The mechanism and development of avian navigation

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Manx shearwater (*Puffinus puffinus*) in flight, Skomer Island. 25th July, 2018. Photo by the author.

Abstract

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The mechanisms by animals navigate are central not only when considering how animals interact with the environment, but also how the environment shapes and guides animal evolution. Some of the most remarkable feats of navigation in nature are undertaken by birds, with long-distance, trans-continental and trans-oceanic migrations found throughout the avian clade. However, despite being of fundamental interest, the development of avian navigation remains imperfectly understood. In this thesis I seek to use historic ringing data alongside modern biologging technology to investigate the mechanism and ontogeny of long-distance movement, using both correlative and experimental analyses and drawing on examples from across the avian phylogenetic tree. First, I consider the mechanisms of outbound migratory inheritance, finding that Manx shearwaters (*Puffinus puffinus*) are unlikely to follow their parents on first migration. I suggest that this implies that shearwaters are likely to inherit migratory information genetically, and speculate that genetically inherited information could also underpin return migration even in animals where outbound and return migratory routes differ. Second, I find that great frigatebirds (*Fregata minor*) exhibit a rapidly learnt ability to compensate for wind drift, and I suggest that such an ability could be predicated upon either visual information or sensory gradients cues. I propose that a learnt ability to compensate for drift may arise early in development, and could be of use to migratory taxa more generally. Third, I find evidence for the use of magnetic spatial information in both a songbird (the Eurasian reed warbler; *Acrocephalus scirpaceus*) and a seabird (the Manx shearwater) when relocating the natal/breeding site ('philopatry') following migration. Specifically, I find that magnetic inclination, learnt prior to departure, might be used as a uni-coordinate 'stop-sign' on a return migratory vector to guide return migration. Further, by mathematically modeling year-on-year variation in the Earth's magnetic field, I suggest that the use of uni-coordinate magnetic information might be less affected by magnetic secular variation than a bi-coordinate magnetic 'map', and hence might be a more evolutionarily advantageous solution to the problem of natal homing. Finally, using a twilight cue manipulation paradigm, I find evidence for the use of a magnetic compass by a pelagic seabird, the Manx shearwater. I find that rotations in the Earth's magnetic field at dusk predict deflections from the beeline during homewards orientation, with the magnitude of these deflections predicted by discrepancies between the inclination of the artificially applied magnetic field and the inclination of the normal magnetic field. I suggest that this inclination sensitivity is consistent with the use of an inclination compass, as seen in songbirds. Overall, I discuss the evolutionary and environmental determinants of navigational mechanism, and propose future experiments and analyses that could elucidate the development and mechanism of long-distance navigation across avian taxa.

Acknowledgements

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I should probably start by thanking Tim Guilford for the last 6 years, who's been endlessly supportive and stimulating ever since I presented my undergraduate project from an upturned washing up bowl. Along the way I've had so many wonderful memories, and quite a few whiskies, for all of which I'll be forever grateful. Likewise I'd like to thank Ollie Padget for lending an ear to some of my wackier ideas, either over a mist net, a coffee or a beer, and for 5 years of legendary adventures.

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∼ Move to Skomer and Never Leave ∼

Declaration and Author Contributions

The work presented in this thesis is primarily my own. Twenty other authors contributed to the work in this thesis, and their contributions are acknowledged below.

Tim Guilford contributed to the conception, fieldwork, analysis, and manuscript preparation for all chapters.

Oliver Padget contributed to the conception, fieldwork, analysis, and manuscript preparation for all chapters.

Henrik Mouritsen contributed to the conception and analysis of chapters 2 and 3 and contributed to the conception, fieldwork, analysis of chapter 4.

Henri Weimerskirch contributed to the analysis and manuscript preparation of chapter 5.

Emma Borsier contributed to the analysis and manuscript preparation of chapter 7.

Julien Collet contributed to the analysis and manuscript preparation of chapter 5.

Alexandre Corbeau contributed to the analysis and manuscript preparation of chapter 5.

Katrina Davies contributed to the analysis and manuscript preparation of chapter 7 and the fieldwork for chapter 4.

Ben Dean contributed to the fieldwork and manuscript preparation of chapter 6.

Annette Fayet contributed to the fieldwork of chapter 4 and the analysis and manuscript preparation of chapter 6.

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Matyna Syposz contributed to the fieldwork of chapter 4.

Chris Tyson contributed to the fieldwork and manuscript preparation of chapter 6.

The following letter has just reached me:

> *Dear Sir,*
>
> *On December 23rd a Swallow was caught in the farmhouse of the farm 'Roodeyand', 18 miles from Natal, with a metal label round its leg, with the words: 'Witherby, High Holborn, London', and on the other side 'B.830'. The farmer, Mr. J. Mayer, took the label off and has it in his possession. As I am interested in birds of any sort and the migration of same, I shall be glad to know if you receive this letter safely.*
>
> *Yours truly,*
>
> *C. H . Ruddock*

The ring B.830 was put on an adult Swallow (Chelidon r. rustica) by Mr. J. R. B. Masefield, at Rosehill, Cheadle, Staffordshire, on May 6th, 1911. This bird was one of a pair (Mr. Masefield thought the female) which nested in a porch. Its mate was also caught and ringed. At the same time Mr. Masefield ringed another pair nesting in the same porch. In the summer of 1912 he again caught the Swallows which had come to nest in his porch and found that only one of them had a ring, viz. B.827, which was one of the birds nesting there the year before. Neither its mate nor the other pair of which the present B.830 is one had returned to this particular spot.

That this Swallow breeding in the far west of Europe should have reached so far to the south-east of Africa as Natal, seems to me extraordinary. Unfortunately the few records we have as yet of ringed Swallows recovered during migration do not afford a clue to the routes taken and it seems to me unreasonable to suppose that our birds proceed southwards down the east side of Africa as might be inferred from this Natal record.

It is, indeed, quite impossible to theorize on a single recovery of this kind and we must be content at present with the bare fact—perhaps the most startling fact that the ringing of birds has as yet produced.

We are most thankful to Mr. Ruddock for reporting this extremely interesting recovery and we hope that the details of it will become widely known in South Africa and thus produce further results.

—Harry F. Witherby, *British Birds, Volume 6, Issue 9*

Contents

1

Introduction

Contents

> *"A huge percentage of the stuff that I tend to be automatically certain of is, it turns out, totally wrong and deluded."*
>
> – David Foster Wallace, *This Is Water*

1.1 Introduction

The ability to move is near-ubiquitous amongst animals, to the extent that it is a near-defining characteristic. Movement is, therefore, at the centre of how animals interact with their environment and, in turn, how the environment shapes their evolution. Efficient movement over any scale is predicated upon the twin processes of orientation and navigation, with orientation here defined as the ability to position one's self relative to allocentric directional information, and navigation defined as organised movement towards a goal (Wiener et al., 2011; Holland, 2014; Padget et al., 2018). Amongst animal taxa, the greatest navigators are perhaps the birds. For instance, Arctic terns (*Sterna paradisaea*) are capable of navigating from the Arctic Circle to the Antarctic Circle (Egevang et al., 2010), whilst willow warblers (*Phylloscopus trochilus*) navigate between Northern Europe and Central Africa (Lerche-Jørgensen et al., 2017) and *Pterodroma* petrels traverse entire oceans to provision for their young (Ventura et al., 2020). The sensory and cognitive basis of these and similar feats have fascinated humans for centuries (e.g. Gätke, 1879), though it is perhaps only within the last half-century that humans have begun to understand the sensory, cognitive and developmental underpinning of long-distance navigation. This is perhaps owing to a series of technological and methodological advances.

Chief amongst these advances is perhaps the advent of 'biologgers'; miniaturised animal-borne data loggers that present the opportunity to study navigation in wild animals. This allows not only for hitherto unparalleled realism in the study of navigation (Guilford et al., 2011a), but for a drastically wider ecological context within which navigation can be studied. Different life histories necessarily lead to a diverse array of navigational challenges and, consequently, we might expect navigational mechanisms to vary across taxa. For example, it is unlikely that that the same systems underlie the metre-by-metre movement of dung beetles (e.g. Dacke and El Jundi, 2018) and trans-continental migration of songbirds (e.g. Schmaljohann et al., 2012). As such, drawing from a wide variety of ecological and phylogenetic contexts is essential when considering the mechanisms underlying navigation at any spatial scale. Perhaps one of biologging's greatest utilities is the ability to study the movements of animals we otherwise have very little contact with, such as marine organisms. Nowhere is this more true than amongst seabirds, where ocean-going ('pelagic') species have, until recently, led lives far from human observers. Consequently, whilst elegant experimentation has led to remarkable advances in the study of seabird navigation throughout the 20th century (e.g. Matthews, 1953), it has only recently become possible to study seabird navigation experimentally in exquisite detail.

Increases in the utility of biologging devices have moved in lockstep with increases in the computing power available to biologists, which in turn has allowed for the re-analysis of historic datasets. When contextualised within remotely-sensed and modeled environmental/physical variables, for example the International Geomagnetic Reference Field ('IGRF'; Thebault et al., 2015) or the Normalized Difference Vegetation Index ('NDVI'), such data can be tremendously powerful. For example, historic teleost fish abundance data have been linked to year-on-year ('secular') variation in the Earth's magnetic field (Putman et al., 2013; Putman et al., 2014a; Putman et al., 2015), whilst similar trends have been observed in the breeding densities of sea turtles on the Atlantic coast of North America (Brothers & Lohmann, 2015). Correlative analysis of navigation is not, however, limited to historically gathered data and more recent studies have also utilised biologging (e.g. Thorup et al., 2017; Padget et al., 2019) and genetic data (e.g. Brothers and Lohmann, 2017).

Both *in situ* experimentation and correlative analyses have considerable utility in the contemporary study of navigation. As such, this thesis aims to utilise both in its exploration of the sensory mechanism and cognitive basis of avian navigation, and how such mechanisms develop and change through an individual's life. It aims to draw on examples from across the avian clade, from warblers to frigatebirds, to paint a picture representative of the sheer diversity observed amongst birds. Below I will briefly outline 'the state of play' in the contemporary study of animal navigation, with a particular focus on navigational ontogeny, before exploring the general methods used in this thesis and setting out its aims. Within this thesis plural pronouns will be used in data chapters, whilst singular pronouns will be used in the introduction and discussion. This is to denote both the fact that many of the chapters have specific contributions from multiple authors and, more generally, that much of the synthesis presented in the introduction and discussion has resulted from discussions between several people. The precise contributions of various authors are recorded in the preamble to this thesis, and in total 20 authors have participated either intellectually or in experiments/analyses.

1.2 A short history of avian navigation

Until surprisingly recently, it was a subject of some debate whether long-distance avian migration actually existed. Whilst there is evidence for a human understanding of migration in the Old Testament, in the books of Job and Jeremiah (*The New Jerusalem Bible*, 1985), and early Polynesian folk stories make repeated reference to the migration of Pacific golden plover (*Pluvialis fulva*; Richter-Gravier, 2019), early European scholars were equivocal in their understanding of bird migration. On the one hand Aristotle (and later Pliny the Elder) recorded common crane (*Grus grus*) migration from Scythia to Egypt, but on the other both subscribed to the idea that songbirds wintered underwater (Lincoln & Peterson, 1979). This claim was predicated upon the fact that many songbird species, specifically hirundines (swallows and martins), roost in reedbeds. This, they reasoned, was in preparation for overwinter underwater hibernation.

Amongst English-speaking ornithologists, this assertion was first challenged by Gilbert White who cited a lack of torpid swallows in the waterways of his native Isle of Wight as the source of his skepticism (White, 1789). This was compounded by another 18th century author, Thomas Bewick, who cited anecdotal observation of swallows crossing the Mediterranean as evidence for migration from Europe to Africa (Bewick, 1797). Half a century later this Afro-European migratory flyway was reinforced by the discovery of a so-called *Pfeilstörche* in Germany; a white stork within the neck of which an African arrow was embedded (Kinzelbach, 2005). A further 25 *Pfeilstörche* were subsequently recorded, further confirming the likelihood of bird movement between Europe and Africa.

Perhaps the first truly ‘scientific’ attempts to study bird migration were instigated by Heinrich Gätke, who from 1843 lived on the island of Heligoland (in the German Bight) and who formed the Heligoland Bird Observatory in 1891 (Gätke, 1895). Gätke initially documented and collected specimens of rare birds, though his successors, starting with Hugo Weigold in 1910, moved away such practices and towards the ‘ringing’ of migratory birds: attaching uniquely numbered metal rings to a birds’ legs. Around the turn of the century several ringing schemes were established across Europe, the first of which was administrated from Rossitten (now Rybachy) on the Courish Spit. Owing to the engagement of both professional ornithologists and keen amateurs, such ringing schemes have produced huge amounts of data over the intervening years, with Heligoland alone recording > 800,000 birds ringed (and > 7,000 birds recovered and their rings read) over the first century of its existence (Hüppop & Hüppop, 2011). Similar ringing schemes have subsequently been established the world over, with a barn swallow (*Hirrundo rustica*) ringed in Staffordshire under the British ringing scheme finally dispelling the myth of underwater hibernation with its recovery at a farm in Natal, South Africa (Witherby, 1913).

By the post-war 20th century bird migration was, therefore, not as much a question of *if* as much as a question of *how* and *why*. How do birds, in some instances weighing less than a teaspoon, navigate across multiple continents and, further, why would they do this? A central tenet in the modern study of animal navigation has been that a navigator requires 2 pieces of information: where they are, and which way they are facing (Kramer, 1950). This thesis, first proposed by Gustav Kramer, split efficient goalwards movement into 2 distinct phases: a ‘map’ phase and a ‘compass’ phase. Whilst in this context the ‘map’ and ‘compass’ in question are metaphorical, they nonetheless serve as useful academic devices when considering the mechanistic underpinning of navigation.

1.2.1 Of compasses...

If a navigator is to understand the relationship between the egocentric direction in which its facing and the allocentric map within which it understands its position, they require a link between an animal's egocentric and allocentric frames of reference. Such a link is typically thought to be provided by a compass; a device which provides direction within an allocentric frame of reference. Information regarding the orientation of a navigator could, in principle, be extracted from very local cues. For example, orientation relative to distant mountain ranges could provide directional information as long as the mountains remain within sight (a 'heading indicator'; Guilford and Taylor, 2014). However, such orientation would not provide directional information within the navigator's 'map', which necessarily limits the utility of the heading indicator. As such, in this chapter I will focus primarily upon global compass cues when considering avian orientation decisions.

Since the Earth spins on an axis, it follows that the centre of this rotation could in principle give directional information that could be sensed anywhere on Earth. If a navigator were receptive to such cues, via any sensory modality, they could orient relative to the Earth's axis and hence could determine direction anywhere on the planet. One such cue, to which birds have been repeatedly shown to be receptive, is the apparent rotation of celestial bodies (Emlen, 1967a, 1967b). Whilst it is long established that stars do not rotate around the Earth, their apparent movement forms a centre of rotation the azimuth of which aligns with either the north pole (in the northern hemisphere) or the south pole (in the southern hemisphere). It follows, therefore, that the rotation pattern of the stars could inform on direction, and in birds this seems to be the case (Emlen, 1967a, 1967b). The avian star compass has been shown to be time-independent, meaning that birds are not attentive to the position of specific stars at specific times, and instead pay attention to the general rotational pattern and aim relative to the centre. This has been shown both through experimental manipulation of the centre of rotation in planetaria, and through clock-shifting so as to demonstrate time-independence (Emlen, 1967a, 1967b; Mouritsen & Larsen, 2001; Pakhomov et al., 2017).

Clockshifting, experimentally shifting the photoperiod so it is misaligned with the natural photoperiod (in turn altering the endogenous rhythm by which animals keep track of time over the day), has also been of some use in exploring another rotational compass: the sun compass. Again owing to the rotation of Earth, the apparent position of the sun moves in a predictable way through the daily photoperiod. If a navigator knows what time of day it is, and knows where the sun usually is at that time, it follows that they can determine orientation relative to the sun (akin to a sundial in reverse). Therefore, a clockshifted bird will deflect in a predictable manner, something which has been repeatedly shown in homing pigeons (*Columba livia*; Schmidt-Koenig, 1961; Biro et al., 2007; Armstrong et al., 2013) and, more recently, seabirds (Padget et al., 2018) and songbirds (Wiltschko & Balda, 1989; Duff et al., 1998). Time-compensating the sun's apparent position is, however, not the only way birds might use to determine orientation using the sun. As light from the sun enters the atmosphere, dust and water cause it to polarise, with the most polarised light being that reflected at 90^o from the light source. Hence, as the sun's light is incident upon the edge of Earth's atmosphere, an observer looking at the part of the sky that creates a 90^o angle between the observer, the particles reflecting the light and the light source will be the part of the sky with greatest polarisation. Such a 90^o angle is true for a plane across the sky, which moves with the sun as the sun's azimuth changes throughout the day. The plane's azimuth is therefore identical in movement to the sun compass, but through a 90^o shift. This axis can, therefore, be used either to navigate in its own right or, alternatively, can be used to calibrate other compasses at dusk so as to correct for any inaccuracies (Muheim et al., 2006; Muheim et al., 2007).

The final compass thought to be of some importance in avian navigation is the geomagnetic compass. The Earth's magnetic field is derived from electrical currents caused by the movement of molten iron and nickel within the Earth's core. In turn such movement is caused by convection currents originating from heat generated in the Earth's core, with the rotation of the Earth about it axis causing such convection currents to form a magnetic field approximating a dipole with a north-south axis offset from the geographic north-south axis by around 10^o (for a review, see Roberts and Glatzmaier, 2000; see Figure 1.1). This process, known as a 'geodynamo' (Larmor, 1919), has in the present day formed a magnetic north pole in the geographic south and a magnetic south pole in the geographic north. However, the location of the 2 poles switches regularly through geographical time, inverting ever 100,000 years or so '(Glatzmaiers & Roberts, 1995).

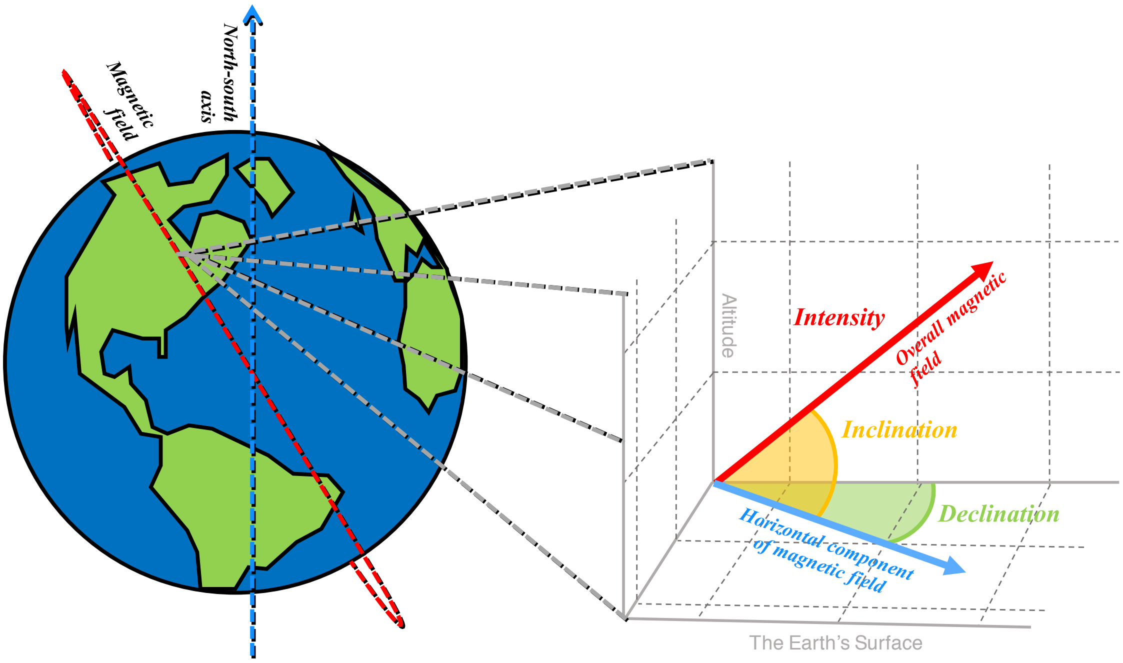

Figure 1.1: The geomagnetic field of Earth. A figure showing (left) the axis of the Earth's magnetic field relative to the axis around which the Earth spins, with (right) the 3 main parameters extracted from the Earth's magnetic field (inclination, declination and intensity) shown relative to the Earth's surface. All distances and angles are not accurate, and are accentuated for ease of understanding. Arrowheads show field directions relative to convention, though in practice the magnetic field vector in the present-day northern hemisphere is oriented towards the centre of Earth.

In principle, sensitivity to the polarity of the Earth's magnetic field would give a compass system that functions the world over. Indeed, human magnetic compasses have been predicated upon polarity for much of recorded history. However, whilst polarity-sensitive magnetoreception has been used to explain the 'fixed direction response' of birds orienting in complete darkness, where a supposedly innate tendency to head north is seemingly observed (Wiltschko et al., 2007; Stapput et al., 2008), most studies suggest that the day-to-day magnetic orientation of birds is agnostic to polarity and has instead been shown to utilise a different component of the Earth's magnetic field: magnetic inclination (Wiltschko & Wiltschko, 1972; Wiltschko et al., 2006; Schwarze et al., 2016). The Earth's magnetic field can be considered a vector in 3 dimensions, with both a magnitude and direction (see Figure 1.1). The inclination of the Earth's magnetic field is, then, the angle between the Earth's surface and the geomagnetic field, with the acute inclination angle always oriented towards the pole. Sensitivity to inclination is thought to reflect the mechanism by which birds, and specifically songbirds, sense the Earth's magnetic field.

It has been suggested that songbirds might utilise a light-dependent quantum physical reaction in the eye to sense the Earth's magnetic field, with the yield of such a chemical reaction linked to the spin states of a radical electron pair (for a review, see Hore and Mouritsen, 2016). Spin state is, in turn, thought to be influenced by a) the strength of an externally applied magnetic field and b) the sensor's orientation relative to such a field. Repeated head saccades through the magnetic fields are thought to be important in magnetosensation (Mouritsen et al., 2004), and under this model of magnetoreception such 'head scanning' behaviour is first used to determine the direction of the horizontal component of the magnetic field, i.e. the north-south axis, before second resolving the vertical inclination angle and hence determining which end of the north-south axis axis is polewards. There is an increasing body of evidence in favour of the 'radical pair mechanism' of magnetoreception, with both the light-dependence of magnetoreception (Wiltschko et al., 1993) and the apparently disorienting effects of radio waves (Ritz et al., 2000; Ritz et al., 2004; Engels et al., 2014) both cited as key lines of evidence. An alternative hypothesis suggests that the avian magnetic sense is predicated upon a magnetite receptor located in the upper beak (Fleissner et al., 2003; Falkenberg et al., 2010). Indeed, it does seem that severing the opthalmic branch of the trigeminal nerve, which innervates the upper beak, inhibits magnetoreception in songbirds (Pakhomov et al., 2018). However, similar experiments in other taxa have not found the same effect (Wikelski et al., 2015), and similarly exposure to extremely powerful magnetic pulses seemingly has little effect on orientation (Gagliardo et al., 2006; Gagliardo et al., 2008, 2009; Holland et al., 2013). Indeed, more recently the putative magnetite receptor has been suggested to in fact be macrophages (Treiber et al., 2012). As such, the radical pair mechanism posited has, perhaps surprisingly, become surprisingly plausible when considering avian magnetoreception.

Insensitivity to the polarity of the Earth's magnetic field means that birds are necessarily unable to tell the difference between north and south, and are only capable of discerning polewards from equatorwards. This makes equator-crossing using a simple inclination compass impossible, and indeed virtual magnetic displacement experiments suggest that birds are unable to navigate in equatorial magnetic conditions (Wiltschko & Wiltschko, 1992). Additionally, both the time-compensated sun compass and the rotational star compass provide different information depending on the hemisphere occupied. The rotational centre of the star compass shifts from the North Star in the northern hemisphere to the Southern Cross in the south, whilst the sun's arc traverses the southern sky in the northern hemisphere and the northern sky in the southern hemisphere. Compass cues are, therefore, not globally informative in the truest sense and often require context for correct interpretation. This is not only true when considering equatorial crossing, but also as animals move through both time and space more generally. The sun's location at a given time of day, for example, changes through the year and with latitude, whilst the difference between magnetic and true north ('magnetic declination'; see Figure 1.1) leads to variance in the course represented by a given magnetic compass bearing. Such inaccuracies have led to the principle of compass 'calibration', where less accurate compass systems are calibrated to more accurate compass systems (Cochran et al., 2004). This is thought to occur at twilight, when all 4 major compass systems are thought to be accessible simultaneously (Cochran et al., 2004; Muheim et al., 2006; Muheim et al., 2007). We might expect, therefore, a degree of redundancy in the compass systems used by birds.

1.2.2 ...and maps

Thus far, I have considered only the mechanisms by which birds determine their orientation, and have not considered how they might position themselves. One of the simplest mechanisms by which a navigator might determine position relative to the goal is via path integration (or 'dead reckoning'), using the cumulative sum of the directions and distances taken on the outward journey to calculate an overall homewards vector (for a review, see McNaughton et al., 2006). Path integration is widespread amongst in animals, with desert ants an oft-cited example where solar cues and step counting are used to give the overall distance and direction taken on the outbound leg (Muller &

Wehner, 1988). Such a system could in principle underpin movement on a larger scale, especially as all that is required is seemingly a compass and a means to measuring distance. However, path integration mechanisms necessarily accumulate error over time, and hence have been traditionally considered too inaccurate for long distance navigation. Allocentric maps have, therefore, been suggested as an alternative.

Amongst long-distance migrants, it has been suggested that navigational ‘maps’ may be predicated on position relative to 2 or more gradient cues: if a navigator were sensitive to a given sensory gradient, and could recall the position of the target within the same frame of reference (i.e. know the gradient value of the target), then in principle they could effect goalwards movement. 2 main sensory modalities have been suggested to be of some use when discerning position, the first of which is olfaction. In 1971 Floriano Papi discovered that the ability to home is, in racing pigeons, contingent on an intact olfactory nerve (Papi et al., 1971) and subsequent empirical investigation has reiterated the importance of olfaction in pigeon navigation, with anosmic pigeons shown to be unable to home (Benvenuti and Gagliardo, 1996; Budzynski et al., 1998; for reviews, see Wallraff, 2005; Gagliardo, 2013). Further, pigeons exposed to olfactants at one site, before being made anomsic and subsequently released at a second site (‘false release site’ experimentation), orient as if released from the original site (Benvenuti & Wallraff, 1985), lending further credence to the idea that pigeons position themselves relative to the loft using olfactory cues. Olfactory navigation has also been implicated in seabird navigation, where anosmia is also seen to impair homewards navigation (Gagliardo, 2013; Pollonara et al., 2015; Padget et al., 2017). Evidence for olfactory navigation is, however, equivocal in extremely long-distance songbird migrants, hence the generalisability of olfactory navigation is the source of some debate (Holland et al., 2009; Kishkinev et al., 2020).

Amongst songbirds there instead exists evidence for navigation using different gradient cues, namely quantities extracted from the Earth’s magnetic field. 3 magnetic parameters have been postulated to be navigationally useful to birds, the first of which is the previously mentioned magnetic inclination. Magnetic inclination varies near-linearly with distance from the pole, hence could in principle be used to determine latitude (see Figure 1.2

for inclination isolines in Europe). Inclination has been implicated in the navigation of both teleost fish (Putman et al., 2013; Putman et al., 2014a) and sea turtles (Brothers & Lohmann, 2015, 2018) and there is even some evidence for inclination-based spatial positioning in songbirds too (Fransson et al., 2001). Inclination could, therefore, provide latitudinal information in avian taxa also.

The second magnetic cue implicated in animal navigation is the overall intensity of the Earth's magnetic field. As with magnetic inclination, intensity has been suggested to underlie teleost and sea turtle navigation (Putman et al., 2011; Putman et al., 2014b; Scanlan et al., 2018), and there is even some evidence that a magnetite-based receptor in the beak of birds may also inform on magnetic intensity (Bookman, 1978; Mora et al., 2004; Dennis et al., 2007; Wiltschko et al., 2009; Holland & Helm, 2013). However, as mentioned above, the potential magnetic intensity receptor in birds has been recently shown to probably be macrophages rather than any sensory tissue (Treiber et al., 2012). Therefore, whilst magnetic intensity varies substantially across the globe, correlating approximately with latitude and hence being an ideal candidate for long-distance gradient navigation (see Figure 1.2), its role in avian navigation is unclear.

Both inclination and intensity have been suggested to have their greatest utility when informing on latitude. However, the final magnetic cue suggested to be navigationally useful in birds, declination (i.e. the angle between true and magnetic north; see Figure 1.1), correlates better with longitude (see Figure 1.2). As such, a map comprising both declination and one (or both) of inclination/intensity has been been suggested in songbirds, with evidence stemming from the apparent ability of songbirds to compensate for longitudinal magnetic displacement (Chernetsov et al., 2017; Pakhomov et al., 2018; Kishkinev et al., 2021). However, this ability is seemingly not widespread amongst songbirds (Chernetsov et al., 2020), and hence further investigation into a declination map is necessary.

