parameters of interest, namely, the intercept and slope of the relationship

between inclination change and the remaining variation, on top of the null hypothesis, in delta latitude.

For each individual, we calculated the total latitudinal bias in sampling effort in the years that followed, accounting for decreased probability of recapture owing to mortality (survival = 0.95 [21]) and retained the difference between this mean and the latitude of ringing to give, for each bird, a change in latitude probabilistically expected owing to sampling alone given the assumption of random latitudinal recruitment of a proportion of ringed birds.

$$\Delta Lat_{exp} \sim Lat_R - \frac{\sum_{n=0}^{P-R} \overline{Lat_R} \times 0.95^n}{\sum_{n=0}^{P-R} 0.95^n}$$

Lat_R = Latitude focal bird ringed at; R = year ringed; P = last year for which ringing data collected.

For this analysis we also assume that the proportion of birds ringed and subsequently recovered is closely related to the overall sampling effort at a given site in a given year.

We find that biases in the sampling latitude, as outlined above, are a significant predictor of the latitude at which birds are recovered (LM; $F = 71.3764$, $p = 2.2 \times 10^{-16}$). This suggests that there are, unsurprisingly, changes in where birds were sampled between years, and that the change in latitude observed per bird is in part influenced by these changes. This, we believe, is because the probability of ringing recovery is dependent on sampling effort and as such by including this in the model alongside our parameters of interest (inclination/intensity) we account for systematic change in sampling latitude, which suggests that the significant effect of magnetic inclination on latitude is unlikely to be due to a confound with sampling bias.

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