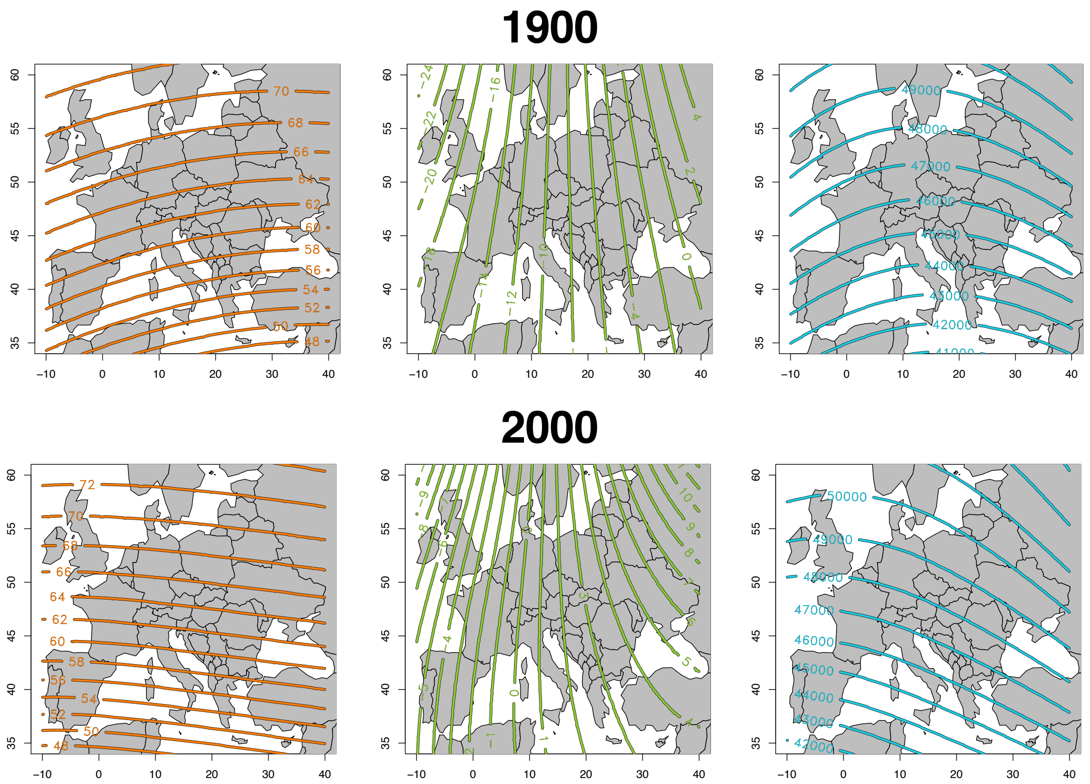

Figure 1.2: The Earth's magnetic field in Europe over the last century. Magnetic isolines of inclination (left), declination (centre) and intensity (right) in the years 1900 (top) and 2000 (bottom) for Europe and North Africa. All magnetic values are derived from the International Geomagnetic Reference Field (Thebault et al., 2015). Declination and inclination isolines are given in degrees, whilst intensity isolines are given in nanoteslas.

1.2.3 Inheriting trajectories in 3 dimensions

Thus far I have considered how an animal might a) discern their position and b) determine their orientation. However, I have left the development of these feats unconsidered. Similarly, I have yet to touch upon how migratory trajectories might be inherited.

As discussed above, there exists some evidence that experienced avian navigators can determine their position relative to some form of 'map'. However, such an ability has been seen to be largely absent in naïve individuals. Efforts to test this have focused primarily upon displacement experiments, where birds are taken from their traditional migratory route and released in hitherto unvisited locations. The expectation is that individuals navigating using a map would be able to compensate for such manipulations, ending up at the intended destination, whilst animals orienting using simpler systems would be unable to do so. The first such displacement experiment was conducted by A.C. Perdeck, who caught starlings (*Sturnus vulgaris*) travelling along the north coast of Europe and displaced them to Basel, Switzerland (Perdeck, 1958). Consistent with map-based navigation, adult starlings were recovered in north-west Europe (i.e. the normal wintering site). Immature birds, however, were recovered largely in Iberia, suggesting that they were unable to compensate for displacement and instead proceeded along a parallel course (see Figure 1.3 for a summary). Whilst Perdeck ringed and subsequently displaced > 10,000 starlings, the displacement paradigm has been successfully replicated using both laboratory-based orientation assays (Mouritsen & Larsen, 1998) and biotelemetry (Thorup et al., 2007), with both immature pied flycatchers (*Ficedula hypoleuca*) and white-crowned sparrows (*Zonotrichia leucophrys*) seemingly unable to compensate for long-distance displacement. Instead, as with Perdeck's starlings, immature birds in both experiments oriented along a parallel trajectory as if they'd not been displaced.

Such agnostic responses to displacement have been suggested to reflect an innate program of orientation within naïve birds, with bird unaware of where they are and instead executing a series of fixed orientation responses. Such a program could lead birds to the wintering ground if birds knew both the directions to take, and the distance to travel. It has been suggested that migratory distance could be encoded as time spent in flight, and there is some evidence for such a migratory 'clock'. Specifically, it has been observed that even within a species the extent of migratory restlessness ('*zugunruhe*') is well correlated with the distances birds have to travel (Gwinner & Wiltschko, 1978; Berthold & Querner, 1981). Taken alongside a compass, this inherited 'clock and compass' vector has become the prevailing theory when considering avian migratory inheritance. Further credence has been lent both by the fulfillment of theoretical expectations of vector orientation (Mouritsen, 1998) and, more recently, by a series of remarkable *in situ* biologging studies where streaked shearwaters (*Calonectris leucomelas*) were shown to fly seemingly maladaptive routes over inland mountain ranges (Yoda et al., 2017; Yoda et al., 2021). Such orientation decisions are, it can be reasoned, reflective of the

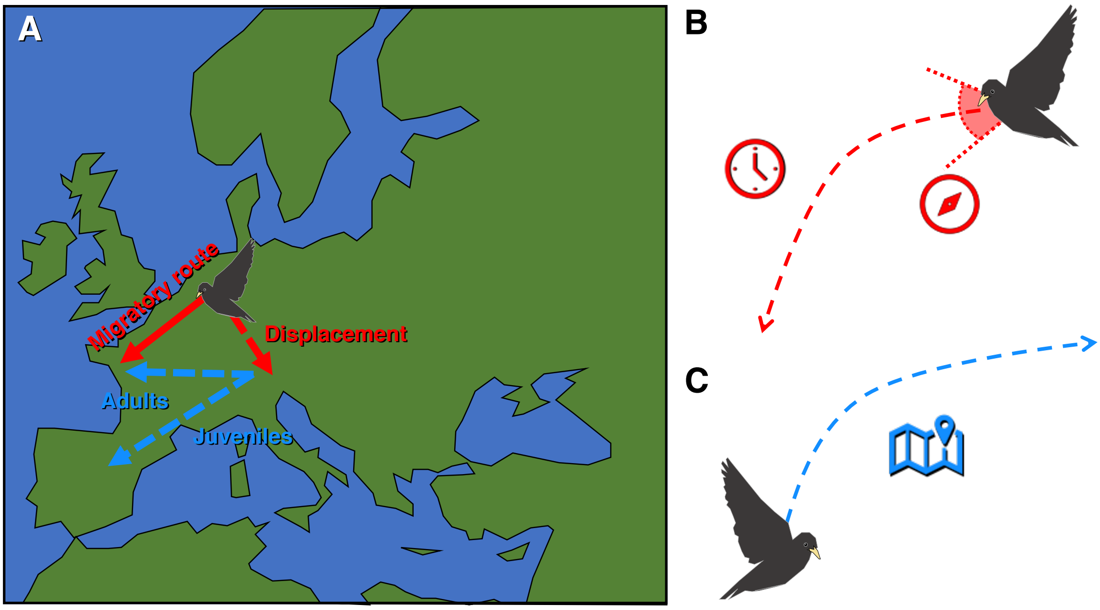

Figure 1.3: The ‘clock and compass’ theory of migratory inheritance. A) Summary of A.C. Perdeck’s 1958 starling displacement, with the solid red arrow indicating the normal migratory route, the dashed red arrow showing the displacement treatment and both blue arrows showing the responses of chicks and adults to the treatment. B) Visual caricature showing the information available to first-time migrants under clock and compass theory. C) Visual caricature showing the information available to experienced navigators on migration.

limitations of vector orientation. Alternative theories of inheritance have, however, been postulated. Specifically, the ability of juvenile common cuckoos (*Cuculus canorus*) to apparently compensate for displacement (Thorup et al., 2020) has been suggested to show that birds are born with some kind of ‘map’, as is seemingly the case in salmonid fish and sea turtles (e.g. Putman et al., 2011; Naisbett-Jones et al., 2017; Scanlan et al., 2018). Further experimentation is, then, necessary to resolve the apparently conflicting evidence found in different taxa.

Whatever birds inherit, it is apparent that it is at least in part inherited genetically or epigenetically (for a review, see Merlin and Liedvogel, 2019). A series of by-now classic cross-breeding experiments report that the progeny of southeast-migrating and southwest-migrating Eurasian blackcaps (*Sylvia atricapilla*) orient in an intermediate southwards direction, suggesting that additive genetic variance determines migratory direction (Helbig, 1991; Helbig, 1996). This has been further hinted at in correlative studies conducted in the ‘transition zone’ between southeast-migrating and southwest-migrating blackcaps, where consistent with additive genetic variance an intermediate migratory direction has been reported (Delmore et al., 2020). Additive genetic variance cannot, however, completely explain the variance seen in free-flying birds.

Firstly, extremely divergent migratory routes can evolve and persist and in blackcap populations seemingly undergoing genetic panmixia (Plummer et al., 2015; Delmore et al., 2020). If migratory route were entirely determined by additive genetic variance, then extremely maladaptive intermediate phenotypes would presumably arise and selection away from highly divergent migratory routes (or towards speciation) would occur. It is possible, therefore, that some of the genetic inheritance of migration is non-additive, and it has been suggested that migratory routes might be inherited relative to a bipolar migratory axis (Thorup, 1998). In principle, Mendelian variance in such a bipolar axis could reconcile the problem of additive genetic variance and diametrically opposing migratory routes in a panmixing population.

Secondly, several migratory species have been observed to execute different trajectories when removed from their conspecifics, suggesting that there might also be a cultural component to long-distance migration. Many of these studies have focused upon birds being held behind or displaced prior to first migration (as has been observed in white stork, *Ciconia ciconia*; Chernetsov et al., 2004), though more recent studies have taken advantage of artificial reintroduction projects to chart the cultural development of migratory route over successive generations (e.g. in whooping cranes, *Grus americana*; Mueller et al., 2013). However, cultural inheritance needn’t necessarily involve related conspecifics, and indeed in white storks the relative migratory speeds of immature and adult birds suggests that first-year birds would be unable to follow their parents (Rotics et al., 2016). Cultural transmission of migratory route through social learning involving both related and unrelated conspecifics is, then, well established as a means of migratory inheritance. However, many bird species display age-specific differences in migration phenology (e.g. Hake et al., 2003) and hence the opportunity for cultural inheritance is probably not universal. As such, it is likely that (epi)genetic inheritance is of some considerable importance in the vast majority of migratory bird taxa.

In contrast to outbound migration, return migration presents a rather different challenge. Amongst migratory birds philopatry, that is faithful return to the natal/breeding site, is near-ubiquitous (Newton & Brockie, 2008). Such a phenomenon necessarily requires a greater degree of navigational accuracy than the outbound trip, and as such we might expect the mechanism underpinning navigation amongst experienced individuals to be very different. Accurate return to the breeding site following long-distance navigation has been suggested to rely on learnt information (Baker, 1978), and hence below I will explore how learning might inform navigation, both during return migration and more generally.

1.2.4 The roles of experience and learning in avian navigation

It is apparent that we have some idea of the sensory basis of the long-distance ‘map’ used by experienced navigators, and that it is unlikely that such a map is used by inexperienced individuals. As such, we might conclude that such a map is learnt through experience. Is is essential, therefore, to consider how such a map might be structured, as well as how it might be learnt.

In homing pigeons it has been suggested that gradient maps might be learnt using the wind, with different wind directions bringing either different cues (Papi et al., 1972) or different ratios of the same cues (Wallraff, 1990) to the loft location. Birds could, in theory, use this experience to reverse the wind directions associated with the olfactory cues they are currently experiencing in order to determine a direction homewards. This would, however, leave birds with no indication of how far to travel. Such a navigation system has been termed a ‘mosaic map’ (Papi et al., 1972), in instances when different odours represent different directions, or a ‘gradient map’ when cues vary along 2 long-distance non-parallel axes (Wallraff, 1990).

The principles of a gradient map could be further expanded so as to allow for navigation even from outside a navigator's familiar area. If 2 gradient cues, olfactory, magnetic or otherwise, distributed along non-parallel axes, birds could in principle perceive the sign and magnitude of cue differences between those remembered at the home site and those presently experienced (Wiltschko & Wiltschko, 2003). Through this comparison, birds could compute both a distance and a direction home. The computation of distance perhaps elevates the utility of this so-called 'extrapolated map' beyond that of a simple gradient map, and moreover the computation of distance becomes a key predictor of extrapolated map navigation. Indeed, it is thought that procellariform seabirds can compute both distance and direction when homing (Padget et al., 2019), which in turn has been used as evidence that at least amongst seabirds extrapolated map navigation might prevail.

Navigation using an extrapolated map implies that an individual might, in principle, be able to navigate homewards from an area to which it has never previously visited. This ability has been termed 'true navigation', here defined as knowing the distance and direction homewards without outward journey information or goal-emanating cues (Baker, 1978; Phillips et al., 2006; Holland, 2014; Padget et al., 2019). True navigation has been tested in a wide variety of taxa through displacement experiments, and there is growing evidence that adult birds may indeed be able to true navigate (e.g. Perdeck, 1958; Thorup et al., 2007; Chernetsov et al., 2008). It had been traditionally thought that feats such as true navigation must require a dedicated cognitive module, such as the cognitive map suggested to underlie novel short-cutting in mammals (Tolman, 1948). Whilst such considerations are slightly tangential to the aims of this thesis, a 'map' module could in principle comprise a neurological structure with Euclidean properties, and would be parameterised through exploration via path integration. Such a module is controversial, however, and whilst there is limited evidence for a mammalian cognitive map, there is no evidence for an equivalent structure in birds. The alternative to a dedicated cognitive unit comprising the avian cognitive map is, as with much of animal behaviour, classical associative learning using a stimulus-response (SR) paradigm. Map-like navigation is typically considered beyond such simple a mechanism (Jacobs, 2003), though this has recently been the subject of skepticism by some authors (Guilford & Burt de Perera, 2017).

Whilst it is unclear whether associative learning might underpin long-distance navigational ‘maps’, there are certain tasks that an SR paradigm would seemingly be unsuitable for, such as instances where cues must be learnt extremely rapidly without the opportunity for reinforcement through trial and error. An alternative to associative learning through exploration is imprinting, here defined as phase-specific learning during which an individual is attentive to specific cues at a specific point during development (Baker, 1978; Lohmann et al., 2008). If an animal were to associate specific cue signatures with their natal site, for example one or more long-distance spatial gradients, they might be able to identify and return to their natal site (‘philopatry’) after perhaps years have elapsed without needing to build a conventional ‘cognitive map’. There is some evidence that such imprinting might exist in sea turtles and teleost fish, where naïve individuals are thought to imprint on geomagnetic gradients and use them to guide homewards movement (e.g. Putman et al., 2013; Putman et al., 2014a; Brothers and Lohmann, 2017; Naisbett-Jones et al., 2017). Such mechanisms could in principle underlie navigation amongst migratory birds also, though there is as of yet no evidence for geomagnetic imprinting in birds.

1.2.5 Conclusion: the ‘ideal migratory bird’

In avian navigation it is clear, even if nothing else is, that what we know is far outweighed by that which we don’t. Nonetheless, I suggest that we might use the above literature review to build a consensus opinion on how the ‘ideal migratory bird’ navigates. The ideal bird is born with an (epi)genetic migratory program, which probably comprises a series of migratory directions and alongside a time period over which it should remain restless. This bird will likely spend a limited amount of time at the natal site prior to first migration, which upon commencement will be informed by not only the migratory program but possibly also the routes taken by conspecific individuals. In turn, the ideal bird will likely use a variety of compass systems, celestial and magnetic, though we might expect the specific compasses used to reflect both the bird’s ecology and its evolutionary history. We might also expect the ideal bird to regularly pass information between compasses, in order to combat inaccuracies in each system. The ideal migratory bird will arrive for the first time at its wintering ground, as defined by the point at which its *zugunruhe* stops driving it forward, and in spring will return to the breeding site. Unlike outwards migration, the ideal bird is unlikely to utilise inherited information on the return leg. Instead, the ideal bird uses some form of learnt ‘map’ to precisely target its natal site, which in turn will be recalled using learnt, possibly imprinted information. How this map is structured and learnt is unclear, though it will likely rely upon olfactory or magnetic gradients through space. Such a map may even be used on subsequent outbound migrations, underlying most navigational tasks undertaken over the rest of the ideal migrant’s life.

The ideal migratory bird is unlikely to exist. Irrespective, it represents a useful model against which we can test different theories of navigation. Throughout this thesis I will test different facets of this ideal bird, with deviation from the ‘ideal’ representing differences between the empirical work and the theoretical expectation. Such differences necessarily require explanation, which will be incorporated into the discussion sections of each chapter as well as the concluding discussion in this thesis.

1.3 General methods

Owing to the global pandemic dominating much of the period over which this thesis was written, I have been unable to rely primarily upon experimental paradigms when investigating avian navigation. There are, therefore, many empirical and analytical techniques utilised in this thesis. Two methods, however, are prominently featured: using historic ringing data, and using biologging technology. Both techniques are outlined below.

1.3.1 Using historic ringing data to study animal navigation

Uniquely identifying individuals is extremely powerful, with the ability to monitor population size, survival and demographics often predicated upon this ability (e.g.

Halupka et al., 2008; Redfern, 2010; Ockendon et al., 2013). However, individual identification is also extremely useful in the study of navigation, as it allows for the assessment of shifts in position over a given time period. When considering between-year shifts in position, we can use ringing data to therefore investigate whether such shifts correlate with variables of navigational interest, such as the Earth's magnetic field.

As outlined in Sections 1.2.1 and 1.2.2, there are several parameters of the Earth's magnetic field specifically postulated to underlie long-distance navigation. Since the Earth's magnetic field is not a 'true' dipole (in the sense that a bar magnet is), and is caused instead by convection currents in the Earth's core, there is necessarily some variation in the field over time (Putman & Lohmann, 2008). Over small timescales such differences are minimal; if they were large, the magnetic field would be a poor navigational cue. However, between years such changes are large enough to be measured by the magnetic observatories of the world. Such data can either be used in and of itself to track so-called 'secular variation' in the Earth's magnetic field or, alternatively, can be used to model variation in the Earth's magnetic field through time and space. This latter process has led to the creation of the World Magnetic Model (WMM; Chulliat et al., 2015) and the International Geomagnetic Reference Field (IGRF; Thebault et al., 2015), meaning that it is possible to estimate the magnetic field at different points on the globe at different times. In principle, the combination of modeled magnetic data and between-year changes in a given individual's position can be used to determine whether the individual in question is using magnetic information to navigate. For example, in the case of European songbirds returning from sub-Saharan Africa, we might expect them to aim for a magnetic 'target', which in turn may move between years owing to secular variation. How well birds track this measured movement can be used to determine whether they do indeed utilise magnetic spatial cues.

When considering using secular variation to investigate avian navigation, there are very few datasets better than those provided by the various ringing/banding schemes operated across the world. In Europe, for example, 956,221 Eurasian reed warblers (*Acrocephalus scirpaceus*; see Figure 1.4) have been ringed in the last 100 years, with 113,556 common

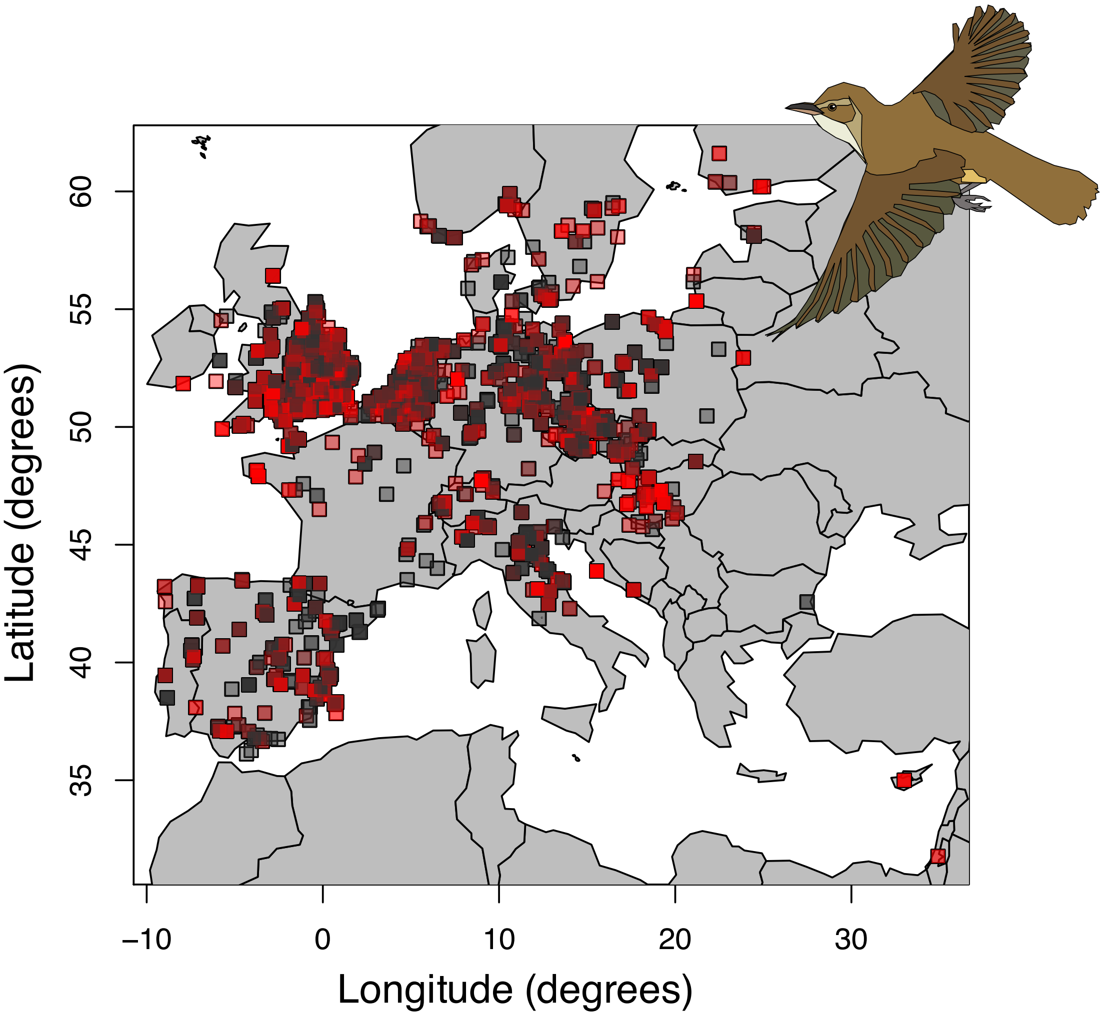

Figure 1.4: European breeding season reed warbler ringing records. The sites at which reed warblers have been ringed (red) or recovered (black) in Europe between 1928-2020. Each point is set to be translucent, hence the more opaque a point is the more birds have been ringed/recovered at that locale.

eider (*Somateria mollissima*), 322,204 white stork (*Ciconia ciconia*) and 103,037 dunlin (*Calidris alpina*) ringed over the same time period (EURING.org). Such records represent an extraordinary resource when investigating the mechanisms that facilitate trans-continental migration. In this thesis we therefore seek to use change in position between ringing and recovery to investigate the cues used during philopatry, attempting to see whether the distance and direction of such movements are predicted by magnetic variables. However, whilst changes in position can undoubtedly be investigated using ringing data, there are 2 obstacles that must first be overcome.

First, not all birds can be reasonably expected to be recovered at all positions. For example, take the case of terrestrial songbirds (e.g. Eurasian reed warblers). Such birds are constrained to certain sites by their ecology, with reed warblers restricted specifically to wetland sites (Leisler et al., 2011). Such sites, whilst widespread, are not ubiquitous if only because of topographic barriers (such as mountain ranges or the sea). The magnetic field could, therefore, shift in such a way that the ‘target’ an individual is aiming for ends up in unsuitable habitat. Again to use reed warblers as an example, the magnetic target that a Dutch bird is homing to might end up in the North Sea. If this is the case we could not reasonably expect the bird to breed at the point estimated based on magnetic variables, and hence the distance/direction moved between ringing and recovery must be influenced by environmental and topographic confounds. A further complication is that between years the availability of suitable habitat might change. In turn, such changes in habitat distribution could in principle confound any variables of interest.

The second problem with using ringing data is that, for a bird to be ringed or recovered, it has to be encountered by an observer. This means that certain movements of birds that might be predicted under a magnetic hypothesis would not necessarily be recorded in reality, simply because no one was present to read the ring of the bird in question. Looking at the reed warbler ringing effort throughout Europe shown in Figure 1.4 it is striking how few records there are from France, despite this being a country within which reed warblers breed extensively (Leisler et al., 2011). As such, the probability of recovery in a given location reflects not only changes in navigational cues and the distribution of habitat, but also the distribution of ringers. Furthermore, if this distribution changes, then this could lead to biases in the direction of movement recorded between ringing and recovery. For instance, let’s for the sake of illustration consider a highly philopatric species that disperses evenly away from the natal site. If ringing effort in this species’ range is gradually moving north (because, say, effort at the northernmost sites is increasing), then despite dispersal being symmetric a northerly movement would be observed.

Given these potential biases, how then do we using ringing data to investigate navigational hypotheses? It is key to set up a null model which takes into account the above confounds: the patchy and changing distribution of ringing effort and suitable habitat. In this thesis we attempt to do this in 2 ways. First, we have attempted to mechanically estimate the effect of changes in the environment and sampling effort and include these as predictors in a model. This we do in Chapter 2, where we investigate the use of magnetic inclination as a latitudinal cue in shearwaters, including in our linear model of changes in latitude both a variable designed to reflect changes in environmental suitability and a variable designed to reflect changes in the latitude at which sampling occurs. By doing this, we attempt to 'soak up' variance that could be attributed to changes in the distribution of environmental variables or sampling effort, meaning that the effect of inclination reported is not confounded by these variables. We expand upon this principle in Chapter 2.

However, this approach is harder to execute when examining position in 2 dimensions. True, separate models detailing longitudinal and latitudinal shifts could be constructed, and in each we could again include variables designed to reflect changes in environmental variables and sampling effort. However, in some species with large longitudinal and latitudinal ranges this might be seen as arbitrary. As such, in Chapter 3 we leave behind parametric statistics and, instead, design a series of bespoke non-parametric randomisation analyses. By mechanistically modeling equal but random between-year movements, and comparing them to the observed movements, we can model where birds can reasonably be expected to be recovered, and hence test whether the observed data fit hypotheses better than chance. This is elaborated upon in Chapter 3.

1.3.2 Biologging and experimentation

In addition to using historic ringing data, I also include in this thesis analyses conducted using biologging data. In total 3 chapters utilise GPS data (Chapters 4, 5 and 6), whilst Chapter 6 also utilises geolocator data.

The Global Positioning System, known almost ubiquitously as ‘GPS’, is a satellite constellation which allows for the precise positioning of a reciever through the comparison of distances from 3 or more satellites. This distance is computed through the comparison of the time at which a radio wave is broadcast and received, with the known speed of light allowing for the calculation of distance. Unlike GPS, geolocator systems (or ‘GLS’) function by ascertaining the time of sunrise and sunset and hence calculating the photoperiod. Between the time of sunrise/set and the length of the photoperiod both latitude and longitude can be determined with surprisingly little spatial error (typically < 250km; For a review, see Lisovski et al., 2020).

Data from 3 different GPS device classes are presented in this thesis. First, we used remote download Platform Terminal Transmitters to download GPS fixes taken from

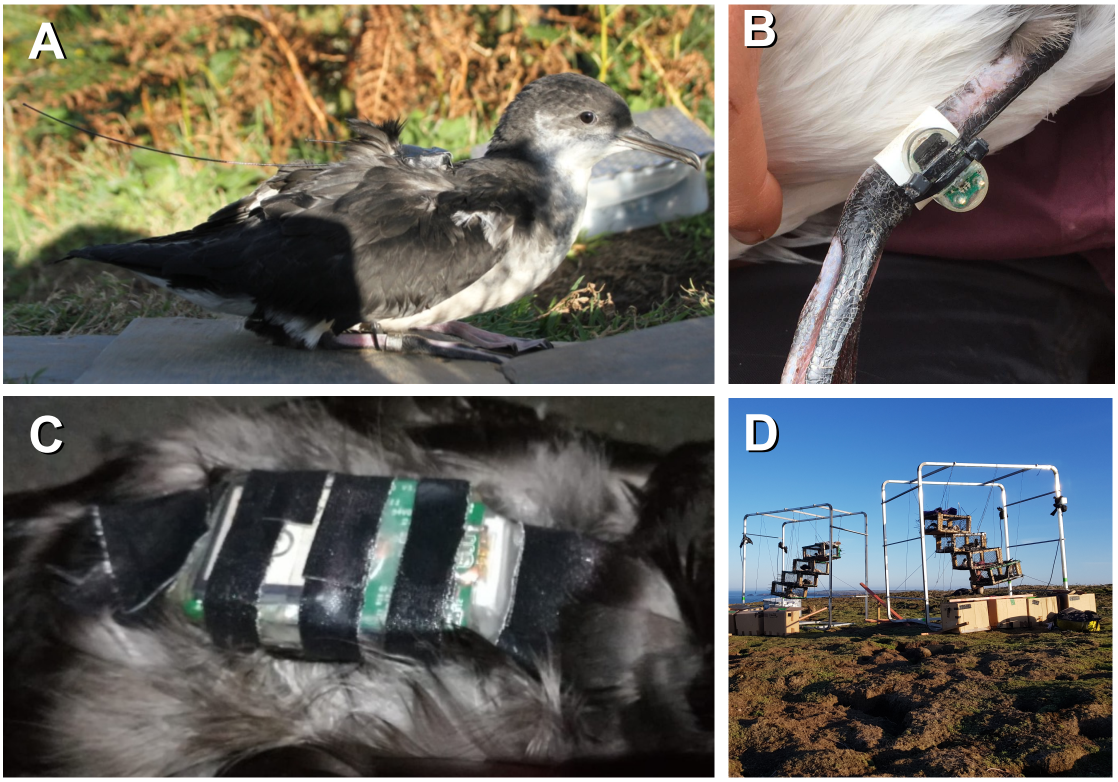

Figure 1.5: Biologging as a correlative and an experimental paradigm. A) Fledgling Manx shearwater fitted with the Lotek PinPoint PTT-GPS used in Chapter 6 of this thesis. B) Manx shearwater with the leg-mounted Migrate Tech C65 geolocator used in Chapter 6 of this thesis. C) Manx shearwater with the dorsally deployed iGotU Mobile Action GPS device used in Chapter 4 of this thesis. D) The Helmholtz coils used to generate artificial magnetic fields in Chapter 4 of this thesis.

fledgling shearwaters (‘PTT-GPS’) via the Argos satellite constellation (see Figure 1.5A). We similarly used archival GLS to track both fledglings and their parents, with the devices retrieved and downloaded subsequently at the colony (see Figure 1.5B). Second, we use commerically available iGotU devices in an *in situ* field manipulation of the local magnetic field (see Figures 1.5C and 1.5D). Finally, we used solar-powered remote-download GPS deployed prior to fledging on frigatebirds, which recorded fixes for between 1 and 3 months post-fledging.

Broadly speaking, biologging devices were used either in correlative analyses (Chapters 5 and 6) or experimental study (Chapter 4). However, since both the aims of the studies and the devices used differ substantially between chapters, details regarding the post-processing used and the analyses conducted are outlined specifically in the methods section of each chapter.

1.4 Objectives and aims of this thesis

This thesis aims to examine the development and mechanism of navigation amongst birds. Each data chapter in the thesis has been written as a self-contained manuscript, hence contains its own introduction, methods, results and discussion sections. At the point of writing Chapter 2 is published in *Current Biology*, Chapter 5 is published in *Proceedings of the Royal Society B*, Chapter 3 is in press at *Science*, Chapter 7 is in press at *Journal of Comparative Physiology A*, Chapter 6 is in press at *Ibis* and Chapter 4 is *in prep* for submission to a peer-reviewed journal.

How birds return precisely to their natal site, after many thousands of kilometres have been traversed and several years have elapsed, is both remarkable and unsolved. Long distance spatial gradients learnt prior to departure could be used to target the natal site (Baker, 1978), hence in **Chapter 2** we tested whether one such gradient, magnetic inclination, was used by Manx shearwaters when returning to the colony for the first time. Using more than half a century of ringing data, we found that changes in position between when birds leave the natal site and return 3 years later (Brooke, 1990) are predicted by changes in the inclination of the Earth's magnetic field. Further, we find that these changes bear out quantitative predictions as to the extent to which birds would be expected to move under a magnetic model of navigation.

Inclination, however, necessarily gives only the latitudinal position of the natal site and hence needs to be combined with longitudinal information. Since Manx shearwaters have an extremely longitudinally constrained range, correlatively investigating the mechanism by which they might determine longitude could be challenging. Consequently, in **Chapter 3** we used Eurasian reed warbler ringing data to investigate a) whether they too used magnetic inclination when returning to the natal site and b) if so, whether they used other magnetic cues (declination and intensity) to determine the precise bi-coordinate position of the breeding site. Whilst we again found evidence for the use of magnetic inclination, we found no evidence for the use of other magnetic cues when locating the natal site. Furthermore, we foumd evidence that reed warblers may in fact only use a single uni-coordinate magnetic cue when locating the natal site, using it as a 'stop sign' in conjunction with a return migratory bearing (Mouritsen, 2003).

Magnetic cues are not, however, suitable only for positional information. Magnetic cues could also provide compass information, as has been repeatedly shown in songbirds (Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1992; Schwarze et al., 2016). However, evidence for magnetic compass use in other taxa remains elusive (e.g. Gudmundsson and Sandberg, 2000). In **Chapter 4**, we used twlight manipulation of the magnetic field experienced by shearwaters in order to assess whether they might use a magnetic compass when orienting within a familiar area. We found that the deflection of shearwaters displaced offshore was predicted by the magnetic treatment, and further found that the extent of this deflection was predicted by the accuracy with which the natural geomagnetic inclination was imitated by the artificially applied field. This is consistent with seabirds orienting using a magnetic inclination compass, hence we suggest that the use of a magnetic inclination compass might be more ecologically and phylogenetically widespread than is currently thought.

Orientation is, however, of little use when moving within a fluid medium if the movement of the fluid in question is not taken into account when making navigational decisions (Chapman et al., 2011). As such, in **Chapter 5** we investigated whether a pelagic seabird, the great frigatebird (*Fregata minor*), can a) compensate for wind drift and b) if so, if this ability is learnt. We found evidence that frigatebirds learn to compensate for wind drift, and that their ability to compensate for wind drift was greater when in-sight of land. We also found that the rate at which frigatebirds learnt to reduce drift was greater out-of-sight of land.

In addition to investigating the role of learning in wind drift, in **Chapter 6** we investigated the relative contributions of learnt and genetically inherited information when considering the distinct outbound and return migratory trajectories taken by Manx shearwaters. By tracking juvenile shearwaters from before fledging, we found little evidence for social learning when considering both outbound and return migration, hence concluding that the characteristic trans-Atlantic 'loop migration' of Manx shearwaters is unlikely to result from cultural inheritance. Further, we suggest that genetic inheritance is likely to underlie outbound migration, and that the return migration trajectory could be built iteratively through a process of 'exploration-refinement' (Guilford et al., 2011b).

In the last analytical chapter (**Chapter 7**) of this thesis we consider, in light of the results of Chapter 3, the potential effects of secular variation on the position represented by different bi-coordinate magnetic maps. Using the IGRF, we found that the position denoted by all magnetic combinations move between years, with the extent of this movement predicted by both the acute angle between field isolines and the direction of field isolines movement relative to each other. Based on this, we suggest that field parameters that vary in a near parallel arrangement are likely unsuitable for use as map cues, and we suggest more generally that the use of magnetic cues as uni-coordinate stop signs may be less affected by secular variation than the traditional bi-coordinate map.

Finally, in **Chapter 8** we will synthesise and summarise our findings, discussing the relevance of the findings presented in our data chapters and considering how they fit into the extant animal navigation literature.

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2

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

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Contents

2.1 Abstract

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). 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. 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.

“See the line where the sky meets the sea? It calls me.”

– Auli’i Cravalho, *How Far I’ll Go*

2.2 Introduction

Natal philopatry is widespread across migratory vertebrate taxa, from reptiles and fish to marine mammals and birds, especially colonial seabirds (Newton & Brockie, 2008). The accurate return of species without post-natal care to breeding grounds after first migration, sometimes called 'natal homing' (Lohmann et al., 2008), constitutes a remarkable behavioural phenomenon. It requires the learning of locale-specific information capable of the homeward guidance of long-distance movements, after perhaps years of elapsed time and based on very limited experience. Unlike first-time outbound migration, which may be at least partly controlled by an inherited vector (Perdeck, 1958; Mouritsen, 1998; Mouritsen & Larsen, 1998; Thorup et al., 2007; Yoda et al., 2017), return to the natal site requires greater accuracy than is achievable by compass, and the underpinning mechanisms remain poorly understood.

Spatial familiarity acquired through exploratory movements and outbound migration may be an important component of natal homing in many species (Baker, 1978; Guilford & Burt de Perera, 2017). Nevertheless, imprinting by neonates prior to first migration on locale-specific values of a wide-ranging gradient cue, such as the intensity or inclination of the Earth's magnetic field, 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'. Support for a 'Geomagnetic Imprinting Hypothesis' (Lohmann et al., 2008) has been found in sea turtles (Chelonioidae) and salmon (Salmoniformes), where natural variation in the Earth's magnetic field and contrasts induced by local topography suggest the use of magnetic cues specific to the natal site when navigating (Putman et al., 2011; Putman et al., 2013; Putman et al., 2014; Brothers & Lohmann, 2015; Putman et al., 2015; Brothers & Lohmann, 2017). Experimental sensory manipulation in loggerhead turtles, *Caretta caretta*, also suggest that magnetic cues could play a role in neonatal navigation (Irwin & Lohmann, 2005; Fuxjager et al., 2014).

Although much is now known about magnetoreception in birds, specifically the role of the inclination angle of Earth's magnetic field in the compass orientation of night-migrating passerines (Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1992; Hein et al., 2011; Schwarze et al., 2016), the potential role of geomagnetic imprinting in avian natal philopatry has not been investigated.

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 Procellariform seabird with a trans-equatorial, trans-Atlantic migration pattern. Manx shearwaters breed on islands in the East Atlantic across a latitudinally diverse but longitudinally constrained range (c.-5°E to -10°E, c.45°N to 65°N). From ringing recoveries (Brooke, 1990) and geolocators (Guilford et al., 2009), 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 their second summer, with breeding commencing several years later (Brooke, 1990). Since 1954, some 2996 Manx shearwaters from British colonies have been ringed as chicks and later recovered as returners (>1 year later) at or close to a breeding colony, with around 4% of these birds recovered at non-natal colonies. The species thus exhibits a high degree of natal philopatry.

To address whether this natal philopatry might be informed by magnetic cues, we investigated whether, for birds that apparently recruited to a colony other than the natal colony, the switch correlated with latitudinal changes in the Earth's magnetic field between fledging and recruitment. Both magnetic inclination angle and total magnetic intensity vary latitudinally, with a greater inclination angle and higher intensity associated with more northerly latitudes (for locations in the northern hemisphere). As such, both could inform on the latitudinal position of the natal site. Minor fluctuations in the earth's magnetic field mean that, for a given latitude, inclination and intensity can increase or decrease year on year. This is associated with a corresponding northward or southward movement in the latitude at which specific parameter values occur (see Figure 2.1 for magnetic shifts over the sampled period). Thus, if Manx shearwaters make use of magnetic parameters during natal homing, such changes might be reflected in the errors or biases associated with where they return to breed, allowing for the following qualitative prediction: with decreased magnetic intensity/inclination values, birds will be more likely to recruit to the north of their natal colony, whilst increases will lead to a greater chance of recruiting to the south (see Figure 2.1 for a graphical representation). Further, if inclination/intensity is being used to infer latitude, then we can make two further quantitative predictions. First, we predict that the intercept of the linear regression of latitude against inclination/intensity should be zero (i.e. when there is no change in inclination/intensity there is also no change in latitude). Second, if inclination is used to infer latitude, the gradient of the inclination vs latitude linear model should be approximately 1.34, as this is the ratio of degrees inclination to degrees latitude in the British Isles (it is not a 1:1 ratio as inclination isolines are closer together at the the equator). By comparing the magnetic field at the point when a fledgling leaves its colony and the field at the point it returns (c2.5 years later; Brooke, 1990) we can calculate a change in the magnetic field parameters of interest. We can then assess how this change predicts the change in latitude at recruitment.

2.3 Methods

2.3.1 Data collection

5988 Manx shearwater ringing recoveries were obtained from the BTO, representing 3336 unique individuals ringed as chicks and recovered as breeding adults. 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. Of the 2996 fledglings recovered 109 had changed colony, moving a mean distance of 134km (± 90km; see Figure 2.3). 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

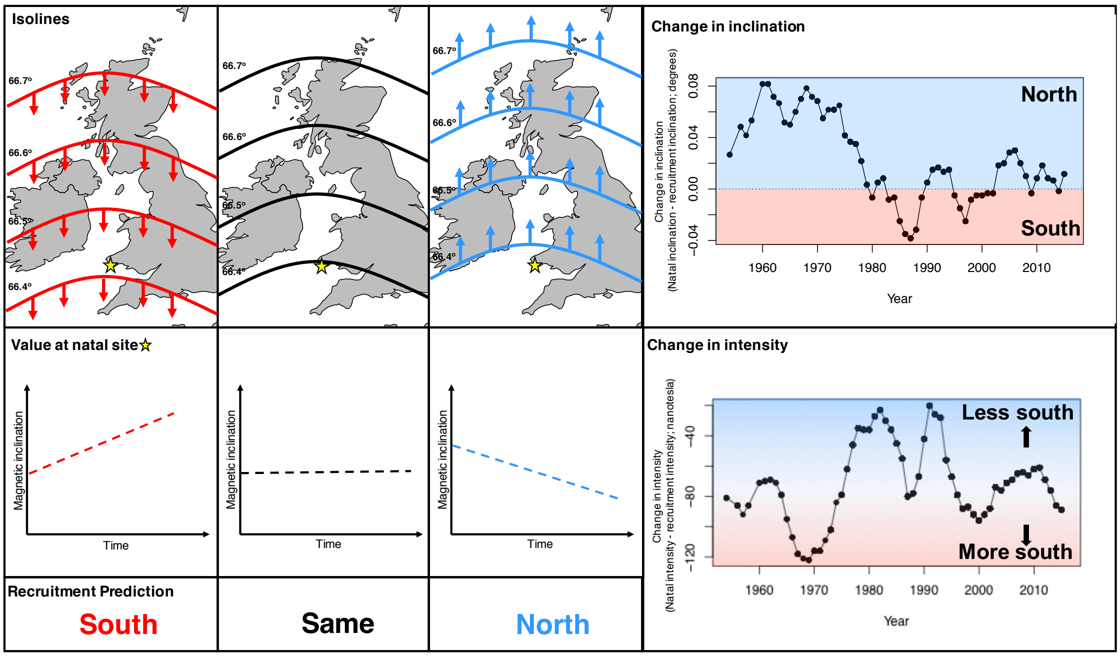

Figure 2.1: Changes in magnetic field parameters and their predicted effects. (left) The effects of changes in inclination on (top) isolines, (middle) recorded inclination at a given site and (bottom) predicted shifts in recruitment. (right) The changes in magnetic inclination (top) and intensity (bottom) in the British Isles 1954-2019.

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. We, additionally, calculated a change in sea surface temperature (SST) based on data derived from the European Environment Agency. This we used to assess whether any correlations between magnetic variables and latitude were better explained by changes in climate.

2.3.2 Parametric statistical analysis

All statistical analyses were performed in R (R Core Team, 2017).

To test whether changes in magnetic parameters 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. We, additionally, tested whether changes in sea surface temperature predicted changes in the latitude to which birds returned. All linear models were fitted using least squares.

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 observed under the null hypothesis if changes in sampling effort across the latitudinal range of Manx shearwaters lead to an apparent non-zero 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 birds that moved north between ringing and recovery would be disproportionately represented in our dataset. Consequently, since ringing effort at colonies of different latitudes has not necessarily remained constant, 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.

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; Brooke, 1990) 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:

$$\Delta Lat_{exp} \sim Lat_r - \frac{\Sigma_{n=0}^{p-R} L\bar{a}t_R \times 0.95^n}{\Sigma_{n=0}^{p-R} \times 0.95^n} \tag{2.1}$$

Where Lat_R = Latitude focal bird ringed at, R = year ringed and P = the last year for which ringing data collected. ΔLat_{exp} was then included in all linear models as a predictor designed to model the expected latitudinal bias owing to sampling. This variable makes the assumption 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.

2.3.3 Non-parametric statistical analysis

In addition to assessing the relationship between different magnetic parameters and recruitment latitude using parametric statistics, rank-order randomisations were also carried out to ensure than any results were not driven by non-normally distributed data. Qualitative directions were assigned 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^o). Shifts in latitude were then 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.

2.4 Results

2.4.1 The effect of the Earth's magnetic field on recovery latitude

We found that shifts in recruitment latitude were significantly predicted by shifts in inclination (LM; F = 34.7935, $p < 0.0001$, Figure 2.2). 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. This too suggested a significant effect of inclination shift on recruitment latitude ($p < 0.0001$), 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 was 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).

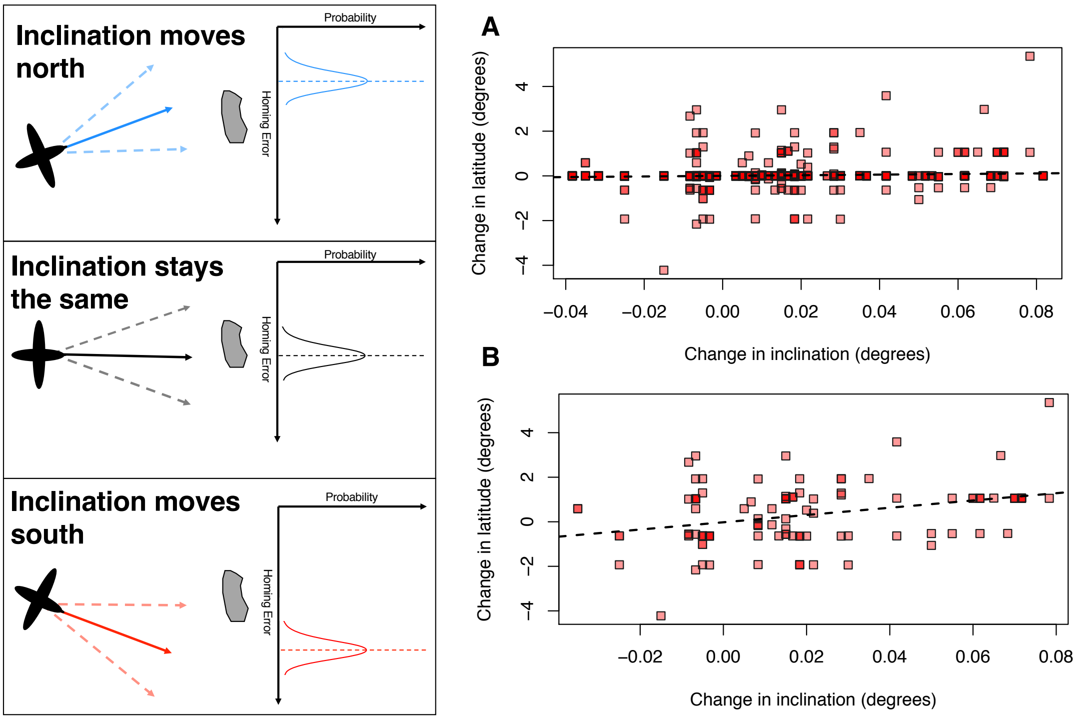

Figure 2.2: The recruitment of Manx shearwaters with magnetic inclination. (left) The expectation of homing biases based on changes in inclination. We expect that small shifts in the Earth's magnetic field will interact with an existing probability of changing colonies (due to, for example, imprecisely 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 B) changes in inclination plotted against changes in latitude for birds that changed colony (n = 109). Regression lines in A) and B) represent least mean squares regression lines.

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.

2.4.2 The effect of sampling effort on recovery latitude

We found that changes in the sampling latitude, as outlined in equation 2.1, were a significant predictor of the latitude at which birds were recovered (LM; F = 71.3764, p <0.0001). 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 in sampling distribution. This, we believe, is because the probability of ringing recovery is dependent on sampling effort. 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.

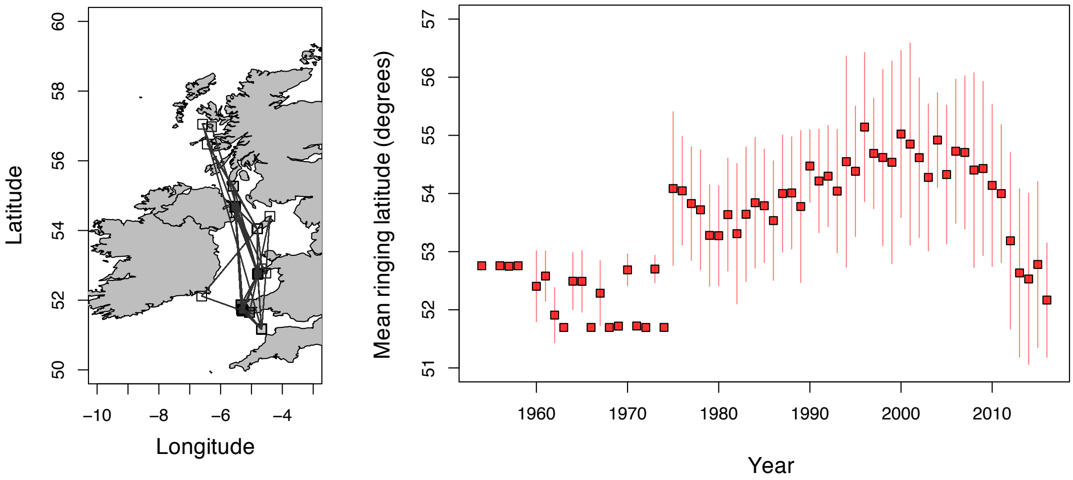

Figure 2.3: The latitudinal shifts between ringing and recovery recorded in Manx shearwaters, and the changing latitudes at which Manx shearwater were ringed. (left) Changes in colony between ringing and recovery for each shearwater that was ringed and recovered at different colonies (n = 109). Each bird is represented by a translucent point, hence the opacity of each line is proportional to the number of birds executing that precise change. (right) The mean latitude (± standard deviation) at which shearwaters were ringed for each year in our analysis dataset. A lack of error bars indicates a year for which only 1 bird was encountered.

2.5 Discussion

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; $F = 77.708$, $p < 0.0001$), 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. However, we found no effect of changes in sea surface temperature on recruitment latitude, which would probably be the most plausible non-navigational driver of post-natal dispersal in a pelagic seabird. As such, given how precisely the data fit the magnitude and direction of our *a priori* predictions, we believe that the most parsimonious explanation is the direct use of magnetic inclination in seabird natal philopatry.

Baker (1978) postulated that natal philopatry in migratory birds might be enabled by the learning of locale-specific cues pertaining to the natal site, perhaps utilising exploratory movements (e.g. Mukhin et al., 2005) or information gathered on the first outward migratory journey. The mechanisms involved have, however, been seldom investigated. Unlike the learning of a detailed familiar area map, or a larger scale extrapolated navigational map, around the home site, the specific task of first returning to the natal site long after fledging (and a potentially rapid first autumn migration like that seen in shearwaters; Brooke, 1990) may favour a targeting mechanism based on some form of imprinting which requires no exploratory experience. Our results suggest that, as in sea turtles and teleost fish taxa (Lohmann et al., 2008; Putman et al., 2013; Putman et al., 2014; Brothers & Lohmann, 2015; Putman et al., 2015; Brothers & Lohmann, 2017), shearwaters might imprint onto the 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 focusing 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 2.2). 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 (Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1992; Wiltschko et al., 1993; Schwarze et al., 2016), currently thought to be underpinned by the differential reactivity of quantum-entangled electrons (Ritz et al., 2000; Ritz et al., 2004; Engels et al., 2014; Kobylkov et al., 2019; Xu et al., 2021; for a review, see Hore and Mouritsen, 2016). The use of magnetic information for non-compass navigational cues has also been postulated in migratory birds such as reed warblers (*Acrocephalus scirpaceus*; Chernetsov et al., 2008; Kishkinev et al., 2013; Kishkinev et al., 2015; Chernetsov et al., 2017; Pakhomov et al., 2018) and Silvereyes (*Zosterops lateralis*; Fischer et al., 2003). However, in the diurnal homing pigeon the consensus is that magnetic cues are at best of secondary importance in homeward navigation (Wallraff, 2005; Holland et al., 2013a, 2013b). Interestingly, in procellariforms, 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 (Benhamou et al., 2003; Bonadonna et al., 2003; Bonadonna et al., 2005; Gagliardo et al., 2013; Pollonara et al., 2015; Padget et al., 2017). 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 procellariforms 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 (Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1992; Schwarze et al., 2016).

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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3

Magnetic ‘stop signs’ signal a European songbird’s arrival at the breeding site following migration

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Contents

3.1 Abstract

Each year, billions of trans-equatorial, trans-continental, night-migratory songbirds return from the tropics to breed across temperate latitudes. Although it is known that these birds can navigate back to their breeding grounds with remarkable precision, it has remained a mystery how they know when and where to stop migrating. Here, using nearly a century of Eurasian reed warbler (*Acrocephalus scirpaceus*) ringing recoveries, sampled from across the species' range, we investigated whether fluctuations in the Earth's magnetic field (EMF) predict variation in the exact sites to which birds return. The 17,799 ringing recoveries specifically imply that magnetic inclination is learned prior to departure and is subsequently used as a uni-coordinate 'stop sign' when relocating the breeding site. Surprisingly, this suggests that a simple single coordinate navigation system, rather than a bi-coordinate map may underlie philopatry in songbirds. However, many locations have the same inclination angle. Data from populations with different migratory return directions indicate that birds solve this ambiguity by stopping at the first place where the right inclination is encountered on the bird's return vector. If this mechanism underpinned songbird migration more generally, it could explain long-term trends in the annual movement of billions of animals with implications for ecosystems across the globe.

"You know what kind of plan never fails? No plan. No plan at all. You know why? Because life cannot be planned."

– Ki-taek, *Parasite*

3.2 Introduction

Every autumn, billions of songbirds (Passeriformes) leave their breeding sites and migrate towards their wintering grounds. The first outbound migration undertaken by migrating songbirds is thought to be underpinned by a genetically inherited migratory program (Helbig, 1991). This is typically, though not universally (Thorup et al., 2020), thought to involve a 'clock and compass' mechanism a clock to tell an individual how long to travel for (Perdeck, 1958; Thorup et al., 2007; Yoda et al., 2017). The information that allows birds to return, often extremely precisely, to their natal/breeding site ('philopatry') is, however, less well understood.

It has been postulated that experienced navigators of multiple taxa utilise learnt, bi-coordinate maps for navigation (Perdeck, 1958; Mouritsen, 2003; Thorup et al., 2007; Padget et al., 2019). Such maps may comprise 2 or more gradient cues. Various gradient cues have been proposed, including 3 magnetic parameters extracted from the Earth's geomagnetic field. These are magnetic inclination, the 'dip angle' between the Earth's magnetic field and the Earth's surface; magnetic declination, the angular difference between magnetic and true north; and magnetic intensity, the overall strength of the Earth's magnetic field (for reviews, see Holland, 2014; Mouritsen, 2018). On average, inclination and intensity vary with latitude and declination varies with longitude. Maps comprising 2 or more of these components have been suggested to be navigationally important in sea turtles (Brothers & Lohmann, 2015), teleost fish (Putman et al., 2013), and songbirds (Fransson et al., 2001; Chernetsov et al., 2017; Kishkinev et al., 2021). Specifically, it has been suggested that songbirds use magnetic declination alongside inclination and/or intensity as a bi-coordinate 'map' (Chernetsov et al., 2017; Chernetsov et al., 2020). Whilst studies into songbird magnetic map navigation have focussed primarily on compensating for extremely long-distance displacement, such a mechanism might also allow songbirds to use magnetic information learnt prior to migratory departure, alongside other cues, to locate the natal/breeding site. Such information could be learnt via phase-sensitive imprinting (Baker, 1978; Lohmann et al., 2008) or, alternatively, through pre-migratory exploration (Mukhin et al., 2005; Guilford & Burt de Perera, 2017).

How magnetic cues might be used in avian navigation is unclear. Classically, it has been considered that gradient cues could be utilised as some form of 'extrapolated map', with bi-coordinate position derived relative to 2 or more gradient cues (Wiltschko & Wiltschko, 2003). Such a map would allow in principle an individual to know the distance and direction to a target from anywhere on Earth (Padget et al., 2019), which could be of some use when considering the navigation of trans-continental migrants. An alternative system of navigation has been suggested to utilise a single sensory gradient, which could act as a uni-coordinate 'stop sign' on an otherwise predetermined migratory bearing (Mouritsen, 2003). Such a system could perhaps make sense, given the apparent vector orientation of first-time migrants (Mouritsen, 1998; Thorup et al., 2007; Yoda et al., 2021).

Here, we attempted to ascertain whether Eurasian reed warblers (*Acrocephalus scirpaceus*; 'reed warblers'), a trans-Saharan migratory songbird (Leisler et al., 2011), utilised magnetic information when returning to the natal/breeding site and, if so, how. Reed warblers are night-migrating songbirds breeding in wetland habitats across the temperate Western Palearctic from Iberia to western Russia (Leisler et al., 2011). Because there are slight (but detectable) year-on-year shifts in the Earth's magnetic field (Putman & Lohmann, 2008), the magnetic parameter values characteristic of an individual's birth or breeding site will exist in a slightly different location in the following year. Hence, if birds were to use magnetic parameters to determine the location of their breeding site, we would expect a) that birds actively minimise changes in specific magnetic parameter values between years and b) that positional changes between fledging and breeding, or consecutive breeding attempts, reflect changes in the geographic location of specific magnetic field parameters over the same time period. We investigated these expectations using a dataset comprising 17,799 reed warbler ringing recoveries made between 1940 and 2018.

3.3 Methods

3.3.1 Ringing data

In our analysis we used only recoveries made in consecutive years that were likely to represent individuals at their natal or breeding sites.

Ringing data were derived from the EURING scheme (euring.org) based on a search query for any reed warblers ringed and recovered in subsequent years. Many reed warblers are ringed not at the breeding site but instead on migration. As such, ringing/recovery events were filtered so as to restrict the records used to breeding birds. Previous studies suggest that reed warblers commence breeding in late May in southern Europe and mid-June in northern Europe (Chernetsov, 1999; Halupka et al., 2008; Ockendon et al., 2013; Ceresa et al., 2020) whilst ringing totals at coastal sites both in northern Europe (Portland Bird Observatory; Southern England) and southern Europe (Gibraltar Bird Observatory; Iberia) do not record migrant reed warblers in large numbers until August. Consequently, we believe a late July cut-off is sufficient to remove the majority of migrant birds. However, it is possible that birds ringed/recovered in May and June are on northward migration. To remove these birds, we used a linear regression model of Julian date against longitude and latitude trained on ringing records of adults with a brood patch in order to estimate the point at which breeding likely commenced at a given longitude/latitude.

Based on this model we estimated, for each ringing/recovery's longitude/latitude pairing, a cut-off Julian date where breeding was likely to commence at that specific location. We then removed ringing records that fell before this date, reasoning that such records may represent birds on migration rather than breeding birds. For the birds used in our study, cut-off dates varied between the 16th June (in the southernmost latitudes of the range) and 8th July (in the northernmost latitudes). Through this process, some 75,000+ ringing recoveries were reduced to 17,799 where the ringing event occurred after the cut-off date (but before 31st July). This subset broke down into 10,784 birds ringed and recovered as adults, and 7,015 birds ringed as nestlings/fledglings and recovered as second calendar year adults. In total, our analysis used birds ringed between the years 1940 and 2018.

The above outlined latitude/longitude-specific cut-off date allows us to select for birds likely to be breeding, whilst simultaneously allowing for the largest possible sample size. Consequently, we believe that this mechanism represents the optimum trade-off between maximising sample size and minimising the probability of erroneously including migrant birds in our dataset. However, ensuring that any results are robust to the precise selection process used is essential. We have, therefore, conducted re-analyses of 3 further subsets of our data selected using different criteria. These subsets are birds captured/recovered between 15th June - 15th July, birds for which a sex had been determined (at both the ringing and recovery events) and nestlings subsequently recovered as adults at or north of the breeding site. For the first of our subsets we reasoned that it was extremely unlikely these birds were on migration given previous studies into reed warbler breeding phenology (Chernetsov, 1999; Halupka et al., 2008; Ockendon et al., 2013; Ceresa et al., 2020). For our second subset we reasoned that, given sex-determination in reed warblers requires examination of breeding-specific phenotypical features (brood patch or cloacal protrusion; Svensson, 1970), sexed birds were very likely to be recovered at the breeding site (e.g. Ceresa et al., 2020). We used positive sex identification, rather than the presence/absence of a brood patch/cloacal protrusion, as our criteria for inclusion in this analysis because the latter is not widely reported in the EURING data. For our fourth subset, we reasoned that for nestlings the ringing event had to take place at the breeding site (by definition), and that birds captured at or north of the breeding site were extremely unlikely to be still be on northwards migration when re-encountered. Therefore, by analysing these additional subsets in addition to our main dataset, we sought to ensure that the results presented in our main text were robust to the selection process used to determine which ringing recoveries to use and, further, ensure that our findings did not result from the inclusion of migrating birds in the analysis dataset. These analyses are included as an Appendix of this chapter.

In addition to testing subsets of our data selected using different selection criteria, we also reanalysed our data including a 'constant effort' cohort so as to ensure our result was not driven by a handful of year's data and was instead caused by a trend observed across all years. Our constant effort cohort comprised 50 ringing records selected at random from every year since 1967, the first year for which we have 50 records, upon which we repeated all our analyses. These are presented in the Appendix.

A not insubstantial number of reed warblers (n = 1,321) have been caught more than twice in consecutive years, and hence there is the possibility that the inclusion of such records in our analysis might be pseudoreplicative. To investigate whether this were the case, prior to our main analysis we regressed the distance between the first encounter site and the second encounter site against the distance between the second encounter site and the third encounter site. These distances were used as a proxy for philopatric faithfulness and, if faithfulness was consistent between years, we reasoned multiple records from the same bird could not be included in our analysis. We found, however, that this was not the case (LM; F = 0.0462, p = 0.830). Consequently, since we found no within-individual consistency in movements between years, we reasoned that philopatry in one year was unlikely to predict philopatry in the next and hence all records could be included in our analysis.

3.3.2 Magnetic and environmental data

Magnetic data were derived from the International Geomagnetic Reference Field 12 at a spatial resolution of 0.2° longitude and 0.2° latitude (Thebault et al., 2015). Bilinear interpolation was used to resample magnetic parameters onto a precise 2.5km x 2.5km grid, so as the grid resolution was constant throughout the range. For each year included in the study, magnetic parameters were sampled on a 2-weekly basis, and from the 16 values obtained per year a mean was derived at each location for each of inclination, declination and intensity. Using this, each ringing/recovery event was assigned a magnetic inclination, intensity and declination value based on the closest possible grid cell (maximum distance to nearest grid cell = 1.25km).

In addition, a total of 4 environmental variables were derived and their correlation against different magnetic variables investigated. These were: surface air temperature, the normalized difference vegetation index (NDVI, a proxy for live vegetative cover), the Fraction of Absorbed Photosynthetically Active Radiation (fAPAR, a proxy for live vegetative cover) and the proportion of days where a temperature of $< 0^{o}$C was recorded ('proportion frost days'). All environmental variables were gathered over the largest possible temporal range for all positions across Europe,and stored as a raster grid. For each grid cell, data were gathered for dates in May-July and a mean value for each position was calculated to represent the environmental phenology in that area in a given year. Temperature data were derived from the National Center for Environmental Prediction reanalysis dataset at a spatial resolution of 0.5^{o} longitude and 0.5^{o} latitude. NDVI was derived from the NASA AppEEARS portal for the years 2000-2020 at a spatial resolution of 1km x 1km. The fAPAR and the proportion of frost days were derived from the European Copernicus reanalysis, and were sampled at a spatial resolution of 1km x 1km over the years 1981-2014.

3.3.3 Statistics and analysis

All statistics were conducted in R (R Core Team, 2017).

Parameter shift randomisation analysis

We might expect that if birds attended to specific magnetic cues, they might actively minimise the change in specific magnetic parameters between ringing and recovery. We would, therefore, expect that the observed magnetic parameter shift between ringing and recovery would be smaller in the focal bird's observed movement than in equivalent but random movements. As such, we reasoned that we can test whether birds actively attend to magnetic parameters by comparing their movements to realistic but random null 'movements' in a randomisation analysis.

It is essential, therefore, that a realistic 'null' expectation is established for reed warbler philopatry. Based on previous studies, we may expect birds to be recovered close to their natal/breeding site (Paradis et al., 1998). However, the potential value of appropriate habitat (rather than precise location) when considering fitness maximisation, coupled to any potential inbreeding costs, the theoretical optimal precision of philopatry is unclear (Baker, 1978; Waser & Jones, 1983). Consequently, we derived our null model for natal/breeding philopatry from the empirically gathered ringing recoveries, so as the philopatry of our null birds reflected that of real birds.

Additionally, not all changes in position are available to all birds and it is essential that any null model takes this into account. For example, if a reed warbler attempting to return to the Netherlands encountered a northward shift in the Earth's magnetic field then its expected recovery position, under a model of solely magnetic navigation, would likely end up in the North Sea. This is impossible as, even if birds did respond precisely to such magnetic shifts, they would never be recovered owing to a lack of offshore ringing effort. Hence, we might expect that, given the topography of the coastline and the distribution of ringing effort, the most likely recovery position is on the nearest adjacent land. This might result in unpredictable changes in distribution with magnetic parameters; to take the above example, the longitude may change with inclination alongside latitude due to the shape of the coastline. It is, therefore, essential that the null distribution against which any hypotheses are tested takes into account not only the topography of Europe but, additionally, the patchy distribution of ringing effort over the reed warbler breeding range. This can be achieved by limiting 'null' recoveries to the sites at which real birds have been encountered.

To establish null expected recovery positions for a given bird we first sampled, with replacement, the empirically observed distances between ringing and recovery, so as our null reed warblers moved the same distances with the same frequencies as real reed

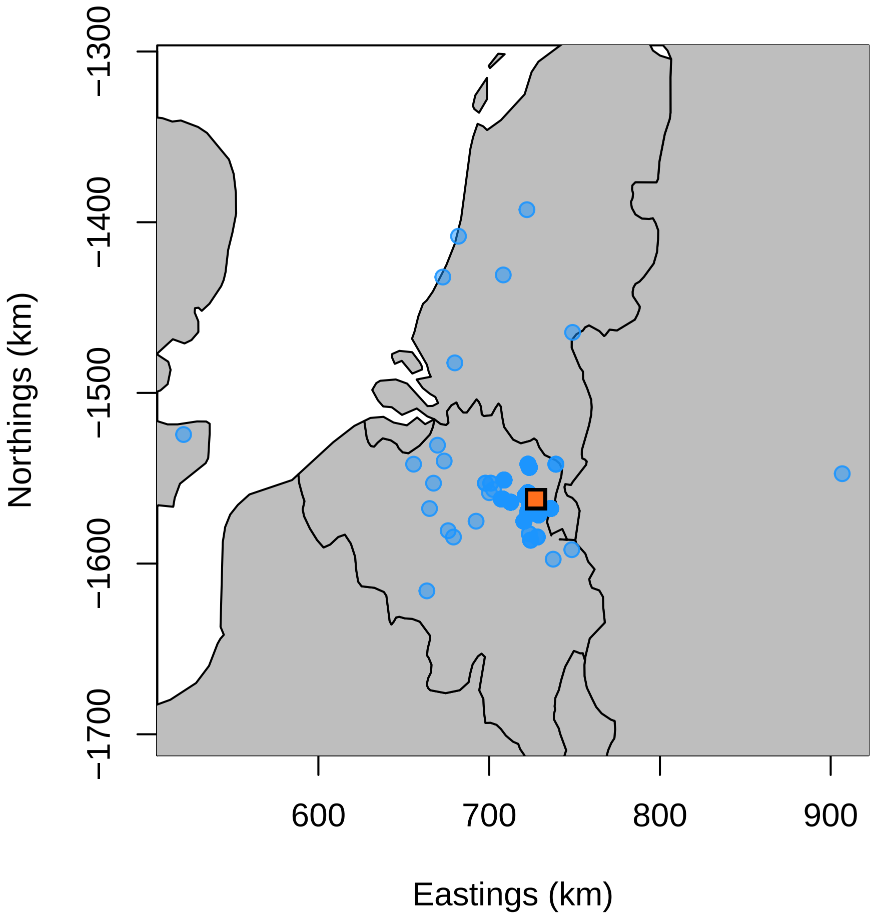

Figure 3.1: The null between-year movements of Eurasian reed warblers to which real movements might be compared. Using our randomisation procedure (see Methods), the above represents 1,000 potential recovery sites for a reed warbler breeding in northeastern Belgium. Orange/black square denotes the breeding site, translucent blue circles represent null expected recovery sites.

warblers. The distances used to generate null positions in adult birds were only drawn from distances derived from other adult birds, and likewise the distances used to generate null positions in 1st year birds were only drawn from distances derived from other 1st years. This meant that, if there were differences in the accuracy of homing between adult and 1st year reed warblers, these were taken into account in our null distribution. For each bird we then selected a recovery site from the sites at which reed warblers had been ringed/recovered that were within 1km of the sampled between-year distance. If no such point existed, we selected the point that was closest in distance to the sampled between-year distance. This ensured that every null recovery site was an observed recovery location, hence our null model didn't include unrealistic recovery sites (such as over the sea or in an area with no ringing effort; see Figure 3.1). In turn, this allowed us to account for the patchy distribution of ringing effort and habitat availability across Europe. Since the longitude and latitude at which ringing occurred didn't change significantly over time (latitude LM; F = 1.69, p = 0.190; longitude LM; F = 0.99, p = 0.590), and because changes in the longitude/latitude at which birds were ringed/recovered did not predict changes in longitude/latitude between ringing and recovery (latitude LM; F = 1.59, p = 0.201; longitude LM; F = 0.672, p = 0.413), we allowed our null birds to be recovered at any site reed warblers had been encountered at irrespective of the dates at which the site was active. This allowed for the greatest possible variation in the movement of our null birds (see Figure 3.1).

Whether birds were attentive to magnetic cues was assessed using a randomisation, iteratively comparing our null model of reed warbler movement to the movements of real reed warblers. For each null 'movement' we calculated the associated change in each magnetic parameter, before calculating the mean and median changes in the parameters of interest per iteration. This process was repeated 1,000 times, and the distribution of median/mean changes in the magnetic field per iteration were used as our null distribution. If birds were using the parameter in question to guide homewards movement, we reasoned that the true median and/or mean change in magnetic parameters derived from real ringing/recovery events would be significantly smaller than those generated by simulating random but equivalent movements. Thus, by assessing the proportion of times the null median/mean shift in a given magnetic parameter was smaller than the observed median/mean shift, we could ascertain whether a statistically significant preference for magnetic inclination, declination or intensity was observed.

Linear regression analysis

In our analysis we sought to test specifically 2 different hypotheses of magnetic navigation: bi-coordinate navigation using an extrapolated map and uni-coordinate 'stop sign' navigation (Mouritsen, 2003; Wiltschko & Wiltschko, 2003). Regarding the latter, we might expect that error in the sites to which birds home should distribute along the migratory vector taken from the wintering site. Specifically, we might expect that birds distribute along the vector connecting the breeding site to the point at which they cross the Mediterranean. We reasoned that linking the natal/breeding site to this crossing point was a reasonable estimate for a putative migratory compass bearing, since outbound migration in reed warblers (and European passerines more generally) is thought to involve a series of migratory bearings, the most northern of which is thought to connect the breeding site with the Mediterranean crossing point (Gwinner & Wiltschko, 1978; Chernetsov et al., 2008). Reed warblers breeding in northern and western Europe cross the Mediterranean Sea in southwestern Europe whilst, conversely, birds breeding southeast of the Austrian Alps are known to cross the Mediterranean Sea in southeast Europe (Leisler et al., 2011; Zwarts et al., 2012; Prochazka et al., 2018). For reed warblers, this is a southwest-northeast axis for birds breeding in northern and western Europe, and a southeast-northwest axis for birds breeding in southeastern Europe (Leisler et al., 2011). If error in the site to which birds homed distributed along each population's pre-determined migratory axis, this would be consistent with magnetic 'stop sign' navigation.

To test whether this were the case, we regressed changes in longitude (as 'eastings' in kilometres, so as to control for the differing size of longitudinal degrees with latitude) against changes in latitude (as 'northings' in kilometres, so as to make linear model output coefficients more easily interpreted). The difference between the 2 populations was then assessed as an interaction term in the model, with the expectation that the gradients of each populations should oppose each other and align according to our *a priori* expectations. Linear models were fitted using least mean squares.

O-E comparison analysis

Under any hypothesis of magnetic navigation defined *a priori*, there is a precise location at which a bird is expected to be observed. For example, a bird navigating using a bi-coordinate map comprising magnetic inclination and magnetic declination would be expected to be recovered at the intersect of the previous year's inclination/declination isolines observed in the subsequent year (see Figure 3.2). As such, we can test how birds use specific cues by comparing their recovery location to that expected under a given hypothesis.

To do this, we attempted to test specifically whether the movement of reed warblers between ringing and recovery correlated with 'movement' in the site occupied by the magnetic parameter values previously found at the natal/breeding site in the previous year. For instance, if the latitude and longitude of magnetic values X_1 Y_1 (e.g. inclination/declination) moved between years, there would be some correlation between this movement and the movement between ringing and recovery of birds if they aimed specifically for coordinates in the cues hypothesised. To test whether this was the case, we isolated the exact geographic position to which a bird is expected to home under a specific model of navigation. In our analysis we included 6 potential magnetic hypotheses, each containing either 2 magnetic parameters used as a bi-coordinate map or a single magnetic parameter utilised alongside a return compass bearing as a stop sign. These hypotheses were: inclination/declination, inclination/intensity, intensity/declination, inclination/bearing ('inclination stop sign'), declination/bearing ('declination stop sign') and intensity/bearing ('intensity stop sign'; see Figure 3.2).

For bi-coordinate magnetic map hypotheses we defined the expected recovery position as the intersect between the isolines denoting the magnetic parameter values associated with the natal/breeding site in the natal/breeding year. For the stop sign hypotheses a likely compass bearing was derived for each bird by connecting each bird's natal/breeding site with the likely point at which each bird crossed the Mediterranean Sea (Leisler et al., 2011; Zwarts et al., 2012), with the resultant line's intersect with the magnetic isoline of interest giving the predicted recovery location for each bird. We reasoned that linking the natal/breeding site to the point at which each bird was likely to cross the Mediterranean Sea was a reasonable estimate for a putative compass bearing, since birds on outbound migration are thought to navigate along a series of inherited migratory bearings, the most

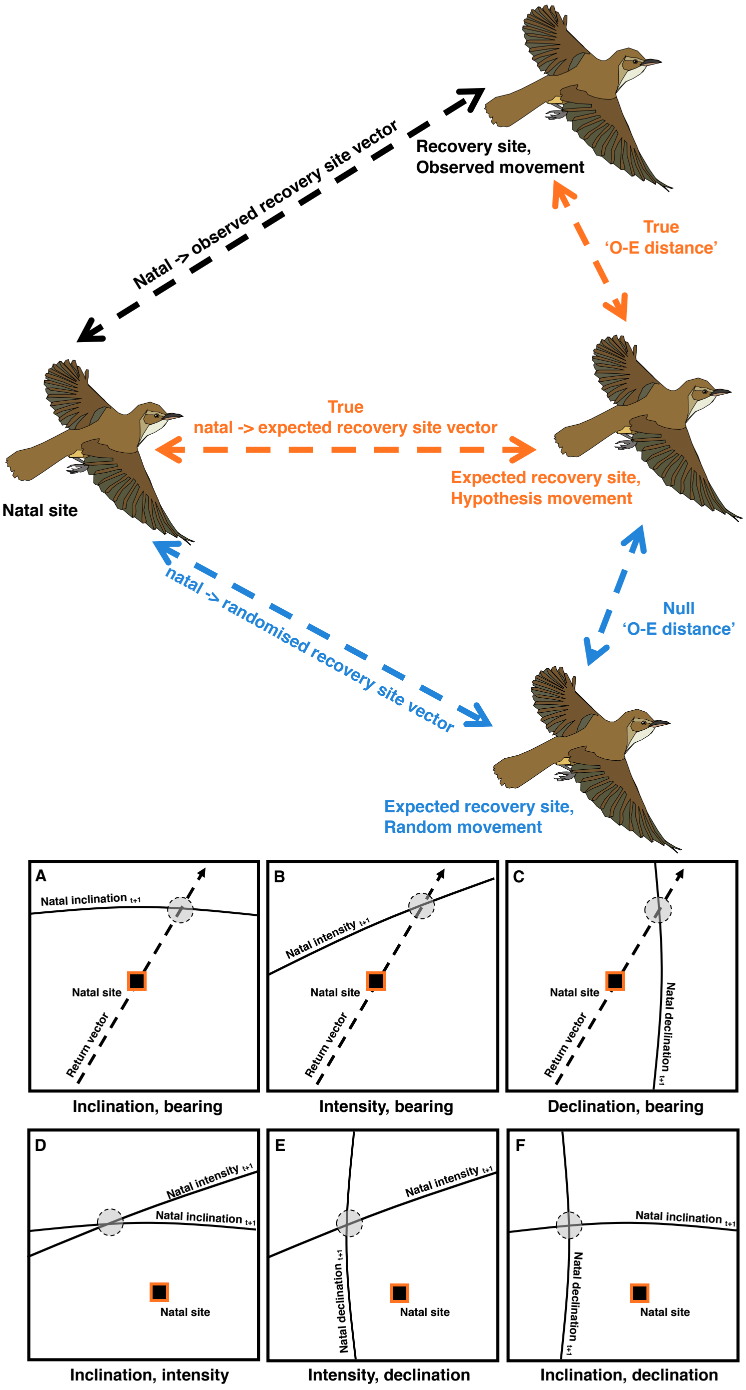

Figure 3.2: The O-E distance method of testing navigational hypotheses. A visual representation of how the distance between the expected recovery site (under a given navigational hypothesis) and the observed recovery site can be used to test how well ringing data fit different hypotheses. (top) The expected recovery site, under a given model of navigation, can be estimated (orange labels) and the distance to the true recovery site ('True O-E distance') can be calculated. The smaller the true O-E distance, the closer the expected and observed positions and hence the better the hypothesis fits the data. By comparing this distance to the distance between the estimated recovery site and equal but random movements ('null O-E distance'; blue labels) we can calculate a likelihood of the hypothesis out-performing chance and hence calculate a p-value. (bottom) Panels A to F show how the expected recovery positions under each hypothesis are calculated.

northern of which is thought to connect the natal/breeding site with the Mediterranean crossing point (Gwinner & Wiltschko, 1978; Chernetsov et al., 2008). If a bird were to re-capitulate a series of innate bearings we would, therefore, expect the final leg of such a series would intersect the Mediterranean Sea crossing site. For birds breeding in western and northern Europe the Mediterranean crossing point was estimated as the Straits of Gibraltar, and for birds breeding in south-eastern Europe the Mediterranean crossing point was estimated as the western coast of Lebanon. Whilst it is extremely unlikely that all birds pass precisely through these positions we reasoned that, given how great the distance is between most breeding sites and the crossing points, even relatively large discrepancies between the hypothesised and observed crossing points will have a fairly small impact on any subsequent analysis.

If, for a given hypothesis, the expected recovery site was at a probabilistically impossible site (for example in a mountain range, over the sea or in an area where no ringing occurred) we reasoned it would be unrealistic to suggest that such a site is the 'expected' recovery site. As such, for each hypothesis we defined the expected recovery site as the site where ringing occurred closest to the site where a bird was expected to be recovered under a given hypothesis.

For each bird we measured the geographic distance between the observed recovery site and the recovery site expected under a given model of navigation (the observed vs. expected 'O-E' distance), a process which we repeated for each navigational hypothesis. The smaller this distance, the better the fit between the ringing data and the hypothesis in question. In order to assess the relative likelihood of different magnetic models of navigation, we compared the O-E distance for each bird to the distances between the expected recovery site and a null recovery site (the 'null O-E distance'; see above for a description of our null model; see Figure 3.1 for an example). To test each hypothesis against the null distribution, we iteratively generated a null recovery site for each bird (n = 1000). For each iteration we calculated a mean null O-E distance for each hypothesis, and the distribution of null O-E distances was then compared to the true O-E distance so as to test whether a given hypothesis' observed O-E distance was smaller than would be expected under the null distributions (i.e. was smaller than would be expected if birds were inattentive to the Earth's magnetic field). P-values were calculated as the proportion of null mean O-E distances that were smaller than the observed mean O-E distance.

Environmental confound analysis

It is possible, given the correlative nature of the study, that any correlations between bird movement and secular variation result from a confound between magnetic inclination and another variable. One possible confound is environmental phenology, something to which migratory birds have repeatedly (e.g. Thorup et al., 2017; Alves et al., 2019; Fandos et al., 2020), though not universally (Wang et al., 2019), been shown to be receptive. Changes in environmental phenology could cause birds to extend/truncate return migration, causing them to alter their breeding sites non-randomly and, in turn, possibly confounding changes in the Earth's magnetic field.

To test whether this was the case, we examined whether our focal magnetic parameters correlated with 4 variables related to environmental phenology: spring air temperature, the proportion of frosty days in spring, the Fraction of Absorbed Photosynthetically Active Radiation (fAPAR; a proxy for live vegetative cover) and the normalized difference vegetation index (NDVI; a second proxy for vegetative cover). All variables were derived at each position where reed warblers had been encountered, with each variable derived for as many years as possible. Each variable was normalised, and then all variables were regressed against each other in a series of uni-variate linear regressions. Because variables were normalised the gradients of different models could be directly compared, with a gradient of +1 indicating a strong positive correlation, a gradient of -1 representing a strong negative correlation and a gradient of 0 representing no correlation.

3.4 Results

3.4.1 Parameter shift randomisation analyses

First, we sought to investigate whether birds actively minimised changes in specific magnetic parameters (inclination, declination and intensity) between ringing and recovery. This, we reasoned, would indicate whether birds were attentive to specific cues when locating the natal/breeding site. Using a randomisation analysis, we compared the observed reed warbler movements to those expected under our null model. We found that the median observed change in inclination (randomisation; $p < 0.001$), but not declination ($p > 0.99$) or intensity ($p = 0.18$), was smaller than would be expected under our null model of philopatry. We found, however, that the mean changes in inclination, declination and intensity were not significantly different to those expected under our null distribution (randomisation; inclination, $p > 0.99$; declination, $p = 0.4$; intensity, $p = 0.38$). Because the distribution of distances moved between ringing and recovery is necessarily long-tailed (Tittler et al., 2009), it is perhaps not unsurprising that the mean and median changes in a given magnetic parameter yield different results. Further, since the change in any magnetic parameter is inevitably linked to how far the bird in question moves, this disparity may imply that the processes driving long-distance dispersal may not be as closely linked to magnetic secular variation.

To test this, we re-ran our randomisation analysis with birds from the 1st percentile for ringing to recovery distance removed as they were, by definition, moving very large distances. Birds moving long-distances were removed for both adults and chicks separately, so as to ensure the proportion of birds of each age class was consistent in subsequent analyses. We found that amongst the remaining birds the observed mean change in inclination was smaller than would be expected by chance (randomisation; $p < 0.001$), but that the changes in intensity (randomisation; $p = 0.96$) and declination (randomisation; $p = 0.69$) were not, suggesting that our result is indeed primarily driven by birds moving shorter distances between ringing and recovery and not by birds moving longer distances.

3.4.2 Change in longitude vs. change in latitude

Taken together, the above results imply that birds target the area denoted by the inclination value encountered at the natal/breeding site a year prior. However, position relative to a single coordinate dimension, referenced alone, cannot give the position of the natal/breeding site. birds could, however, in principle recall the location of their natal/breeding site using only one coordinate dimension if they also knew the compass bearing(s) between the wintering and breeding sites (as is seen on outbound migration; Perdeck, 1958; Thorup et al., 2007; Yoda et al., 2017).

If this were the case, we would expect that changes in latitude would correlate with changes in longitude between ringing and recovery. Specifically, if reed warblers utilise magnetic 'stop signs' on compass bearings during return migration, we should expect

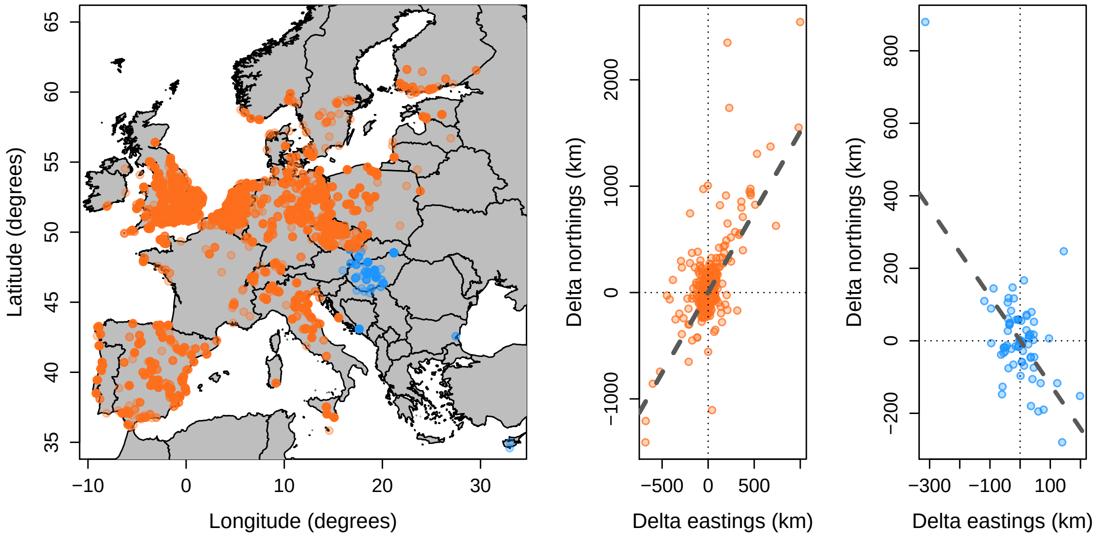

Figure 3.3: Changes in position between ringing and recovery for Eurasian reed warblers. (left) Map of ringing sites for Eurasian reed warblers, coloured orange for birds expected to migrate via the western Mediterranean and coloured blue for birds expected to migrate via the eastern Mediterranean (Leisler et al., 2011; Zwarts et al., 2012). (middle) Changes in longitude ('eastings' in kilometres) plotted against changes in latitude ('northings' in kilometres) for birds breeding in north/west Europe and (right) changes in longitude ('eastings') plotted against changes in latitude ('northings') for birds breeding in southeast Europe. In all panels point opacity indicates the number of overlapping datapoints. Regression lines were fitted using least squares.

changes in the longitude/latitude of the breeding site between ringing and recovery to distribute a) along a southwest to northeast axis for northern and western European birds and b) along a southeast to northwest axis for south-eastern European birds. When changes in latitude (as 'northings' in kilometres) were regressed against changes in longitude (as 'eastings' in kilometres) for both populations of reed warblers, we found a significant change in latitude per unit change in longitude (LM; F = 143,445, $p < 0.0001$) and, further, found a significant difference in the direction of this effect between migratory populations (LM; F = 1,579, $p < 0.0001$; see Figure 3.3). We found that the north-western European population of reed warblers showed significant eastwards movement with northern movement (gradient = 1.51 ± 0.0480), whilst the south-eastern population showed significant westwards movement with northwards movement (gradient = -1.21 ± 0.0675; see Figure 3.3). This was consistent with our *a priori* expectations, suggesting that birds may indeed be using magnetic inclination as a 'stop sign'. Such a result is, however, also consistent with our findings being driven by birds being caught on migration and, therefore, could be a consequence of ineffective exclusion of still actively migrating birds. This might seem unlikely, given the time of year at which ringing/recovery events included in our analysis occurred and given the breeding phenology of reed warblers (Halupka et al., 2008; Ockendon et al., 2013). Nonetheless, we sought to ensure our result was robust to the selection criteria by re-running our analyses with 3 different, more stringent subsets (birds ringed in a more restricted core breeding time window (15th June-15th July); birds recovered at or north of their original natal/breeding site; and birds sexed at capture, which requires identification via phenotypical changes linked to breeding (cloacal protrusion or brood patches). These analyses are presented in the Appendix.

3.4.3 'O-E' randomisation analysis

The results of our previous analyses are consistent with the use of magnetic inclination as a 'stop sign' on a return migratory trajectory, with birds targeting the inclination value encountered at the natal/breeding site the previous year during philopatry. Such a hypothesis necessarily predicts the precise location at which a bird might be expected to be recovered (as the intersect between the natal/breeding inclination isoline and the return compass bearing; see Figure 3.2). A similarly precise recovery location can be estimated for any *a priori* magnetic navigation hypothesis, including both 'stop sign' and bi-coordinate models of magnetic navigation. Consequently, we aimed to create bespoke randomisation analyses to assess whether specific navigational hypotheses explained ringing recoveries better than would be expected by chance. This 'O-E' randomisation is outline in the methods section.

Based on this method, we found that the only hypothesis that significantly out-performed the null model was inclination acting as a stop-sign on a return compass bearing (randomisation; $p < 0.001$; see Figure 3.4). The O-E distance of all other models were shown to be no smaller than would be expected if birds moved randomly, implying that not only was the inclination stop sign the best fit model of those proposed but was also

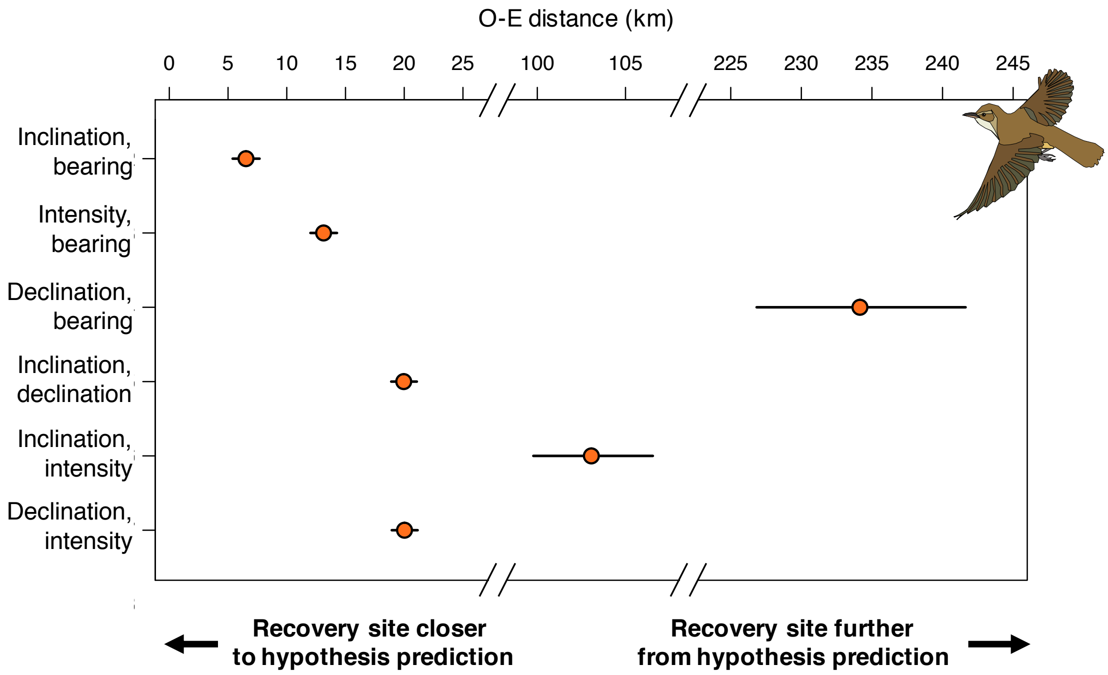

Figure 3.4: The O-E distances for all magnetic navigational hypotheses tested. A comparison of the mean observed to expected ('O-E') distances (see Figure 3.2) for all hypotheses tested in our analyses, with a smaller mean O-E value representing a better fit between the hypothesis and the observed data and a larger value representing a poorer fit between the hypothesis and the observed data. Error bars represent bootstrapped 99% confidence intervals. Note the breaks in the scale on the horizontal axis.

the only model that performed better than would be expected by chance. Furthermore, despite 1st years moving further between ringing and recovery (mean = 11.51km ± 0.607) than adults (mean = 4.388km ± 0.390), consistent with previous studies (Mouritsen, 2003), we found that the O-E distance for the inclination stop sign hypothesis was significantly smaller than chance when considering both adults (randomisation; $p < 0.001$) and 1st years (randomisation; $p < 0.001$) separately, implying that even though adult birds were more accurate in their homing birds of all ages attended to magnetic stop signs. Additionally, and remarkably, we also found that the O-E distance for the inclination stop-sign model was significantly smaller than the distance between the ringing and recovery sites (Mann-Whitney U test; $p < 0.0001$), implying that following return migration birds were recovered closer to the site predicted by the inclination stop-sign model than they were even to their own breeding/natal site. As with our previous analysis, we re-ran our O-E analysis with 4 additional datasets selected using more stringent selection criteria, so as to ensure our analysis was robust to the filtering methods (see Appendix).

3.4.4 Environmental confound analysis

Whilst we found a substantial positive correlation between magnetic inclination and magnetic intensity (gradient = 0.31 ± 0.007), and a substantial negative correlation between magnetic inclination and magnetic declination (gradient = -0.57 ± 0.0061), we found that none of the examined environmental variables correlated notably with any magnetic variables (see table 3.1). The largest gradient between inclination and an environmental variable was between inclination and air temperature, with a gradient of only 0.021 (±0.0073). Based on this, we suggest that, whilst it is possible our results are the product of a confound between magnetic secular variation and another process, this seems unlikely.

	Inclination	**Declination**	**Intensity**	**fAPAR**	**Average air temperature**	**Proportion frost days**	**NDVI**
Inclination	NA						
Declination	-0.57 (± 0.0061)	NA					
Intensity	0.31 (± 0.0070)	0.031 (± 0.0073)	NA				
fAPAR	-0.047 (± 0.01)	0.019 (± 0.0099)	-0.021 (± 0.0075)	NA			
Average air temperature	0.021 (± 0.0073)	0.009 (± 0.0077)	0.048 (± 0.0073)	0.021 (± 0.014)	NA		
Proportion frost days	-0.017 (± 0.0081)	0.024 (± 0.0080)	0.0057 (± 0.0087)	-0.13 (± 0.017)	0.19 (± 0.0084)	NA	
NDVI	-0.0029 (± 0.0084)	0.008 (± 0.00709)	-0.02 (± 0.0068)	-0.053 (± 0.012)	0.018 (± 0.085)	0.11 (± 0.011)	NA

Table 3.1: Regression matrix detailing the strength of the correlation between different magnetic parameters and potential environmental confounds. Correlations are presented as the gradient of the regression lines between normalised variables, meaning that +1 represents a strong positive correlation, -1 a strong negative correlation and 0 represents no correlation. Gradients are presented with the 95% confidence intervals in brackets.

3.5 Discussion

Using both conventional parametric analysis and our novel, non-parametric ‘O-E’ analyses we infer that a mechanism based on learnt magnetic inclination acting as a stop sign along an axis defined by migratory direction explains the positions at which reed warblers are recovered better than would be expected if birds move randomly, better than other models of magnetic navigation and, remarkably, better even than the natal/breeding site. Since this is a correlative analysis it is, necessarily, possible that our findings are the result of a confound between movements of the magnetic field and some other parameter. However, given that a) we found no substantial confound with any of the environmental variables investigated, b) we found no difference in our results when analysing different subsets of the data (see Appendix) and c) there are no long-term temporal trends in longitudinal/latitudinal shift between ringing and recovery (latitude LM; F = 1.69, p = 0.190; longitude LM; F = 0.99, p = 0.590), we believe that the most parsimonious interpretation of the result is that magnetic inclination is used as a stop sign by birds of all ages during philopatry.

This might make sense, since magnetic inclination has been repeatedly implicated in avian navigation over the last 50 years (for a review, see Mouritsen, 2018) and, further, other magnetic gradient-derived positions move substantially more with secular variation than inclination thus making the proposed mechanism potentially advantageous. The position of the natal site as estimated using inclination and declination as a bi-coordinate map would move, on average, 18.5km (± 0.0760km) between years; intensity and declination 20.4km (± 0.0510km) between years; and intensity and inclination 98.2km (± 2.60km) between years (see Chapter 7 for more information). In contrast, the location of the breeding site as denoted using inclination as a stop sign on a compass bearing moves only 1.22km (± 0.0133km) between years. By remembering a breeding location relative to the most stable cue, and limiting the impact of secular variation by referencing it alongside an unchanging compass bearing, we therefore suggest that the observed strategy minimises the effect of secular variation on philopatry. However, whilst navigating using an inclination stop sign reduces a bird's exposure to the effects of secular variation, it cannot be the only cue used by birds during natal site return. If it were, even slight magnetic secular variation would inhibit successful philopatry. Consequently, other cues must complement magnetic inclination when pinpointing the end goal of migration (Mouritsen, 2018).

Whilst our results shed light on the sensory and developmental underpinnings of breeding site philopatry, our results may also imply that magnetic secular variation is of some importance when considering the drivers of range shifts in migratory taxa. As with any correlative contrasts drawn using natural environmental variance, we suggest that experimental verification of our suggested mechanism is an essential next step. Nonetheless, we believe our findings provide evidence for a novel mechanism of long-distance navigation, both within birds and migratory animals more generally.

3.6 Appendix

Extended subset analyses

In addition to our main analyses, we repeated all statistical tests using different subsets of the ringing data, so as to ensure that the trends discussed in our main text were robust to the selection criteria used to subset ringing data. In total, we conducted 4 additional analyses.

Ringed at the nest site, recovered north of the nest site

Firstly, we repeated our analyses for a subset of birds ringed at the nest and recovered at or north of the breeding site. Such birds, we reasoned, were extremely unlikely to represent birds caught on migration in either instance. Based on this subset we found, consistent with our main analyses, that the shift in median inclination (randomisation; $p < 0.001$; see methods) but not declination (randomisation; $p = 0.87$) or intensity (randomisation; $p = 0.13$) was smaller than would be expected if birds had moved randomly. We additionally found a significant change in latitude per unit longitude (LM; $F = 4,360$, $p < 0.0001$) and, again consistent with our main analysis, we found that the direction of this effect was different for different breeding populations (south-eastern vs north/western Europe; LM; $F = 47.4$, $p < 0.0001$). Finally, as in our main analysis, we found that birds were significantly closer to the expected recovery location under an inclination/bearing model of navigation than would be expected by chance (randomisation; $p < 0.001$; see methods). This was not the case for any other hypothesis examined.

15th June to 15th July

Our second subset analysis focused on birds caught between the 15th June and 15th July. Based on previous studies, this date range represents the most likely breeding window for Eurasian reed warblers. Therefore, this is when birds are least likely to be on migration (Halupka et al., 2008; Ockendon et al., 2013; Ceresa et al., 2020). When considering birds ringed between these dates, consistent with our main analyses, we found that the shift in median inclination (randomisation; $p < 0.001$; see methods) was smaller than would be expected if birds had moved randomly. This was not the case when considering declination (randomisation; $p = 0.87$) or intensity (randomisation $p = 0.13$). Further, we found that changes in longitude were significantly correlated with changes in latitude (LM; $F = 7{,}576$, $p < 0.0001$) and, again consistent with our main analysis, we found that the direction of this effect was different between the south-eastern and north/western European reed warbler populations (LM; $F = 554$, $p < 0.0001$). Finally, we found that birds were significantly closer to the expected recovery location under an inclination/bearing model of navigation than would be expected by chance (randomisation; $p < 0.001$; see methods). This was not the case for any other hypothesis examined.

Sex-determined birds

Our third subset analysis concerned birds for which sex had been determined. Given the overlap in plumage and biometrics between male and female reed warblers, sexing typically relies on the presence of a brood patch/cloacal protrusion (Svensson, 1970). Sexed birds are, therefore, likely to be breeding. Amongst birds sexed at both ringing and recovery, we found that the shift in median inclination (randomisation; $p < 0.001$; see methods) was smaller than would be expected if birds had moved randomly. This was not the case when considering declination (randomisation $p = 0.99$) or intensity (randomisation $p = 0.47$). Additionally, we found that changes in longitude were significantly predicted by changes in latitude (LM; $F = 12{,}196$, $p < 0.0001$) and, again consistent with our main analysis, we found that the direction of this effect was different between the south-eastern and north/western European reed warbler populations (LM; $F = 34{,}349$, $p < 0.0001$). Finally, we found that birds were significantly closer to the expected recovery location under an inclination/bearing model of navigation than would be expected by chance (randomisation; $p = 0.006$; see methods). This was not the case for any other hypothesis examined.

Additionally, we further repeated our analysis of sexed birds that were also included in our original analysis (i.e. were both sexed and additionally ringed/recovered after a cut-off date specified for their ringing longitude/latitude). Amongst these birds we again found that the shift in median inclination (randomisation; $p < 0.001$; see methods) was smaller than would be expected if birds had moved randomly. This was not the case when considering declination (randomisation; $p > 0.99$) or intensity (randomisation $p = 0.48$). Further, we found that changes in longitude were significantly correlated with changes in latitude (LM; $F = 46.7$, $p < 0.0001$) and, again consistent with our main analysis, we found that the direction of this effect was different between the south-eastern and north/western European reed warbler populations (LM; $F = 26.9$, $p < 0.0001$). Finally, we found that birds were significantly closer to the expected recovery location under an inclination/bearing model of navigation than would be expected by chance (randomisation; $p < 0.001$; see methods). This was not the case for any other hypothesis examined.

Constant effort cohort

Our final subset analysis concerned a ‘constant effort’ cohort, including 50 birds ringed every year since 1965 (the first year in which 50 birds were ringed and subsequently recovered). This analysis was included so as to ensure our results were not disproportionately influenced by a handful of years’ data. This is particularly important given that crustal anomalies, diurnal variation, or variability in the magnetic field owing to space weather are not modeled completely by the IGRF. Amongst these birds we again found that the shift in median inclination (randomisation; $p < 0.001$; see methods) was smaller than would be expected if birds had moved randomly. This was not the case when considering declination (randomisation; $p = 0.94$) or intensity (randomisation $p = 0.010$). Further, we found that changes in longitude were significantly correlated with changes in latitude (LM; $F = 46.7$, $p < 0.0001$) and, again consistent with our main analysis, we found that the direction of this effect was different between the south-eastern and north/western European reed warbler populations (LM; $F = 26.9$, $p < 0.0001$). Finally, we found that birds were significantly closer to the expected recovery location under an inclination/bearing model of navigation than would be expected by chance (randomisation; $p < 0.001$; see methods). This was not the case for any other hypothesis examined.

Based on our supplementary multiple-subset analyses, we find that our result presented in the main text is repeatable using subsets of ringing data selected using multiple different (and more stringent) criteria. In turn, this implies that the results presented in the main text are robust to the precise mechanism by which breeding ringing records are parsed from migrating conspecifics and, therefore, we suggest that it is unlikely that the inclusion of migrant birds in the analysis dataset is driving the results presented.

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4

Twilight cue manipulation reveals magnetic inclination compass use in a pelagic seabird

With contributions from: Padget, O., Kobylkov, D., Mouritsen, H., Fayet, A.L., Syposz, M., Gillies, N., Davies, K., Trapp, S., Hewitt, J. and Guilford. T.

Contents

4.1 Abstract

Amongst long-distance navigators the ability to orient relative to a compass is essential. Whilst magnetic compass orientation has been repeatedly implicated in songbird navigation, evidence for magnetic compass orientation in other bird taxa remains elusive. Here, we tested whether a pelagic seabird, the Manx shearwater (*Puffinus puffinus)*, uses a magnetic compass during homeward navigation. By rotating the magnetic field experienced by birds at dusk, and tracking their return to the breeding colony following displacement, we found that the deflection angle between a bird's track and the homeward beeline was predicted by the magnetic treatment. We further found that the magnitude of this deflection was in part predicted by variance in the inclination experienced by the bird during the magnetic treatment, suggesting that birds paid less attention to the artificial magnetic field when the inclination was less representative of their normal geomagnetic conditions. We suggest that this is consistent with a magnetic inclination compass being used in twilight calibration, providing the first experimental evidence for magnetoreception in a free-flying non-passerine, and propose therefore that avian magnetic compass orientation may be more phylogenetically and ecologically widespread than is currently understood.

> *"There's an island hidden in the sound,*
> *Lapping currents lay your boat to ground.*
> *Affix your barb and bayonet,*
> *The curlews carve their Arabesques,*
> *And sorrow fills the silence all around.*
> *Come and see..."*
>
> – The Decemberists, *The Island*

4.2 Introduction

Egocentric orientation is understood to be essential for efficient goal-oriented movement, when considering both animals moving within a restricted area (e.g. Wiltschko and Balda, 1989) and trans-continental migrants (e.g. Perdeck, 1958; Thorup et al., 2007; Yoda et al., 2017). Such orientation over a variety of spatial scales is often thought to rely on compasses.

A compass provides a link between an animal's egocentric and allocentric frames of reference, providing global allocentric directional information that an animal can align themselves with reference to for orientation. Amongst experienced navigators compasses are typically used in combination with locational 'map' information, either as a 2-step process (Kramer, 1950) or directly to discern position relative to landmarks (Biro et al., 2007). Compass orientation is also thought to be key in the inheritance of migration trajectories, with migratory destination inherited as a 'clock' (to encode distance) and a 'compass' (to encode direction; Perdeck, 1958; Thorup et al., 2007; Yoda et al., 2017). A variety of cues are known to provide animals with compass information, most notably time-compensated visual solar cues (Schmidt-Koenig, 1961), solar polarisation cues (Muheim et al., 2006), visual celestial rotation cues (Emlen, 1967a, 1967b) and magnetic cues (Wiltschko & Wiltschko, 1972). Precisely which compass system is used by a given organism in a given situation is, necessarily, shaped by both the phylogenetic history and present ecology of the species in question. For example, sun compasses are likely prevail amongst diurnal species (e.g. Schmidt-Koenig, 1961; Wiltschko and Balda, 1989; Duff et al., 1998), whilst star compasses are inevitably more useful amongst birds moving at night (such as the night-migratory songbirds; e.g. Emlen, 1967a; Michalik et al., 2014; Pakhomov et al., 2017).

Much of our understanding of avian compass orientation, and specifically magnetic compass orientation, stems from experiments conducted on songbirds (Passeriformes; for a review see Mouritsen, 2018) or homing pigeons (*Columba livia*; e.g. Keeton, 1971), with relatively few investigations focusing on compass orientation in other taxa (e.g. Gudmundsson and Sandberg, 2000). This is particularly true for birds that are incompatible with traditional laboratory-centric experimental paradigms, such as the pelagic seabirds. Navigation amongst seabirds, such as the procellariforms, presents a markedly different challenge to that experienced by terrestrial taxa, and is typically characterised by long distance movement across featureless landscapes (e.g. Guilford et al., 2009; Ventura et al., 2020). Owing to their distinct ecology, it might therefore follow that seabirds orient using different compasses to songbirds. Indeed, evidence for magnetic compass orientation, near-ubiquitous amongst songbirds (Mouritsen, 2018), is seemingly absent in procellariforms (Bonadonna et al., 2003; Mouritsen et al., 2003; Bonadonna et al., 2005; Gagliardo et al., 2013; Pollonara et al., 2015).

It has previously been found that a time-compensated sun compass is involed in seabird compass orientation, (Padget et al., 2018), though it is possible that seabirds utilise multiple compass systems. Indeed redundancy in compass information might be expected, not only because compass systems are sometimes unavailable but also because of inaccuracies and biases in the directional information given by different compasses. Specifically, errors in the magnetic compass are thought to arise from declination in the magnetic field (i.e. differences in the position of true and geomagnetic north; Muheim et al., 2003), whilst error in the sun compass may occur through differences in the sun's position in the sky with latitude and time of year (Muheim et al., 2018). In order to offset the effect of such biases, birds are thought to 'calibrate' their compasses at dusk (Cochran et al., 2004), so as to reduce orientation error. Such calibration events have been demonstrated in both birds and mammals (Muheim et al., 2006; Muheim et al., 2007; Holland et al., 2010; Lindecke et al., 2019). Amongst birds compass solar calibration of the magnetic compass has been associated with high-latitude (where magnetic information is less reliable; Muheim et al., 2003) and long-distance migrations (e.g. Cochran et al., 2004; Muheim et al., 2006), though amongst bats calibration has been implicated in both long and short-distance movements (Holland et al., 2010; Lindecke et al., 2019). Whilst previous studies have primarily demonstrated magnetic calibration of the sun compass, such compass information transfer could in principle occur in reverse (Wiltschko et al., 1987; Cochran et al., 2004), particularly amongst lower latitude species where the effects of magnetic declination are less pronounced. In such instances, magnetic compasses could, in principle, be used to calibrate other compasses (such as the sun compass).

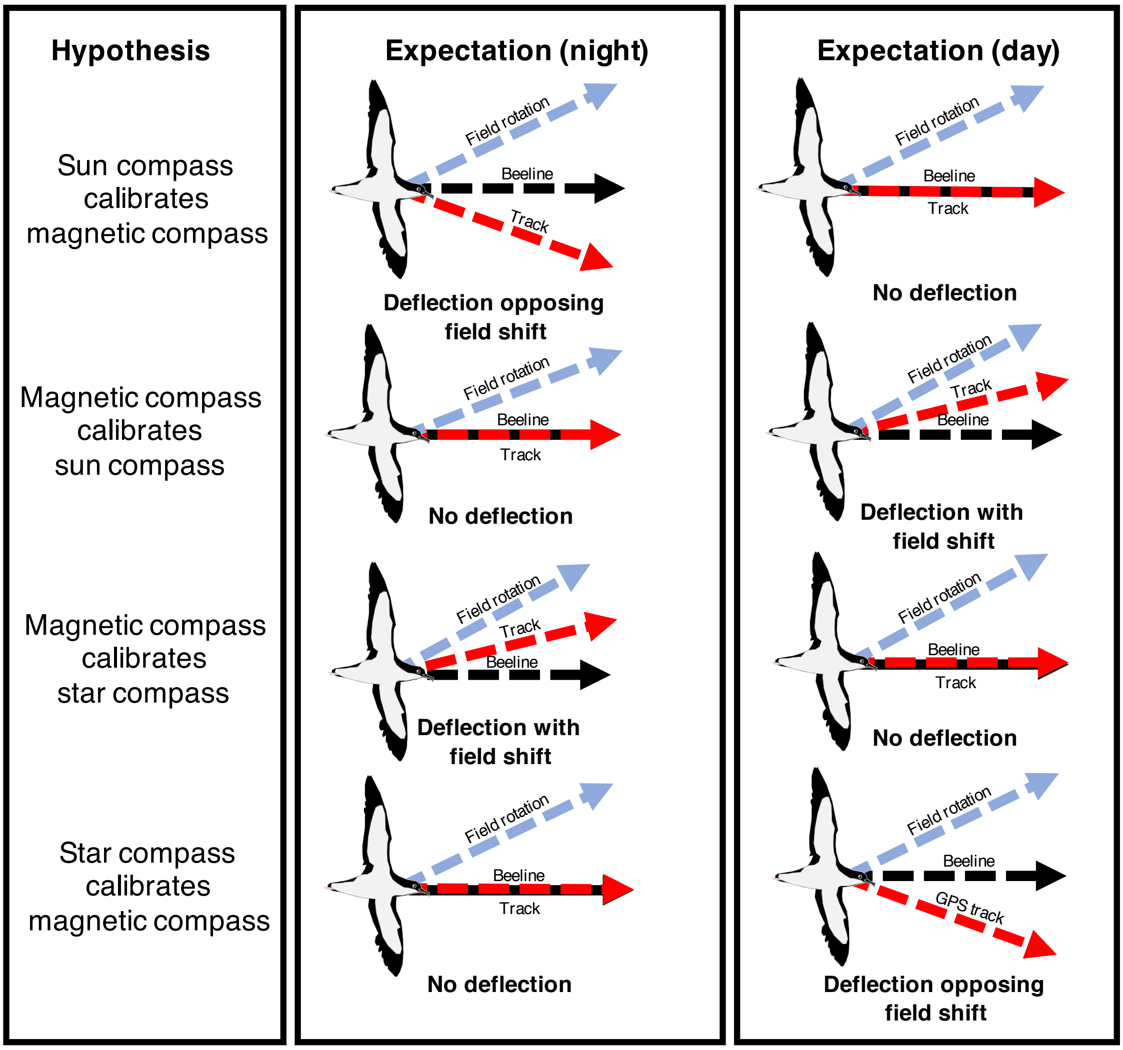

Figure 4.1: The expected effects of different magnetic treatments on deflection. For each potential compass calibration involving the Earth's magnetic field (left) the expected deflection response for homing at night (centre) and day (right) are shown as schematics. All deflections and rotations are not shown to scale, and are scaled to make qualitative predictions regarding deflections as clear as possible.

A now classic paradigm in the study of compass orientation is to manipulate twilight calibration events, so as to determine whether animals are attentive to specific compass cues and, if so, what the direction of information transfer is during compass calibration. This can be ascertained not only by looking for deflections in orientation with twilight compass rotation, but by looking specifically at the direction of deflection (Cochran et al., 2004). Here, we used such an experimental twilight cue manipulation to investigate magnetic compass orientation in a pelagic seabird, the Manx shearwater (*Puffinus puffinus*). By rotating the magnetic field experienced by shearwaters at dusk, and tracking the homing behaviour of manipulated birds following displacement, we sought to investigate whether shearwaters utilise magnetic compass cues during orientation. This we did by measuring the magnitude and direction of deflection from the beeline. For example, if the magnetic field was rotated clockwise and a sun compass used to calibrate a magnetic compass, we would expect the navigator deflect in the opposing direction once removed from the altered field (Cochran et al., 2004; see Figure 4.1). This is because the compass-defined northerly direction would return to it's intrinsic position, and hence the navigator would be deflected in a direction opposing the experimental field rotation. Conversely, we would expect the opposite to be true if the magnetic field were used calibrate a sun compass (Cochran et al., 2004; see Figure 4.1). We would, further, expect to only see deflection at times when a bird is using the compass in question. To take the above example, if a sun compass were used to calibrate a magnetic compass we would expect to see deflections at night (when the sun compass in unviable). Conversely, we would expect a magnetic calibration of the sun compass to be expressed as deflection during the day but not at night (see Figure 4.1).

Further, within our experimental setup we might expect birds to deflect to a lesser extent when the generated magnetic field matches imperfectly with the field normally experienced. Specifically, if shearwaters were, like songbirds, receptive to magnetic inclination (Wiltschko & Wiltschko, 1972), we might expect that disparities between the generated magnetic field and the normal field might reduce the extent by which shearwaters deflect. As such, we sought to ascertain a) whether shearwaters utilised magnetic information when making orientation decisions, b) whether the magnetic compass was used to calibrate a sun compass, or vice versa, and c) whether shearwaters are, like songbirds, receptive to magnetic inclination .

4.3 Methods

4.3.1 Fieldwork and experimental protocol

Fieldwork was conducted on Skomer Island, Pembrokeshire (51.74°N, -5.30°W) over the years 2019 and 2021. In May 2019 46 shearwaters were displaced over 3 nights as part of a preliminary experiment, whilst 60 shearwaters were displaced over 5 nights as part of the main experiment in May-June 2021. The results of our 2019 pilot displacements are presented in the Appendix, whilst the results of our main study are presented here.

Birds were introduced into either one of 2 magnetic treatments (see below) or a control treatment for the 2 hours preceding end of civil twilight, at which point birds were removed from the apparatus. When being introduced to or removed from the experimental apparatus birds were housed in opaque cotton bags, so as to minimise the likelihood of compass recalibration using visual cues as they moved in and out of the altered magnetic field. Following the magnetic treatment birds were displaced 30km in a south-westerly direction (to around 51.63°N, -5.70°W) by boat, then released onto the sea upon arrival. Birds were in transit on the boat for around 45 minutes, hence release times varied between 22:00 and 23:00 GMT. The homeward movements of each bird were logged using dorsally deployed iGotU Mobile Action GPS devices (Guilford et al., 2008), with devices set to record a GPS fix every minute following release. Of the 60 shearwaters released 58 GPS devices were recovered successfully, with complete trajectories retrieved from 50 birds. In some instances birds registered 2 complete homing trips (by homing but not making landfall), hence 59 trips were derived from these 50 birds. Because birds homing on the 2nd night/day post-treatment had experienced dusk in an unaltered magnetic field, it was unclear *a priori* what their response to the magnetic field shift would be. As such we removed these birds from our analyses, keeping only birds homing on the first night (n = 15) or first day (n = 38).

4.3.2 Magnetic field generation

In our experiment we included 3 treatments: a control treatment, an anticlockwise magnetic rotation treatment and a clockwise magnetic rotation treatment. The anticlockwise rotation treatment had a mean declination shift of -114.3° (± 1.81° [SE]), with a mean inclination of 66.08° (± 0.38°) and a mean intensity of 49,366nT (± 82.37nT). The clockwise rotation treatment had a mean declination shift of +114.9° (± 1.81°), with a mean inclination of 66.41° (± 0.49°) and a mean intensity of 49,746nT (± 191.1nT). The control treatment had a mean measured declination shift of 0° (± 0.077°), with a mean inclination of 66.83° (± 0.26°) and a mean intensity of 49,746nT (± 36.62nT). Error was recorded in the inclination, declination and intensity of the control treatment owing to slight variation in the precise direction the magnetometer was facing.

Magnetic field treatments were generated using Helmholtz coil systems (Cochran et al., 2004), powered using variable-current Kepco BOP 50-4M power supplies (Kepco Inc, Flushing, NY, USA; e.g. Kobylkov et al., 2019). Each coil system measured 2m x 2m, with the 2 coils within each coil system separated by a distance of 1m. Birds were housed in one of four experimental arenas, each measuring 0.4m x 0.4m x 0.2m. Arenas were suspended in the centre of the Helmholtz coil system, and were constructed out of entirely non-magnetic material (wood, plastic, aluminium and copper). Arenas overlapped each other by 0.2m, ensuring that the overall dimensions of the structure was 0.8m x 0.8m (see Figure 4.2 for a schematic of the coil design). The field within each arena was measured using an MEDA FVM-400 magnetometer (MEDA, Washington D.C., USA) accurate to the nearest 1nT. We systematically varied which coil system was used to produce which treatment, so as to remove any unknown idiosyncrasies associated with a given coil system as a potential confound in our experimental design.

The control treatment group were kept outside of both coil systems on a non-magnetic table set to an identical height. Control arenas were identical in construction to the experimental arenas, and were located adjacent to the experimental coils. Each coil/control treatment was separated from each other treatment by approximately 5m, so as to ensure that the field generated by a each coil did not impact birds in other treatments.

4.3.3 Track processing and analysis

All processing and analysis was conducted in R (R Core Team, 2017)

Only the homing section of each trajectory was analysed since this was the only part of the trip where the destination could be estimated *a priori*. Homing behaviour was, as in similar analyses, isolated using backwards path analysis (Bonadonna et al., 2005; Padget et al., 2018). Moving back along a given bird's track from the point at which

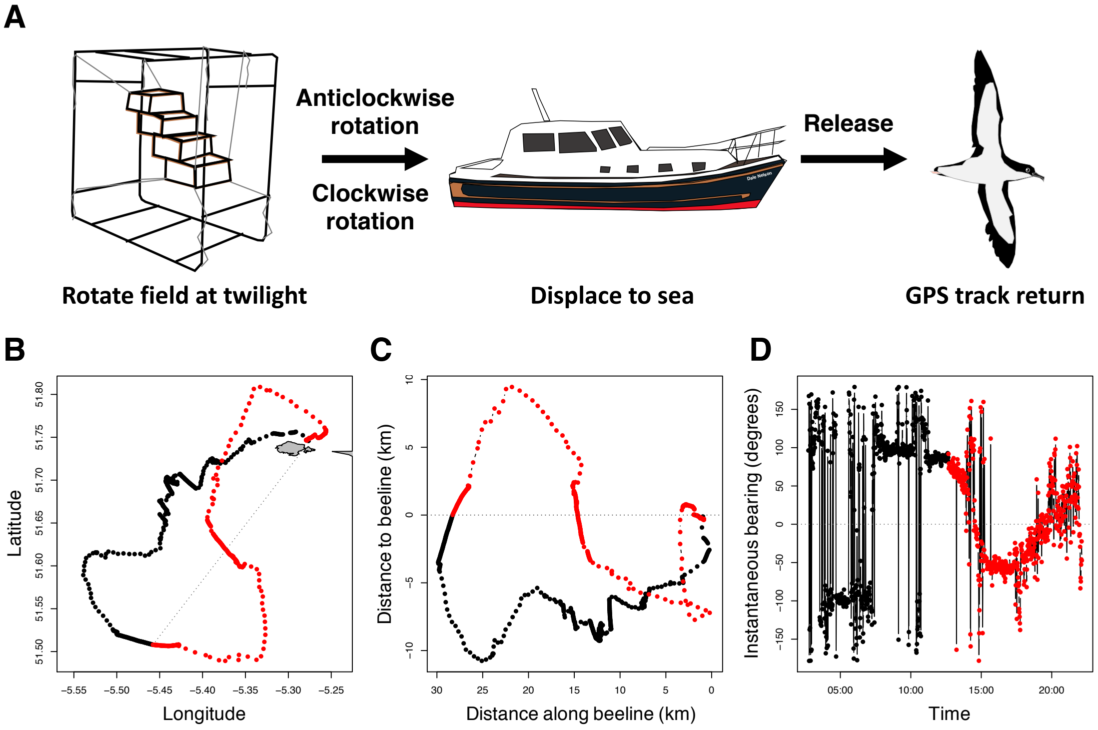

Figure 4.2: The experimental protocol and GPS track processing used in the experiment. A) Graphical illustration of the experimental protocol, including a schematic showing the design of the experimental arena. B) The complete GPS track from bird EA59477, with the homewards beeline shown as a dotted grey line. C) The GPS track from bird EA59477 transformed around the beeline, so as the point at which the bird starts homing is positioned at [n,0] where n is equal to the distance from the colony at the point of homing. D) The instantaneous deflection from the beeline for all points along the GPS track for bird EA59477. In all plots homing behaviour is highlighted in red.

birds reached the colony, we isolated the point where the beeline distance from the colony stopped changing linearly over time with respect to the length of the backward path (see Figure 4.2). This, we considered, was the point at which birds started homing. As in similar studies of compass orientation within a familiar area, we then used the instantaneous deflection from the beeline as our response variable (Armstrong et al., 2013; Filannino et al., 2014; Padget et al., 2018). At each point along the homewards trajectory a beeline to the colony was isolated, and an instantaneous deflection from this beeline was calculated (see Figure 4.3). If birds were to orient differently following the magnetic treatment, we would expect that the magnitude of the instantaneous deflection angle would increase, equating to birds 'spiralling' in towards the colony.

The effect of the experimental treatment on instantaneous bearing was assessed using linear mixed-effect models (LMMs; Bates et al., 2015). Because our declination rotation treatment could be considered to be a single treatment with three ordered levels, we fitted an LMM with magnetic rotation as a continuous predictor (+115^o, 0 or -115^o). Likelihood ratio (LR) tests were then used to obtain p-values, with the full model compared to a null model (with treatment as a predictor removed). Additionally, we modeled our treatment as an ordered factor within an LMM so as to obtain estimates for deflection in each treatment. We also conducted post-hoc pairwise t-tests, Bonferroni-correcting the p-values, for each of the between-group comparisons (control $\sim$ anticlockwise, control $\sim$ clockwise and clockwise $\sim$ anticlockwise). Bonferroni corrections took into account the 6 treatment groups: first-night control, first-night anticlockwise, first-night clockwise, first-day control, first-day anticlockwise and first-day clockwise. In all LMMs trip ID was included as a random effect, nested within bird ID (so as to account for the potentially pseudoreplicative effect of including in the analysis 2 tracks from the same bird).

In addition to testing whether there was an overall effect of the treatment, we also sought to test whether there was a significant effect of heterogeneity in the applied magnetic field on deflection during homing. Specifically, we might expect birds to be sensitive to magnetic inclination, as this has been repeatedly implicated in songbird magnetic compass orientation (e.g. Wiltschko and Wiltschko, 1972; Wiltschko et al., 2006; Schwarze et al., 2016), and hence pay less attention to the artificially changed magnetic field ('CMF') when inclination is less representative of the normal geomagnetic field ('NMF'). We also investigated whether this was true of magnetic intensity, something to which other avian taxa have also been suggested to be sensitive (Semm & Beason, 1990; Holland, 2010).

We tested these hypotheses by first measuring the inclination/intensity within each arena of the Helmholtz coil with no current flowing through coil, before turning the coil on and measuring the induced change in inclination/intensity. From this we could calculate an 'absolute change in inclination/intensity', which if larger would indicate a greater effect of the magnetic coil on inclination/intensity. We then tested whether greater departures in the inclination/intensity between the NMF and the CMF predicted reduced deflection using an LMM, regressing the absolute deflection in orientation against the absolute change in inclination/intensity. To ensure that any effects of inclination/intensity were not caused by a confound between deviation in inclination/intensity and the overall declination shift, we also included in the model the absolute declination shift. We additionally included in the model the location of the arena within which the bird was housed (top, second top, middle or bottom) as a factorial predictor, so as to ensure that this too did not provide a confound.

4.3.4 Ethics statement

All experiments were carried out with the permission of the landowner (with Islands Conservation Advisory Committee approval), under licence from the British Trust for Ornithology with permission from the Oxford University Animal Welfare and Ethical Review Board.

4.4 Results

Using linear mixed-effects models, we investigated whether deflection from the homewards beeline was predicted by the magnetic treatment for both birds homing on the night of release and those homing the following day. Whilst we found that birds homing at night did not deflect significantly from the beeline (LMM; LR test; $\chi^2 1 = 2.39$, p = 0.121), we found that there was a significant difference in the effect of treatment between birds homing on the first night and the first day (LMM; LR test; $\chi^2 1 = 24.234$, $p < 0.0001$), with a highly significant effect of the experimental declination shift on instantaneous deflection observed in birds homing during the first day (LMM; LR test; $\chi^2 1 = 29.434$, $p < 0.0001$). LMM fixed-effect output predicted that birds deflected by 0.187° (± 0.0198°; see Figure 4.3) per degree of twilight field rotation, implying that the direction of deflection was in the same direction as the field shift for birds homing on the first day.

We further found that the significant effect of treatment on birds homing on the first day persisted when the magnetic treatment was modelled as an ordered factor (LMM; LR test; $\chi^2 1 = 29.161$, $p < 0.0001$). Post-hoc pairwise t-tests confirmed that there was a

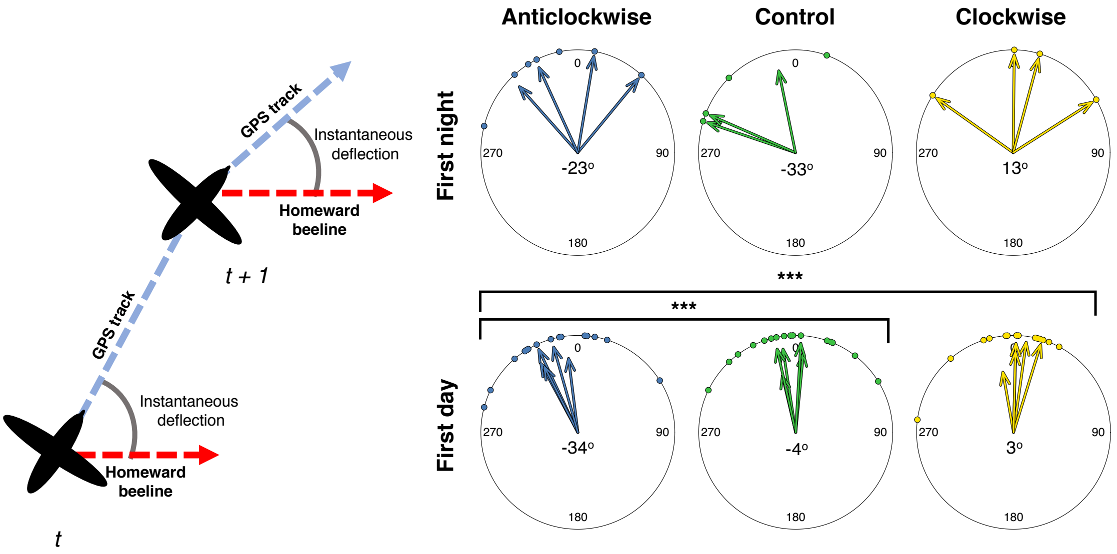

Figure 4.3: Mean instantaneous deflection from the beeline for all birds homing within 24 hours of release. (left) Schematic detailing how instantaneous deflection is extracted from a GPS track. (right) Deflection angle for each bird plotted on a circular diagram for each treatment homing on either the first night (top) or first day (bottom). Grand means for each displacement experiment are shown as arrows in the centre, with the length of each arrow proportional to the Rayleigh value of each group. Significant differences between treatments, as calculated using Bonferroni-corrected post-hoc t-tests, are shown as brackets. *** denotes $p < 0.001$, ** denotes $p < 0.01$ and * denotes $p < 0.05$.

significant difference of -33.08° between the clockwise and anticlockwise rotation experimental groups when considering birds homing on the first day post-release (Bonferroni-corrected t-test; $p < 0.0001$), and that that there was a significant difference of -29.04° between the anticlockwise rotation treatment group and the control group (Bonferroni-corrected t-test; $p < 0.0001$). We found, however, that there was no significant difference between the control and clockwise rotation groups (Bonferroni-corrected t-test; $p = 0.7857$), suggesting that the reported effect was asymmetric between the 2 treatment groups. Consistent with our main analysis we found that, when considering birds homing on the first day, there were no differences between the anticlockwise treatment group and the control group (Bonferroni-corrected t-test; $p = 0.5265$), the anticlockwise treatment group and the clockwise treatment group (Bonferroni-corrected t-test; $p = 0.4476$) and the clockwise treatment group and the anticlockwise treatment group (Bonferroni-corrected t-test; $p = 0.9250$).

As well as testing the overall effect of twilight magnetic field rotation, we also investigated whether the absolute deflection of manipulated birds was predicted by discrepancies between the normal magnetic field and the field generated in our magnetic treatments, both when considering magnetic inclination and magnetic intensity. Whilst we found no effect of magnetic intensity deviation on the observed deflection (LMM; LR test; $\chi^2$1 = 2.09, $p = 0.138$), we found that deviations in magnetic inclination inversely correlated with deflection (LMM; LR test; $\chi^2$1 = 5.43, $p = 0.0109$). Further, we found that the magnitude of this effect differed substantially between treatment groups (LMM; LR test; $\chi^2$1 = 5.97, $p = 0.0145$), with the anticlockwise group showing a highly significant effect of inclination on absolute deflection (a reduction of -10° ± 3.19° deflection per degree inclination discrepancy; LMM; LR test; $\chi^2$1 = 11.18, $p = 0.0008547$) with no detectable effect seen in the clockwise group (LMM; LR test; $\chi^2$1 = 0.259, $p = 0.611$). In turn, this implies that, as with the overall effect of magnetic field rotation, the effect of inclination on deflection was limited to the anticlockwise treatment (see Figure 4.4).

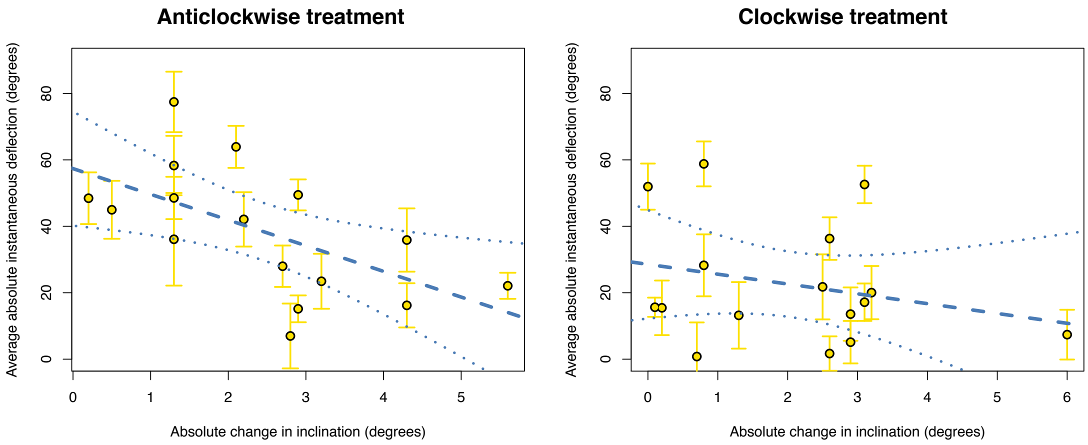

Figure 4.4: The effect of field inclination on instantaneous deflection. The absolute difference in inclination recorded between the CMF and the NMF plotted against the recorded absolute deflection for the anticlockwise declination rotation treatment (left) and the clockwise declination rotation treatment (right). Each point represents the mean deflection per bird (± 95% CI), and the fitted line represents a least means squares regression (± 95% CI).

4.5 Discussion

Using a twilight calibration paradigm, we found that artificial manipulation of the magnetic field at dusk caused Manx shearwaters to deflect during homeward orientation. Since the direction of deflection was in the same direction as the field shift, and was only observed in birds homing during the day, we suggest that this effect is consistent with a magnetic compass being used to calibrate a solar compass. We further found that the effect of the treatment lessened as the disparity between the natural geomagnetic inclination and the treatment field inclination increased, which we suggest is indicative of sensitivity to magnetic inclination. Below we consider why shearwaters might calibrate their sun compass to a magnetic compass, and discuss the magnitude and apparent asymmetry in the effect of the applied magnetic field manipulation.

Whilst deflection from the beeline might simply reflect the stress induced by the experimental treatment, we believe that this is unlikely given that the deflection differs between control and experimental treatments. Given that the overall direction of deflection from the homeward beeline was in the same direction as the treatment, and

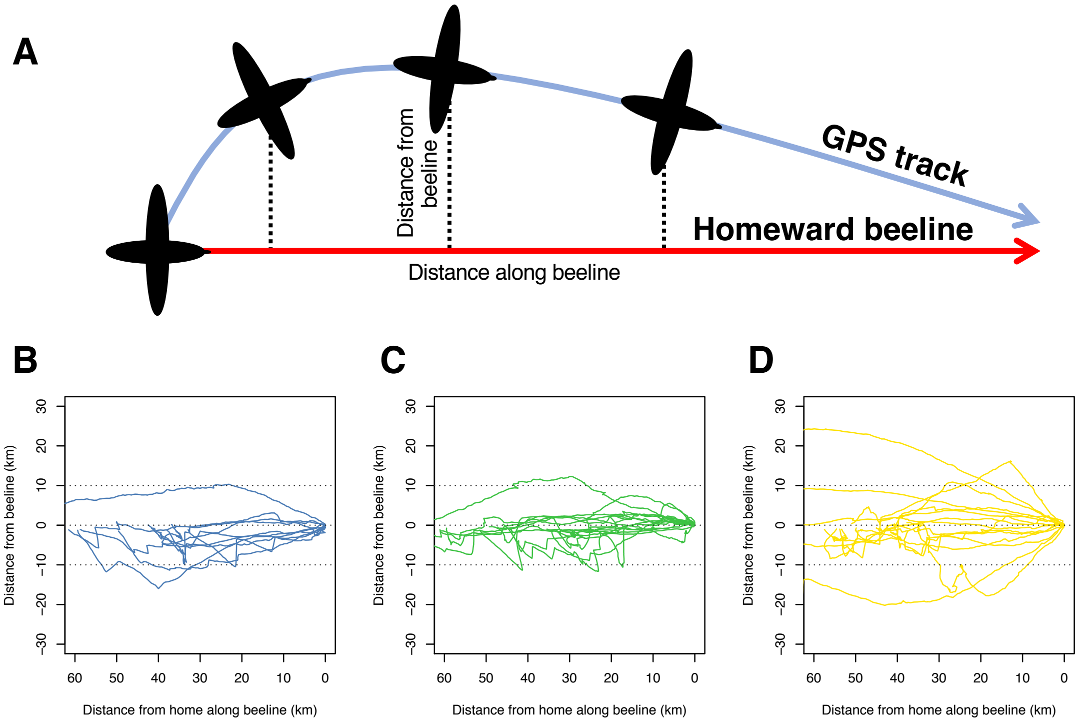

Figure 4.5: The distance from the homeward beeline plotted against the distance along the same beeline for birds homing on the first day post-displacement. A) Schematic showing how the distance from the beeline and the distance along the homeward beeline are calculated for each bird. B-C) The distance along the homeward beeline plotted against the distance from the beeline plotted for the anticlockwise, control and clockwise treatments respectively (after Padget et al., 2018). Birds start homing at [0,n], where n = the distance from the colony at which birds start homing. The home point for each bird is, therefore, at [0,0]. For clarity only the final 60km of each trip are shown, meaning the start of homing is not shown for 6 birds. Dotted lines are included to show ± 10km of the beeline.

given that the deflection was observed during the day but not at night, we propose that in the Manx shearwater system the flow of information within the compass calibration system is from the magnetic compass to a solar compass (Cochran et al., 2004). This is the first time this calibration direction has been reported, with previous studies tending to report the solar calibration of a magnetic compass (e.g. Cochran et al., 2004; Muheim et al., 2006). One hypothesis to account for why shearwaters might calibrate a sun compass from a magnetic compass, rather than the reverse reported in previous studies in songbirds, relates to relative stability of the two compass systems under different life-history conditions. This could be because the accuracy of directional information given by both magnetic and solar compasses varies through both time and space, and access to other frames of references (e.g. local landmarks) may vary, hence the specific ecology of a given species is likely to affect the accuracy of each compass system.

Manx shearwaters have a breeding range constrained almost entirely to Western Europe (Brooke, 1990), within which magnetic declination is fairly constrained (Chernetsov et al., 2017). Over the breeding season shearwaters are capable of long-distance foraging trips to the mid-Atlantic (e.g. Padget et al., 2019), over which the World Magnetic Model (WMM) predicts that declination could change by around 6° (Chulliat et al., 2015). However, such trips are comparatively rare, and breeding Manx shearwaters tend to utilise either the area immediately around the colony or, alternatively, predictable feeding resources within the Irish Sea (Dean et al., 2015; Shoji et al., 2015). Given that the WMM indicates that declination varies by less than 0.5° from the extreme east of the Irish Sea to the extreme west (Chulliat et al., 2015), the declination shifts experienced by shearwaters during the breeding season are therefore comparatively small. In contrast, previous studies of compass calibration have been carried out in the context of migratory birds moving across areas where magnetic declination changes rapidly with longitude, specifically high latitude North America (Muheim et al., 2003; Cochran et al., 2004; Muheim et al., 2007). In such situations, a night-migrating passerine will likely encounter between 5° and 10° of declination shift per day (Cochran et al., 2004; Chulliat et al., 2015). As mentioned previously, the position of the sun at a given time of day changes through the year. For example, the dawn position of the sun on Skomer Island changes by around 74° from the winter solstice to the summer solstice, equating to an average of around 0.4° change per day (Agafonkin & Thieurmel, 2018). If left uncorrected such shifts could accumulate over time hence, since shearwaters experience comparatively small magnetic declination shifts, we might suggest that solar declination might pose a greater barrier to efficient navigation than magnetic declination. Consequently, it perhaps make sense that shearwaters might calibrate a solar compass using another compass system.

In addition to the overall positive correlation between deflection and the applied field rotation, the magnitude of this deflection was reduced significantly by discrepancies between the inclination of the artificially generated magnetic field and the normal magnetic field. Songbirds have repeatedly and empirically been shown to be receptive to magnetic inclination (Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1992; Schwarze et al., 2016) and, given that shearwaters reduce their deflection as inclination becomes less accurate, we suggest that they too are sensitive to inclination. Indeed correlative studies conducted in Manx shearwaters imply that procellariforms might use magnetic inclination as a spatial cue (Wynn et al., 2020), hence empirical evidence for inclination sensitivity in a seabird is perhaps to be expected. Moreover, inclination sensitivity in songbirds has been suggested to reflect the radical pair mechanism by which they sense the Earth's magnetic field (for a review, see Hore and Mouritsen, 2016). We propose, therefore, that the findings of this study are consistent with seabirds using a similar mechanism of magnetoreception to that seen in songbirds.

Whilst we observed an overall effect of our treatment on the instantaneous deflection of homing birds, we found that the effect on orientation was substantially smaller than the field rotation imposed, with a deflection of 0.18^{o} per degree twilight field rotation. Given previous laboratory studies of orientation we might expect birds to deflect with a magnitude equal to that of the field rotation (e.g. Kobylkov et al., 2019), though other *in situ* studies of compass orientation within a familiar area have also found that deflections are often far smaller than would be expected under complete dependence on the deflected compass (e.g. Armstrong et al., 2013). It is difficult to explain why such 'partial deflections' might occur, though it has been suggested that they might reflect compromises in directional information summed from several different sources (Wiltschko et al., 1994). For example, if the mis-calibrated sun compass was not the only directional cue used during daytime orientation, we might expect birds to travel in a 'compromise' direction and hence deflect to a lesser extent than would otherwise be expect. Alternatively, smaller-than-expected deflections may be indicative of the deflected compass system being used when piloting via familiar visual landmarks (Wallraff et al., 1999; Biro et al., 2007; Padget et al., 2018). Under a model of pure pilotage birds would be able to discern the direction home through the comparison of multiple landmark cues, and we would therefore not necessarily expect birds to deflect at all. Birds could, however, compromise between directional cues derived from pilotage and those derived from compasses, which in turn could lead to bird to deflect during homewards orientation (Biro et al., 2007). More recently, it has been suggested that position within a familiar area might be determined using landmarks relative to compass cues, with the distance and direction to a landmark (or landmarks) used to determine position (Padget et al., 2018). For example, position relative to a featureless landmark could be determined if direction to the landmark was also known. Such a system would, when combined with a compass deflection treatment, necessarily lead to partial deflection during homing. Given that the birds displaced in this experiment were moving within an area with which they were likely extremely familiar, this mechanism could in principle explain the partial deflections observed. Alternatively, it has been suggested that an extrapolated gradient map could reduce deviation from the beeline in seabirds, with wind drift compensation specifically suggested to be underpinned by such an ability (Goto et al., 2017). Under such a hypothesis birds have sufficiently high-resolution map that they can reorient very regularly, and a similar ability would also reduce the magnitude of any compass manipulation treatment. It is, therefore, possible that the partial deflections observed in this study reflects the regularity with which the Manx shearwater map allows for reorientation.

However, whilst previous studies of familiar-area compass orientation might suggest smaller deflections are not entirely surprising, the asymmetric effect of the magnetic treatment is not easily explained by either compromise between multiple compass cues or some form of pilotage within a familiar area. Clock-shifted Manx shearwaters deflect to a smaller-than-expected extent but do so symmetrically (Padget et al., 2018), suggesting that whatever mechanism reduces compass deflection does so in both directions. We speculate, therefore, that the asymmetry observed in this study is unlikely to reflect the environment within which our displaced shearwaters orient, since such asymmetry has not been observed in previous studies. Instead, we suggest that asymmetry in the effects of our treatment could be caused by differences in the plausibility of different compass rotations at dusk. This could reflect interactions between compass rotations and visual landmark cues, with the known location of different landmarks relative to each other making certain magnetic field rotations implausible. As discussed above, position can be discerned using a compass direction relative to landmarks, and hence an attempt to discern position using several landmarks and a rotated magnetic compass may have no real-world solution. Given that landmarks rarely move, such instances may lead birds to disregard compass information. Alternatively, shearwaters may not be receptive to magnetic fields where the angle between the setting sun's disc and magnetic north is unrealistic. Over the course of a year the angle between magnetic north and the setting sun changes, which in turn gives a range of 'realistic' values. Magnetic compass rotations that deviate from these values might lead birds to ignore the rotation, in turn leading to asymmetry in the reported deflection. It is, however, unclear how such a 'reality check' would function, and further experimentation (with multiple release sites and homing directions) would necessarily be required to understand why our observed deflection is asymmetric.

Irrespective of this asymmetry, we find an overall effect of twilight field rotation on the bearing taken during homing flight. We believe this equates to the first experimental evidence for magnetoreception in a seabird, and we suggest that inclination sensitivity may point to a shared evolutionary origin between the seabird magnetic sense and that seen in songbirds. We further propose that avian magnetoreception might therefore be more ecologically and phylogenetically widespread than has previously been suggested in birds, and more generally we submit that our experimental paradigm, twilight calibration followed by displacement, may allow others to test for magnetic compass orientation within taxa where classical laboratory experimentation is impossible. We believe this is essential when considering the evolutionary history and ecological generalisability of magnetoreception, a sensory modality about which we know very little.

4.6 Appendix

In 2019, 46 Manx shearwaters were displaced from Skomer Island across 3 nights (n = 16, n = 15, n = 15). On the first night 16 birds were displaced in 4 treatments: a clockwise field rotation treatment, an anticlockwise field rotation treatment, a control treatment and a jostling magnet treatment (see Methods for details regarding the first 3 treatments). The 4 birds in the jostling magnetic treatment did not retain their magnets over the course of the displacement, hence the treatment was not analysed and was not repeated in the next displacement. In this displacement 5 birds were per treatment, which we repeated for the third displacement.

For the first 2 displacements birds were taken 30km south-west of the breeding colony, whilst in the third displacement birds were taken 15km from the colony. In the first 2 displacements birds were placed in the magnetic apparatus for the 2 hours prior to civil twilight (as in the 2021 experiment), whilst in the third displacement birds were kept in the magnetic apparatus for the 2 hours before sunset. Because of the inconsistencies in the treatment in these pilot displacements, the results from these displacements were not combined with the 2021 data. The results are, however, presented below.

The 7 birds that homed on the night of release showed no significant deflection based on treatment as an ordered factor (LMM; LR test; $\chi^2 1$ = 0.199, p = 0.905) or as a continuous treatment (LMM; LR test; $\chi^2 1$ = 0.0617, p = 0.801). We found that birds homing on the first day immediately following manipulation showed significant deflection when the treatment was modelled as both an ordered factor (LMM; LR test; $\chi^2 1$ = 10.118, p = 0.006353; see Figure 4.6) or as a continuous treatment (LMM; LR test; $\chi^2 1$ = 8.9052, p = 0.002844).

Post-hoc pairwise tukey tests showed that the anticlockwise-rotated condition was significantly different to the control group (p = 0.0474) and was significantly different to the clockwise-rotated condition (p = 0.014). The clockwise treatment was, however, not significantly different to the control treatment (p = 0.76) This indicates that whilst overall deflection observed across all 3 groups appeared significant, the effect of this shift was asymmetric. The results derived from the 2019 deflection are, then, consistent with those gathered in 2021.

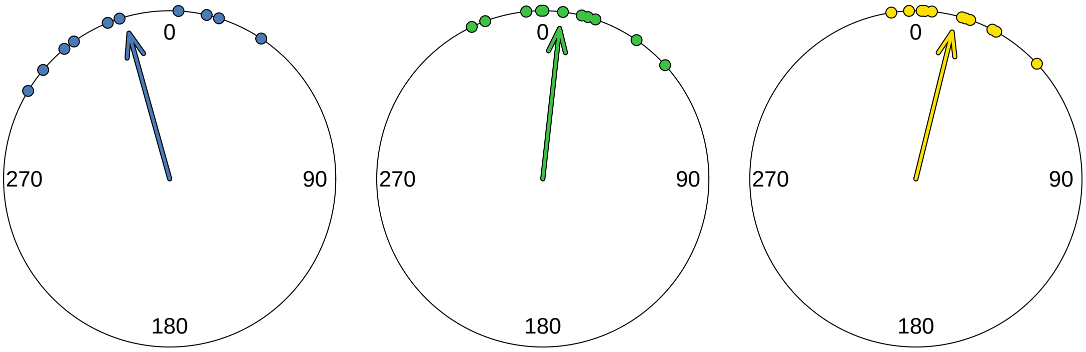

Figure 4.6: Overall deflections from the beeline observed in the 2019 pilot experiment. The circular mean deflections per bird from the beeline observed in the (left) anticlockwise (centre) control (right) clockwise groups displaced for birds displaced in 2019 homing on the first day post-displacement. The overall second order mean is shown as an arrow.

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5

Young frigatebirds learn how to compensate for wind-drift

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Contents

5.1 Abstract

Compensating for wind drift can improve goalward flight efficiency in animal taxa, especially amongst those that rely on thermal soaring to travel large distances. Little is known, however, about how animals acquire this ability. The great frigatebird (*Fregata minor*) exemplifies the challenges of wind drift compensation because it lives a highly pelagic lifestyle, travelling very long distances over the open ocean but without the ability to land on water. Using GPS tracks from fledgling frigatebirds, we followed young frigatebirds from the moment of fledging to investigate whether wind drift compensation was learnt and, if so, what sensory inputs underpinned it. We found that the effect of wind drift reduced significantly with both experience and access to visual landmark cues. Further, we found that the effect of experience on wind drift compensation was more pronounced when birds were out-of-sight of land. Our results suggest that improvement in wind drift compensation is not solely the product of either physical maturation or general improvements in flight control. Instead, we believe it is likely that they reflect how frigatebirds learn to process sensory information so as to reduce wind drift and maintain a constant course during goalward movement.

"If all you've got to do is find peace of mind, come round; you can take a piece of mine."

– Catatonia, *Road Rage*

5.2 Introduction

For motile animals the ability to navigate efficiently through space is essential, and for animals moving over long distances early in life it is necessary that this ability is either innate or develops rapidly. In birds, initial orientation amongst long-distance migrants is thought to be inherited genetically (Helbig, 1991), possibly as a vector (Perdeck, 1958; Mouritsen, 1998; Yoda et al., 2017). However, for any instructions to be meaningful in a stochastic and changeable environment, an animal must account for instantaneous variation in the prevailing conditions, such as wind strength and direction. Any animal moving through a fluid medium is liable to drift, and thus any flying animal moving toward a target is liable to drift with the prevailing air movement. Not all animal movement is goal-oriented, and thus drifting partially or completely with a fluid medium is not necessarily maladaptive (Chapman et al., 2011) and, indeed, moving with the overall movement of a fluid could increase the overall energetic efficiency of long-distance movement (Alerstam, 1979; Liechti, 1995; Lambardi et al., 2008; Hays et al., 2010). However, if an animal is to move efficiently through space towards a pre-determined goal, accounting and correcting for wind drift is likely to be beneficial over both large and small spatial scales (Riley et al., 1999; Srygley, 2001; Krupczynski & Schuster, 2008; Chapman et al., 2011).

'Wind drift compensation' encompasses multiple behaviours that limit the wind's propensity to displace a navigator from their most efficient goalward route. This is typically thought to include the adjustment of the heading so that the track taken is oriented towards the goal (Richardson, 1990), though in practice multiple modifications could be made that contribute to a reduction in wind drift (e.g. increasing the rate at which direction to the goal is updated). Wind drift compensation, by whatever mechanism, is likely to be especially important in seabirds, given their use of wind to efficiently travel vast distances over often visually sparse terrain (Weimerskirch et al., 2003; Gibb et al., 2017; Ventura et al., 2020). At least partial wind drift compensation has been noted in several seabird taxa amongst mature individuals, with the extent to which birds drift postulated to be contingent on the sensory cues available (Tarroux et al., 2016; Goto et al., 2017). Amongst seabirds, great frigatebirds (*Fregata minor*) may be particularly susceptible to wind drift, owing to their reliance on thermalling flight (Weimerskirch et al., 2016) and their inability to land on the water due to non-waterproofed feathering (Nelson, 2005). Whether frigatebirds have an ability to compensate for wind drift, and more generally how such an ability might develop in avian taxa, is, however, unclear. Whilst experience has been shown to affect navigational ability (and migration phenology) across animal taxa (Capaldi et al., 2000; Thorup et al., 2007; Campioni et al., 2020), and age has been specifically implicated as a predictor of drift compensation in birds (Thorup et al., 2003), it is unclear whether improvement in drift compensation with age reflects learning or simply reflects physical maturation (e.g. muscle and feather growth).

Here, we use GPS tracks derived from free-flying fledgling frigatebirds to investigate the development of drift compensation in avian taxa. Frigatebirds have a protracted post-fledging period where they still rely on parental care but are capable of independently moving around the natal site (Nelson, 2005), in doing so refining both biomechanical flight and foraging behaviour (Collet et al., 2020; Corbeau et al., 2020). Because birds were tracked consistently from the moment they fledged, we were able to precisely quantify the extent of individual birds' experience prior to specific excursions from their breeding colony. Using this information, alongside data pertaining to the extent to which land was visible to an individual along its homing trajectory, we sought to investigate a) whether experience correlates with reduced wind drift during homing flight and b) if so, whether this correlation was contingent on the sensory cues available.

5.3 Methods

5.3.1 GPS Tracking

Tracking was carried out on Europa Island in the Mozambique Channel (-22.36°N, 40.37°E) on 13 adult female and 10 juvenile frigatebirds (see Figure 5.1). Adult males were not used in this analysis as their role in chick provisioning is limited and, hence, they show little homing motivation. Devices measured 130×30×12mm and weighed 30g (PS-RF, e-obs GmbH, Munich, Germany), representing between 1.88%–3.55% of the frigatebirds' mass. Devices were deployed dorsally using Tesa tape and were set to record location every 2 or 5 minutes. 3-dimensional accelerometer data were also gathered but is not presented here (Corbeau et al., 2020).

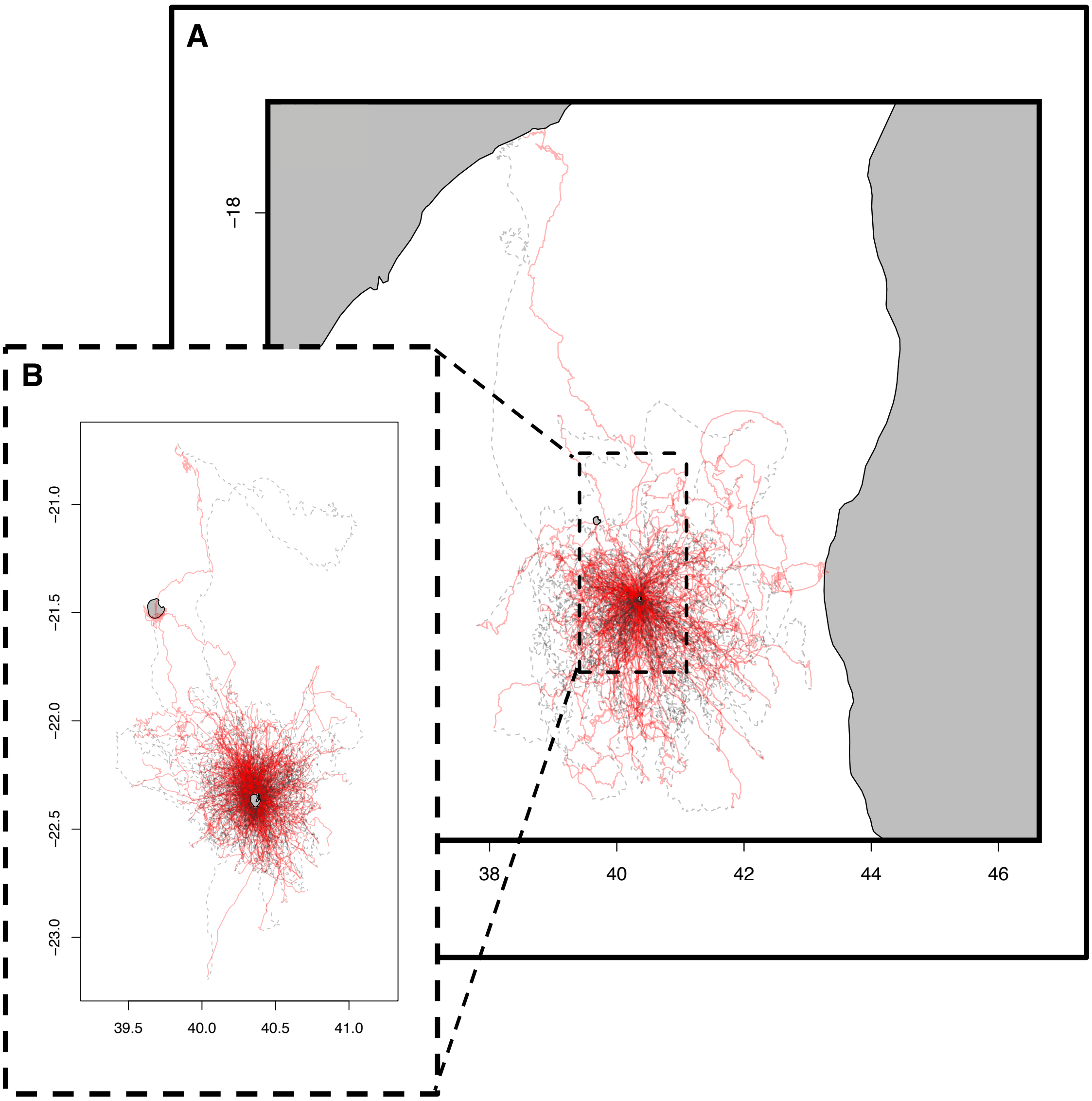

Figure 5.1: The complete GPS tracks used in this analysis. Interpolated GPS tracks from adult female frigate birds are shown in panel A) and interpolated GPS tracks from fledglings shown in panel B), with the dotted black line denoting the juvenile distribution nested within the adult distribution. Homing sections of tracks are highlighted in red whilst outbound sections are highlighted in grey.

5.3.2 Environmental and landmark cue data

Wind data were derived from the NOAA Global Forecast System at a temporal resolution of 3-hours and a spatial resolution of 0.5° longitude and 0.5° latitude. Whether or not birds could see any piece of land was ascertained using their altitude, measured using GPS and smoothed using a rolling median over a window of 4 consecutive fixes; the elevation of local topography, derived from USGS Global Multi-resolution Terrain Elevation Data; and the curvature of Earth. Smoothed altitude was used in analyses as the GPS-derived altitudinal error is substantially higher than that observed in both the longitudinal and latitudinal dimensions (Bouten et al., 2013; Ross-Smith et al., 2016). Birds were assumed to be able to see land if a line of-sight could be drawn between their position and the maximum elevation of any piece of land without the Earth's surface intervening. GPS points taken at night were removed from the analysis because it was not known whether reduced visual salience might affect access to landmark cues, and there were insufficient night-time GPS points to statistically test for an effect of daytime/night-time (980 individual fixes, representing only 24 trips from 6 unique individuals).

5.3.3 Track processing, statistics and analysis

All statistics and processing were conducted in R (R Core Team, 2017). Tracks were interpolated using a cubic spline function (Tremblay et al., 2006) so that fixes were positioned at precise 5-minute intervals. Tracks were also divided into trips out from the colony, with a trip defined as a continuous set of points recorded > 500m from the island's coastline with a minimum distance from the colony of > 3km. Since juveniles were tracked from their very first trips to sea, for a given trip we attempted to quantify the experience of the bird at that point in its development, measuring experience as the number of trips the focal bird had been on prior to the trip in question. In total, 19,732 interpolated GPS fixes were used in the analysis of fledgling frigatebirds, representing 1001 trips from 10 individual birds (with a mean of 100 and a median of 122 trips per individual), whilst

35,430 interpolated GPS fixes were used in the analysis of adult frigatebirds, representing 345 trips from 13 individuals (with a mean of 26 and a median of 12 trips per individual).

We chose to analyse only the homing sections of trajectories as we had an *a priori* expectation of where birds were aiming for. Because we had no expectations about the form of homing behaviour in frigatebirds, we conservatively defined homing as any points that occurred after the maximum distance to the colony was recorded on the trajectory. Due to the mechanisms by which frigatebirds generate lift (principally thermalling) and search for prey items (area restricted search behaviour) we expected individuals of all ages to engage in tortuous, non-navigational behaviours (Weimerskirch et al., 2016) . Track tortuosity was measured using the rolling standard deviation of track bearing over a window of 5 consecutive fixes, and non-navigational behaviours were parsed out using a mixture model to separate GPS fixes into 2 groups based on tortuosity (Benaglia et al., 2009; Dean et al., 2015). Only points with tortuosity lower than the mixture model-defined cut-off (of 52^{o}) were retained for use in navigational analyses. We repeated all analyses with multiple tortuosity cut-off points so as to ensure the significance of any findings were robust and unbiased by the threshold at which points were removed based on tortuosity (see Appendix).

For each point along a homing track, a beeline direction to the colony was assigned along the Great Circle route, from which instantaneous deflection was calculated (Padget et al., 2018). Orientation behaviour was modelled using this instantaneous deflection from the beeline (measured in degrees on a -180^{o} to 180^{o} scale) as a response variable. From the calculated beeline direction home, the cross-beeline and along-beeline wind components were calculated per interpolated GPS position. Using these wind components, we modelled the effect of wind drift in a 3-way interaction between the cross-beeline wind component, fledgling experience and whether or not the bird could see land as a binary factor (see Figure 5.2). The along-beeline wind component was also included in all models. This was because we expected that an increased headwind component might reduce groundspeed, thus halting a bird's forward progress and increasing instantaneous deflection per unit crosswind. By including the along-beeline component we, therefore, sought to standardise model output coefficients with respect to the along-beeline wind component so as the results presented were not the result of a confound between any variables of interest and the along-beeline wind component.

The effect of wind drift was modelled using linear mixed-effects models with trip ID, nested within bird ID, used as random effects (Bates et al., 2015; Padget et al., 2018). P-values were calculated using likelihood ratio tests between the hypothesised (alternative) model and a null model that did not contain the variable or interaction of interest.

5.4 Results

We found that, for fledgling frigatebirds, there was a significant effect of the cross-beeline wind component on deflection from the beeline to home (LR test; $p < 0.001$; see Figure 5.2). Linear mixed effect model outputs suggested that, between consecutive GPS fixes, inexperienced frigatebirds with no line-of-sight to land drifted by 10.5° (± 2.21° [SE]; see table 5.1) per metre per second of crosswind. We found, however, that there was a significant interaction between the cross-beeline wind component and whether or not land was in principle visible (LR test; $p < 0.001$), and that drift per metre per second of wind reduced by 5.73° (± 2.23°) in sight of land. This suggests that juvenile frigatebirds drifted around twice as much per unit wind speed when they could not see land when compared to when they could (see Figure 5.2).

As well as finding evidence that naïve fledglings seemed to drift with the wind, we also found that the magnitude of this effect varied significantly with experience (see Figure 5.3; LR test; $p < 0.001$). For each trip away from the island, the angular effect of wind drift was reduced by 0.0586° (± 0.0214°; see table 5.1) for birds that did not have a direct line-of-sight to land. Since during the tracking period we found that birds undertook a median 122 trips from the colony meaning that, after the median number of trips were completed, birds were estimated to have reduced their drift per metre per second crosswind by 7.14° (± 2.61°) when out-of-sight of land. In contrast, we found that the effect of experience was significantly reduced when birds were in sight of land (LR test; $p < 0.001$; table 5.1), with the effect of experience on drift reduced by 0.0439° (± 0.0216°) when birds could see land, suggesting that the effect of experience was substantially greater when access to visual landmarks is limited.

Whilst there was a significant effect of wind drift on adult frigatebirds (LR test; $p < 0.001$), it was of a markedly lower magnitude compared to that observed in fledglings. The modelled estimate of wind drift was 1.43° (± 0.12°) drift per metre per second of wind in adult frigatebirds when out-of-sight of land (see Figure 5.2). Unlike fledgling frigatebirds, we found that this drift component increased slightly but significantly by 0.701° (± 0.172°) when birds could see land (LR test; $p < 0.001$; see Figure 5.2).

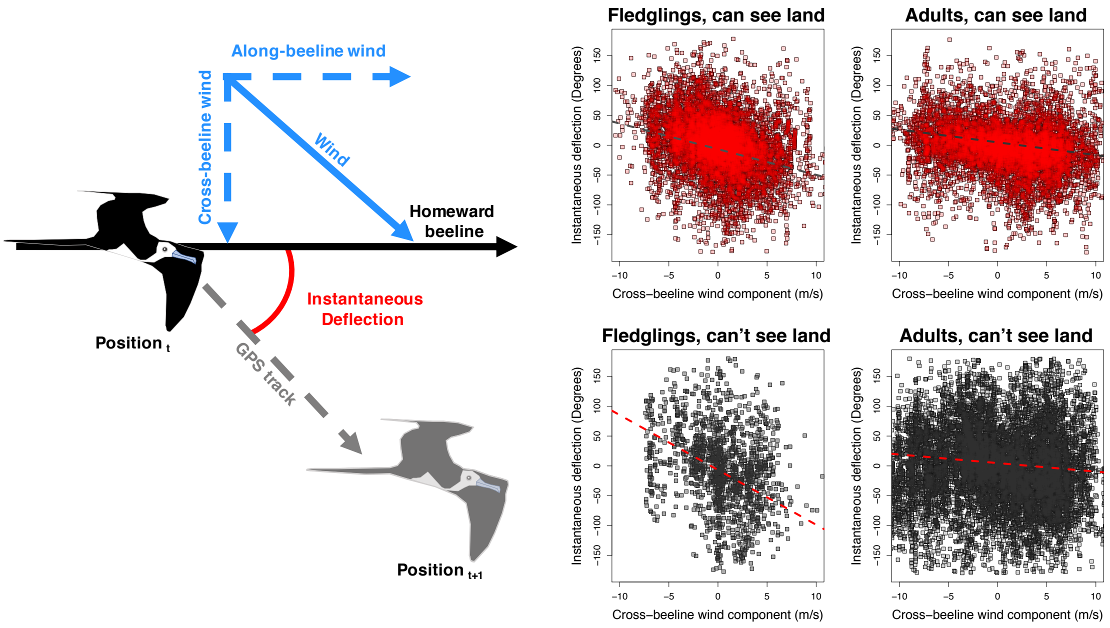

Figure 5.2: The effect of access to landmark cues on wind drift in fledgling and adult frigatebirds. (left) visual representation of modelled quantities and (right) deflection plotted against the cross-beeline wind component in (clockwise from top-left) A) fledgling frigatebirds that could see land, B) adult frigatebirds that could see land, C) fledgling frigatebirds that couldn't see land and D) adult frigatebirds that couldn't see land. Regression lines show the mean effect size as estimated using linear mixed-effects models. Negative values for crosswind component/deflection angle indicate that the crosswind/deflection is anti-clockwise with respect to the bird's movement.

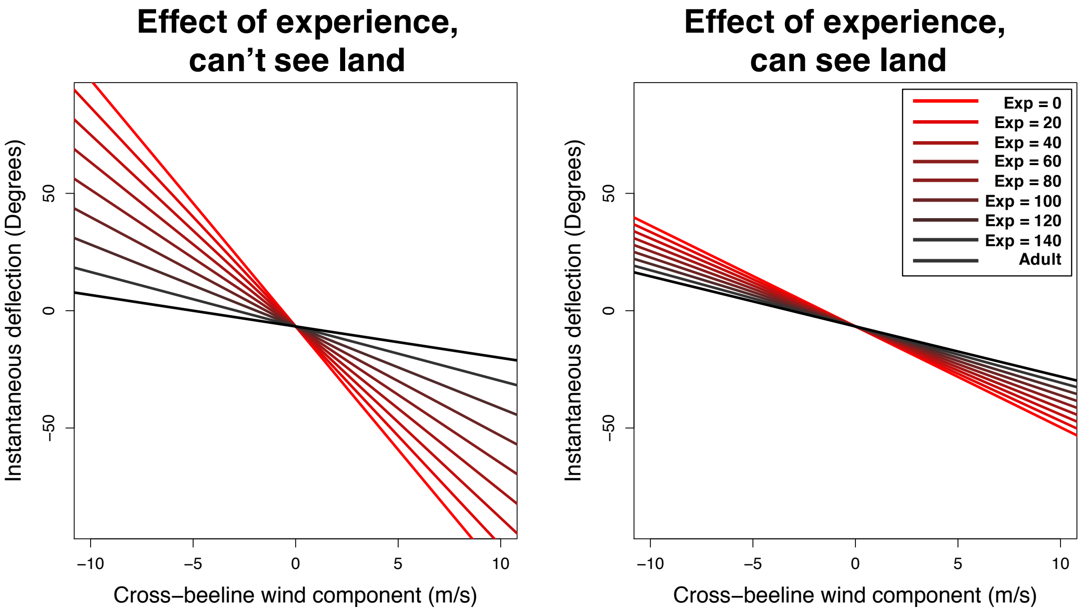

Figure 5.3: The development of wind drift in fledgling frigatebirds. The LMM-estimated mean effect of wind speed on instantaneous deflection for fledglings of varying experiences ('Exp'; the number of trips undertaken) and adults. (left) The estimated effect sizes for birds moving out-of-sight of land and (right) the estimated effect sizes for birds moving in-sight-of-land. As in Figure 5.2, negative values for crosswind component/deflection angle indicate that the crosswind/deflection is anti-clockwise with respect to the bird's movement.

5.5 Discussion

Based on complete GPS records of the free-ranging post-fledging movements of great frigatebirds, we found that wind drift was reduced by both access to visual landmark cues and increased experience. Experience interacted with access to visual cues, reducing wind drift to a greater extent when birds were out-of-sight of land (see Figure 5.2). Whilst previous studies have shown age to be a strong predictor of wind drift compensation in other avian taxa (Thorup et al., 2003), the role of experience has so far remained unclear. Here, we postulate that at least part of the improvement in wind drift compensation with age is a learnt ability, gained progressively, probably involving the interpretation of sensory inputs.

General increases in flight control, due to physical maturation or improvements in the cognitive control of flight, might facilitate successful wind drift compensation and, indeed,

	Instantaneous deflection (degrees)
Experience	−0.166 (± 0.064) **
Can see land	−13.530 (± 6.006) *
Cross-beeline wind	−10.506 (± 2.213) **
Along-beeline wind	−0.083 (± 0.147)
Experience * can see land = TRUE	−0.143 (± 0.060) *
Cross-beeline wind * Experience	−0.058 (± 0.021) **
Cross-beeline wind * can see land = TRUE	−5.724 (± 2.226) *
Cross-beeline wind * can see land = TRUE * Experience	−0.04 (± 0.022) *
(Intercept)	−10.844 (± 6.503)

Table 5.1: Fixed effect estimates for wind drift compensation. Fixed effects, as estimated using a linear mixed-effects model, as used in our analysis of wind drift compensation in fledgling frigatebirds. Because the overall correlation between deflection angle and wind speed is negative (i.e. winds anticlockwise of the beeline displace a bird clockwise and vice versa), a positive effect indicates a reduction in wind drift. The mean estimated effect size is shown in the table, with standard error is shown in brackets. * indicates p < 0.05 and ** indicates p < 0.01, as assessed using a likelihood ratio test.

previous studies have reported differences in wing length between adult and fledgling frigatebirds (Collet et al., 2020). However, we might expect that, if such maturation processes were to underpin the results presented here, the rate of drift both in and out-of-sight of land should reduce at similar rates. In contrast, we find that the change in wind drift with experience is much more prominent out-of-sight of land. Hence, we instead suggest that experience acts on the cognitive processes that transform sensory input into the motor actions required to counter drift. We reason this is the case because experience interacts with access to visual landmark cues, suggesting that the effect of experience is in part contingent on the sensory input available. We suggest that this reflects a process where birds learn, possibly using simple associative learning (Guilford

& Burt de Perera, 2017), how sensory input relates to drift, and in turn use this input to reduce drift on subsequent trips. Although these effects are consistent with processes dominated by individual learning it is also possible that social learning effects, learning involving the observation and mimicry of conspecifics (Hoppitt and Laland, 2008), might also contribute since frigatebirds are a colonially-nesting species.

Drift compensation is typically thought to involve the quantitative adjustment of heading into the wind so as the resultant track taken over the ground is more goalward oriented (Chapman et al., 2011). This process requires that a bird can, first, use sensory input to assess correctly the extent to which it is drifting before, second, adjusting its heading accordingly. Given that we find that birds drift less when in-sight-of-land this could involve visual cues, possibly as optic flow (the relative movement of objects across the field of view) since this has been implicated in wind drift reduction and course retention both in avian taxa and in animals more generally (Esch et al., 2001; Bhagavatula et al., 2011; Ros & Biewener, 2016; Hedenstrom & Akesson, 2017). However, given that multiple cues co-vary with access to visual landmark cues, this is difficult to parse out using only correlative studies.

Heading alteration is not, however, the only mechanism by which wind drift might be reduced with experience. The rate at which birds are displaced by the wind might be reduced by learnt navigational mechanisms that are not specific to wind drift reduction, such as through a more precise understanding of an individual's position; if, at the start of goal-oriented navigation, a bird calculated the bearing home only once and then maintained that heading, then the angle between the bird's realised trajectory and the target would increase if a bird drifted with the wind. Consequently, even a bird inattentive to instantaneous wind conditions could reduce the rate at which it drifts by increasing the rate at which it attends to its displacement relative to the goal. This could be, for example, because of an increase in the resolution at which it perceives spatial information (e.g. an increase in the resolution of a navigational map; Goto et al., 2017). As such, it is unclear from our analyses whether frigate birds learn to attend to specific drift-related cues or whether the observed reduction in wind drift is a product of a learnt ability to attend to more general navigational cues.

In addition to finding that fledglings drift less when more experienced, we find that adult frigatebirds drift less than fledglings (see Figure 5.2). Estimated effect sizes derived from linear mixed-effects models imply that, even after the prolonged pre-migratory parental care period, fledgling frigate birds still drift more than their adult conspecifics (see Table 5.1. Indeed, model output would suggest around 151 trips are required to equal the drift compensation seen in adults when out-of-sight of land. In turn, this suggests that the development of wind drift compensation continues as the fledglings start to migrate. Whilst this is consistent with experience improving drift compensation, we note that, unlike in fledglings, adults drift slightly (but significantly) more when in-sight of land. However, the magnitude of this difference is substantially smaller (by almost an order of magnitude) than the difference observed in fledglings. Given that there is no apparent sensory explanation why drift might be increased with increased salient visual information in experienced individuals, we suggest that such a difference may reflect differences in the motivation to home when approaching the colony rather than an inability to compensate for drift when in-sight of land.

Taken together, our results suggest that frigatebird drift compensation is, at least in part, learnt. As a tropical seabird with an extended post-fledging parental care period that is reliant on thermals to gain lift, it is possible that the development of wind drift compensation in frigatebirds reflects their unique ecology. Further study is, therefore, required in order to investigate the generalisability of these results to other avian taxa. Nonetheless, we believe these results are informative in the context of the development and mechanism of avian navigation, and demonstrate the power of analysing free-ranging GPS tracks when examining the ontogeny of animal behaviour.

5.6 Appendix

Robustness of results to tortuosity cut-off

Due to thermalling and area restricted search behaviour being commonplace in frigatebirds (Weimerskirch et al., 2003; Weimerskirch et al., 2016), we expected there to be, in our dataset, points in which frigatebirds engaged in tortuous, non-navigational behaviour. So as to ensure that such behaviour did not bias the results of our analyses, and so as to increase the signal:noise ratio, we sought to remove these behaviours from the dataset using a threshold model of tortuosity as measured using a rolling standard deviation in track bearing recorded over 5 consecutive GPS fixes (Dean et al., 2015). Because we had no a priori expectation as to the tortuosity value that corresponded to the behaviours we wanted to omit, a threshold value of 52^o SD was selected using a gaussian mixture model (Benaglia et al., 2009). To ensure that the cutoff value chosen did not bias our results or drive the significance observed in our linear mixed-effects model, we re-ran our model with different threshold values. We re-ran the model with the cut-off set at a SD in track bearing of 30^o (Table 5.2), 40^o (Table 5.3), 52^o (mixture model selected cut-off; Table 5.1 in main text), 60^o (Table 5.4) and 70^o (Table 5.5). In Table 5.6 we report the mean and standard deviation of each effect size for all cutoffs tested.

Robustness of results to the inclusion of night-time GPS fixes

In the main-text analysis we removed GPS fixes that fell after dusk because we did not have sufficient sample size to statistically investigate the effect of reduced visual saliency. We include in table S6 analysis of wind drift when these points are included.

	Instantaneous deflection (degrees)
Experience	−0.31 (± 0.07)
Can see land	−27.73 (± 7.24)
Cross-beeline wind	−10.03 (± 2.61)
Along-beeline wind	−-0.25 (± 0.17)
Experience * can see land = TRUE	−0.29 (± 0.070)
Cross-beeline wind * Experience	−0.050 (± 0.031)
Cross-beeline wind * can see land = TRUE	−6.08 (± 2.263)
Cross-beeline wind * can see land = TRUE * Experience	−0.04 (± 0.030)
(Intercept)	−24.47 (± 7.71)

Table 5.2: Wind drift model (tortuosity cutoff = 30°). Estimated fixed effect sizes from linear mixed-effects model of deflection from the beeline regressed against a 3-way interaction between the cross-beeline wind, experience and line-of-sight to land as a binary factor. Along-beeline wind is also included in the model (see main text).

	Instantaneous deflection (degrees)
Experience	−0.31 (± 0.07)
Can see land	−18.9 (± 6.53)
Cross-beeline wind	−10.30 (± 2.41)
Along-beeline wind	−0.25 (± 0.15)
Experience * can see land = TRUE	−0.19 (± 0.070)
Cross-beeline wind * Experience	−0.050 (± 0.021)
Cross-beeline wind * can see land = TRUE	−5.95 (± 2.42)
Cross-beeline wind * can see land = TRUE * Experience	−0.04 (± 0.020)
(Intercept)	−14.92 (± 6.97)

Table 5.3: Wind drift model (tortuosity cutoff = 40°). Estimated fixed effect sizes from linear mixed-effects model of deflection from the beeline regressed against a 3-way interaction between the cross-beeline wind, experience and line-of-sight to land as a binary factor. Along-beeline wind is also included in the model (see main text).

	Instantaneous deflection (degrees)
Experience	−0.13 (± 0.06)
Can see land	−11.4 (± 5.81)
Cross-beeline wind	−9.7 (± 2.05)
Along-beeline wind	−0.26 (± 0.15)
Experience * can see land = TRUE	−0.12 (± 0.06)
Cross-beeline wind * Experience	−0.050 (± 0.021)
Cross-beeline wind * can see land = TRUE	−5.13 (± 2.16)
Cross-beeline wind * can see land = TRUE * Experience	−0.03 (± 0.020)
(Intercept)	−7.67 (± 6.34)

Table 5.4: Wind drift model (tortuosity cutoff = 60°). Estimated fixed effect sizes from linear mixed-effects model of deflection from the beeline regressed against a 3-way interaction between the cross-beeline wind, experience and line-of-sight to land as a binary factor. Along-beeline wind is also included in the model (see main text).

	Instantaneous deflection (degrees)
Experience	−0.11 (± 0.06)
Can see land	−9.72 (± 5.76)
Cross-beeline wind	−9.18 (± 2.04)
Along-beeline wind	−0.16 (± 0.15)
Experience * can see land = TRUE	−0.1 (± 0.06)
Cross-beeline wind * Experience	−0.040 (± 0.020)
Cross-beeline wind * can see land = TRUE	−4.89 (± 2.06)
Cross-beeline wind * can see land = TRUE * Experience	−0.03 (± 0.020)
(Intercept)	−6.71 (± 6.25)

Table 5.5: Wind drift model (tortuosity cutoff = 70^o). Estimated fixed effect sizes from linear mixed-effects model of deflection from the beeline regressed against a 3-way interaction between the cross-beeline wind, experience and line-of-sight to land as a binary factor. Along-beeline wind is also included in the model (see main text).

	Instantaneous deflection (degrees)
Experience	−0.17 (± 0.06)
Can see land	−13.93 (± 5.97)
Cross-beeline wind	−10.86 (± 2.21)
Along-beeline wind	−0.04 (± 0.15)
Experience * can see land = TRUE	−0.14 (± 0.06)
Cross-beeline wind * Experience	−0.060 (± 0.020)
Cross-beeline wind * can see land = TRUE	−6.03 (± 2.06)
Cross-beeline wind * can see land = TRUE * Experience	−0.04 (± 0.020)
(Intercept)	−10.77 (± 6.55)

Table 5.6: Fixed-effect output for wind drift model including night-time GPS points). In the main-text analysis GPS fixes taken at night were omitted from the study (as it was unclear how access landmark cues would interact with reduced visual salience and the night-time sample size was insufficient for statistical analysis).

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6

Early-life development of contrasting outbound and return migration routes in a long-lived seabird

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Contents

6.1 Abstract

Although mechanisms of genetic and social inheritance have been implicated in determining the migratory routes of birds, it is unclear what their relative contributions are in species where outbound and return migration routes differ ('loop migrants'). Here, we used biologging devices to follow Manx shearwaters (*Puffinus puffinus*), a long-lived seabird with a trans-Atlantic loop migration, from before their first migration until their 3rd calendar year. We found that shearwaters undertake first migration without adults, setting off almost immediately upon fledging and moving along a more direct trajectory than adults. Juveniles wintered in the same part of the South Atlantic as their parents before iteratively developing their return migration route over the next 3 years, each time returning—unlike their parents—via a Western Atlantic route. We propose that first outbound migration in Manx shearwaters is broadly consistent with a genetically inherited vector, and that both the outbound and return migration trajectories are unlikely to be learnt from experienced conspecifics. We suggest that return migration in Manx shearwaters, and perhaps loop migrants more generally, may be informed by genetically inherited information and/or local environmental conditions. We further propose that the iterative extension of northbound migration may reflect the 'exploration-refinement' of a return migration route.

> *"You have brains in your head.*
> *You have feet in your shoes.*
> *You can steer yourself any direction you choose.*
> *You're on your own.*
> *And you know what you know.*
> *And YOU are the guy who'll decide where to go."*
>
> – Dr Seuss, *Oh, the Places You'll Go!*

6.2 Introduction

It is essential that naïve migratory animals inherit (by whatever mechanism) information that will allow them to reach their wintering grounds. It is equally important they are also equipped with information that allows them to return to a suitable breeding site. Amongst birds, the outbound migratory trajectory is thought to be underpinned by (epi)genetically inherited information (Helbig, 1991; for a review, see Merlin and Liedvogel, 2019), typically thought to comprise 'clock and compass' vector navigation; a compass to give a direction, and a clock to encode distance (Perdeck, 1958; Mouritsen, 1998; Mouritsen & Larsen, 1998; Thorup et al., 2007; Yoda et al., 2017). In addition, there is evidence that the cultural inheritance of migratory routes can occur through social learning amongst both related and unrelated conspecifics, with the precise migratory route taken at least in part informed by the routes of experienced adults migrating simultaneously (Chernetsov et al., 2004; Harrison et al., 2010; Palacin et al., 2011; Mueller et al., 2013; Rotics et al., 2016). There is also a growing body of evidence for asocial learning in determining migratory route ('exploration refinement'), phenology, destination and efficiency, with individuals of long-lived species honing migratory behaviours over successive attempts (Thorup et al., 2003; Guilford et al., 2011; Campioni et al., 2020; Fayet, 2020; Wynn et al., 2020a).

In contrast to outbound migration, comparatively little is known about the navigational mechanisms underpinning first return migration. The majority of migratory birds exhibit an ability to return precisely to the natal site (Newton & Brockie, 2008), a process known as 'natal philopatry', which is thought to involve learnt cues associated with the natal site (Baker, 1978). Experienced navigators of multiple taxa may use wide-ranging gradient cues during long-distance navigation, with empirical evidence supporting the use of both olfactory (Gagliardo et al., 2013; Pollonara et al., 2015; Padget et al., 2017) and geomagnetic cues (Bulte et al., 2017; Chernetsov et al., 2017; Wynn et al., 2020b). Such cues could act as a bi-coordinate 'map' during long-distance navigation (e.g. Padget et al., 2019), and it has also been suggested that similar cues could be used to target the natal site over very long distances (Baker, 1978; Lohmann et al., 2008). Alternatively, a vector navigation system may be used (as is the case in outbound migration; Perdeck, 1958; Mouritsen et al., 2003; Holland, 2014).

Not all birds follow the same route on both outbound and return migration, with so-called ‘loop migrants’ taking contrasting outbound and return trajectories (e.g. Mellone et al., 2013; Willemoes et al., 2014; Katzner et al., 2016). One such loop-migrant, the burrow-nesting, pelagic Manx shearwater (*Puffinus puffinus*), migrates from Western Europe to the Patagonian Shelf in the South Atlantic, with adults known to migrate south via the East Atlantic and return north via the West Atlantic (Guilford et al., 2009). Scant ringing recoveries in the South Atlantic imply that juvenile shearwaters migrate south almost immediately upon fledging (Brooke, 1990), with colony-based ringing recoveries suggesting that the majority of shearwaters return to the natal colony around their third year post-fledging (Harris, 1966; Perrins et al., 1973).

How juvenile Manx shearwaters undertake their first trans-equatorial migration, and how they then return with almost perfect accuracy to their natal colony (Wynn et al., 2020b), remains unknown. Here, using radio frequency identification (RFID) detectors, archival geolocators (GLS) and remote-download Platform Terminal Transmitter GPS devices (PTT-GPS), we explored a) the mechanism by which juvenile shearwaters inherit outbound migratory information, b) how shearwaters construct their return migratory route and c) whether the time prior to fledging was used by shearwaters to inform navigational mechanisms.

6.3 Methods

6.3.1 GLS tracking

Geolocator deployments were made on Lighthouse Island, Copeland Archipelago, Northern Ireland (54.69°N, -5.530°W). GLS devices (BAS MK19) were deployed on darvic plastic rings on the legs of 54 fledgling Manx shearwaters over the autumn of 2011 (Guilford et al., 2009). 3 of these devices were retrieved with downloadable data over the years 2015 (2 devices) and 2016 (1 device). Of the devices retrieved 1 device recorded for 127 days, 1 for 559 days and 1 for 1041 days. In addition to these 3 juvenile birds, some 38 adult Manx shearwaters were also GLS tracked from Copeland in 2010, 2011 and 2012. These combined 41 GLS tracks, 3 from fledglings and 38 from adults, were processed together.

GLS positions were derived using the GeoLight package in R (Lisovski & Hahn, 2012), with a threshold of 10 arbitrary units and an elevation angle of -4.5° used for all birds. GLS points were retrospectively filtered according to the photoperiod and speed observed between consecutive points in order to filter unrealistic datapoints from any analyses. A photoperiod of > 11 hours and < 14 hours was considered realistic for the Atlantic around the autumn equinox, whilst a maximum speed threshold of 750km per day was imposed based on the average speed of adult Manx shearwaters assuming near-constant movement over the GLS fix time (Guilford et al., 2009). Given that latitudinal information is impossible to discern on either equinox, and error around the equinox makes accurate location of the bird improbable (Lisovski et al., 2020), fixes within 2 weeks of either equinox event removed.

GLS devices also recorded immersion data at 6-second intervals, storing this information as either recorded transitions between wet and dry events or as binned values of the total immersion over a 10-minute period . Devices that recorded dry/wet transitions were subsequently binned to produce 10-minute summaries, so as to make all tracks directly comparable. A threshold model was used to divide binned immersion data by behaviour (Shoji et al., 2015), with an immersion value of 0% immersion classed as flight, a value of 100% immersion as rafting and anything between as feeding.

6.3.2 PTT-GPS tracking

PTT-GPS devices were deployed on Skomer Island, Pembrokeshire (51.73°N, -5.28°W). 10 devices (Lotek Wireless PinPoint) were deployed dorsally using Tesa marine tape (Guilford et al., 2009) on fledgling shearwaters over the autumn of 2019. Devices weighed

5g and were set to record a GPS position every day at midnight GMT, with the positions uploaded to the Argos network every 3 days. Each transmission contained 6 positions, hence each location was transmitted twice. Positional estimates were also ascertained upon transmission using Argos doppler shift and were retained if positional error was estimated at $<$ 1.5km (position class 1 or better).

In addition to tracking fledglings, we also tracked their parents. For each fledgling both parents were fitted with leg-mounted Migratetech C65 geolocators. Of these 20 devices 10 were retrieved, representing the parents of 7 birds (see above for processing details).

6.3.3 RFID monitoring

Radio frequency identification (RFID) detectors were deployed on Skomer Island so as to a) assess the rate of parental visitation in the weeks immediately preceding fledging and b) examine the pre-fledging behaviour of shearwaters.

RFID devices were deployed in the entrances of 70 shearwater burrows in 2018 and 10 burrows in 2019. In 2019, RFID deployment was coincident with PTT-GPS deployment. Both parents and the chick from each burrow were fitted with were fitted with passive integrated transponder (PIT) tags (2 x 12mm EM4102 glass tag, Cyntag Cynthiana, KY, USA), programmed with a unique identification so as to allow for the individual identification of birds as they left the burrow (Tyson et al., 2017). RFID tracking data was augmented by data gathered by the Met Office at the Milford Haven weather station (14.5km from the colony) with wind, precipitation and cloud cover recorded hourly. Moon phase and the timing of moonrise and moonset were derived from the ‘suncalc’ package in R (Agafonkin & Thieurmel, 2018), with both phase and timing to give a combined metric of ‘moonlight’.

6.3.4 Statistical analyses

All statistics were computed in R (R Core Team, 2017). Our formal statistical analysis broke down into 3 broad themes: pre-fledging behaviour, first outbound migration and return migration.

The environmental correlates of pre-fledging activity were examined using a generalised linear mixed effects model (using the 'lme4' package; Bates et al., 2015), with detection events on the RFID reader modeled as a binary response variable. In these models we included wind speed, precipitation, cloud cover and moon brightness. To ensure that temporal autocorrelation did not affect the results, RFID detections were down-sampled to hourly summaries, with hourly average values for all environmental variables calculated.

When considering the outbound migratory trajectory, we sought to investigate a) how direct the migratory trajectories of adults and chicks were, and b) how close adults were to their progeny. How close fledglings and adults were to both the beeline and the shortest over-sea route were examined using a linear mixed-effects model (Bates et al., 2015). The beeline was defined as the Great Circle Route (GCR) between the median adult wintering longitude/latitude and the breeding colony, whilst the shortest over-sea route was defined as the GCR between the breeding colony and the north-east corner of the South American continent and the GCR between the wintering site and the north-east corner of the South American continent (see Figure 6.3). Distance to the GCR was calculated using the 'geosphere' package in R (Hijmans et al., 2017). How close fledglings were to their parents was determined via a stratified randomisation. The distances between each PTT-GPS tracked chick and its parent(s) on a given day was determined for all chicks, from which a minimum chick-to-parent distance could be calculated. A mean distance-to-parent was calculated per chick, and a second-order mean was then taken for all chicks collectively. This was compared to the same statistic calculated with the identity of chicks and their parents randomised (n = 10,000), so as on a given day chicks were compared to random birds (sampled with replacement from the overall pool of tracked parents).

When considering return migration we chose to avoid formal quantitative statistical analysis, owing to the smaller sample sizes associated with the return migration. Instead, we sought to qualitatively compare the phenology and route taken by immature shearwaters to those of adult conspecifics.

6.3.5 Ethics statement

All deployments were carried out with the permission of the landowner (with Islands Conservation Advisory Committee approval), under licence from the British Trust for Ornithology with permission from the Oxford University Animal Welfare and Ethical Review Board.

6.4 Results

RFID analysis of pre-fledging behaviour

We used RFID readers to investigate whether shearwaters may gather potential navigational information on the colony surface prior to fledging. Specifically, we sought to understand whether chick timed forays onto the surface so as to maximise access to rotational celestial cues. Star compasses have been shown to be learnt in songbirds, hence if shearwaters were to utilise a star compass on first migration prior exposure to clear skies would seem essential (e.g. Michalik et al., 2014).

Chicks showed considerable activity in the days and weeks leading up to fledging, with birds recorded on the RFID antennae (i.e. leaving or entering the burrow) on average 7.8 (± 0.58 [95% CI]) unique nights prior to fledging. The instantaneous probability of chicks exploring the surface increased as their fledge date approached (GLMM; LR test; $\chi^2 1 = 689$, $p < 0.00001$), with the probability of chicks being recorded by RFID detectors rising from 0.05% 30 days prior to fledging to 2.5% on the night immediately preceding fledging. In order to investigate whether immature shearwaters timed such trips to the surface so as to maximise access to celestial cues, we looked at whether shearwaters were less likely to be detected on RFID readers on cloudy nights. We, additionally, tested whether birds altered their surface activity in response to conditions not thought to be important when considering compass learning: moon state, rainfall and wind speed. We found that chicks reduced activity on the surface in response to increases in wind speed (GLMM; LR test; $\chi^2 1 = 98.0$, $p < 0.00001$) and rainfall (GLMM; LR test; $\chi^2 1 = 20.4$, $p < 0.00001$). We also found that activity was reduced in response to moonlight (GLMM; LR test; $\chi^2 1 = 5.54$, $p = 0.0129$). We found, however, no effect of cloud cover on activity levels (GLMM; LR test; $\chi^2 1 = 2.28$, $p = 0.131$).

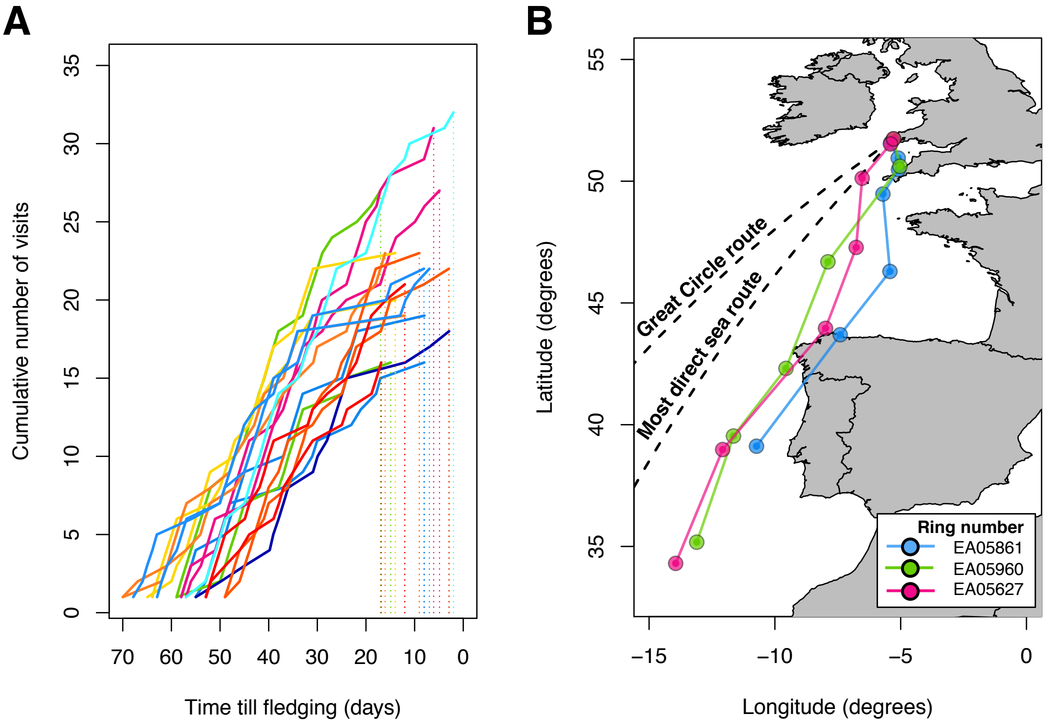

Figure 6.1: The pre-fledging parental provisioning and first migration trajectories of fledgling shearwaters from on Skomer Island. A) the cumulative total number of visits made per parent for each fledgling over the period preceding fledging (with the dotted vertical lines denoting the time of last visitation per parent). B) The first migratory trajectory for the 3 fledglings from which a complete first-week trajectory was recorded via PTT-GPS (see Appendix for all tracks).

Outbound migration

We found that the parents of our tracked chicks stopped visiting the colony on average 9.74 (± 2.42) days prior to fledging, with the chick encountering its final parental visit on average 8.1 (± 2.36) days prior to fledging (see Figure 6.1). No parents were detected at the colony the night that chicks fledged and no parental visits were recorded post-fledging, suggesting that juvenile shearwaters fledged alone.

All three GLS-tracked fledglings migrated towards the Patagonian Shelf, completing the journey in around 2 months (see Figure 6.2). Immersion data implied that the onset of migration following fledging was near instantaneous, with all three fledglings completing a minimum of 10 hours of continuous flight in the first week post-fledging, with one bird completing > 50 hours (see Figure 6.2). This is consistent with data from the PTT-GPS

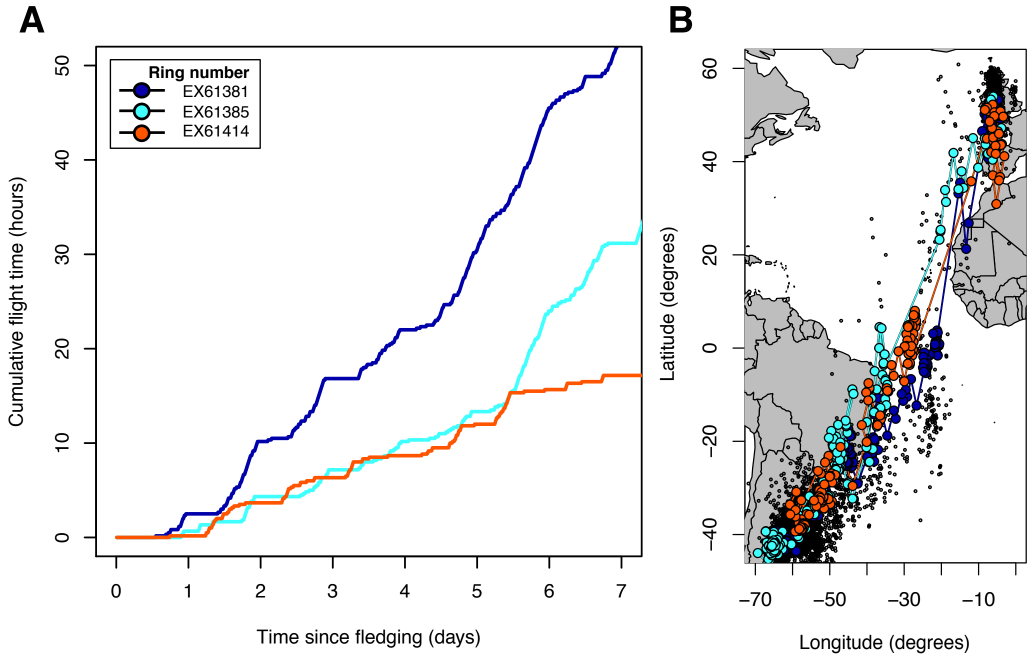

Figure 6.2: The first week's activity and outbound migration trajectory for shearwaters migrating from Copeland, Northern Ireland. A) The cumulative sum of flight events for each bird as defined using immersion loggers. B) The outbound GLS-tracked trajectory for each fledgling shearwater, with GLS positions from adult shearwaters migrating simultaneously shown as black dots.

tracked fledglings, with the three birds for which we have a position on the seventh day post-fledging having moved 890km, 1,837km and 2,036km from the colony respectively (see Figure 6.1). By comparing the positions of the PTT-GPS tracked fledglings to the GLS-estimated positions of their parents, we found that fledglings were likely to have migrated independent of their parents, with fledglings on average 545km away from their parents on any given day over the tracking period. Further, fledglings were not significantly closer to their parents than to randomly selected adults, both when considering the straight-line distance between birds (randomisation; $p = 0.38$) or the longitudinal distance (which is less susceptible to GLS positional error; randomisation; $p = 0.22$). Additionally, GLS-tracked fledglings were significantly closer than adults to both the beeline linking the breeding and wintering site (LMM; LR test; $\chi^2 1 = 5.74$, $p = 0.00249$; see Figure 6.3) and the shortest across-water route to the wintering site (LMM; LR test; $\chi^2 1 = 12.8$, $p = 0.000333$; see Figure 6.3). In turn, this suggests fledglings were moving along a more direct trajectory than their adult conspecifics.

We also found that GLS-tracked fledglings were highly divergent in their outbound migratory trajectories, particularly in the first half of migration, where the maximum distance between them was 1,612km at the equator (Figure 6.2). However, their southern-hemisphere trajectories were highly convergent, with birds only a median distance of 420km (± 200km) apart in the month of December (at the end of their migratory trajectory). Further, we found that all 3 fledglings tracked on first migration stopped for an extensive period on the equator, with all fledglings spending at least a week within 5° latitude of the equator. Indeed, 2 of the 3 fledglings spent as long within 5° of the equator as they did reaching the equator (approximately 3 weeks).

Return migration

In December fledglings had a median latitude of -39.97° (± 4.62°) and a median longitude of -59.04° (± 6.48°), with the positions of adults over the same position very similar, -41.53° (± 1.37°) latitude and -61.94° (± 1.98°) longitude, implying that the wintering distribution of immature and adult shearwaters overlap.

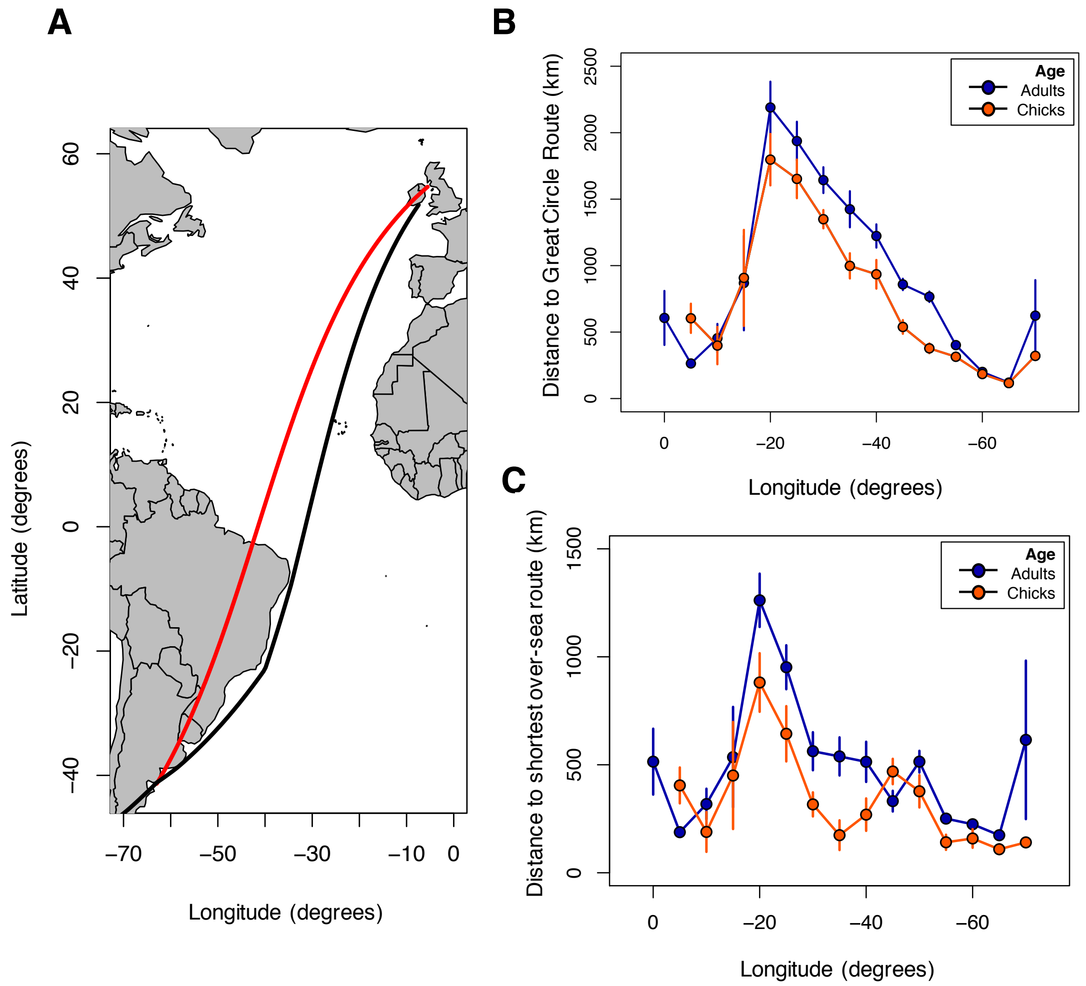

Figure 6.3: The distance from the beeline and most direct overseas route for GLS-tracked adult and fledgling shearwaters. A) Map showing the most direct over-sea route (black) and the Great Circle route (red) from Copeland to the median wintering latitude for Manx shearwaters. B) The distance from the beeline plotted in 5° bins (mean ± SE) for adult and fledgling shearwaters. C) The distance from the shortest over-sea route plotted in 5° bins (mean ± SE) for adult and fledgling shearwaters.

For two of the three GLS-tracked fledglings, the GLS device continued to record into the second calendar year following deployment. Unlike the adult shearwaters tracked over the same period which, consistent with previous studies, had all returned to the North Atlantic by April, both fledglings remained on the Patagonian Shelf until 16th July 2012, at which point they started moving slowly north (see Figure 6.4). This was asynchronous with all recorded adult movements. Both immatures reached around -25° latitude (level with central Brazil) with one bird moving further north on 6th August to reach -2° latitude.

Both immatures returned to the wintering site in early September, with the majority of the adult population immatures joining them by late November (see Appendix).

One GLS device continued recording into the third calendar year post-deployment, meaning that any movement after this date was recorded in just one bird. This bird, now in its second year post-fledging, started northwards migration on May 23rd 2013 (around a month earlier than in the previous year), moving north faster than in the first year (2.81° latitude per day in 2013 versus 0.695° per day in 2012) reaching a maximum latitude of around 52°, approximately the latitude of the breeding colony, on 10th July. Although the timing of the juvenile's northward migration was much later than adult birds tracked over the same season, the juvenile's and adults' routes were similar, following the eastern seaboard of North America northwards before crossing the Atlantic at around 40° north. However, the juvenile did not completely cross the Atlantic but, instead, stopped at around -16° longitude (approximately south of Iceland; Figure 6.4), only around 500km from the natal site. Unlike any recorded adult shearwater from eastern Atlantic colonies, the fledgling then returned to the wintering site via the West Atlantic, arriving back at the wintering grounds in late September (almost exactly the same time as in the previous year; see Figure 6.4).

In 2014, now in its 3rd year post-fledging, the juvenile started northward migration earlier than in the two previous years, with migration estimated to begin on 11th May (again, much later than any adult birds tracked in the same year). Migration speed was comparable with the previous year (mean latitudinal speed = 3.19° latitude per day) and proceeded along a similar route, with the juvenile reaching -30° longitude in late June 2014 (Figure 6.4) at which point the logger stopped recording. The bird was not encountered again until 2015, when it was found dead near to the natal site, and consequently it was not possible to deduce whether it made landfall at the natal colony in 2014.

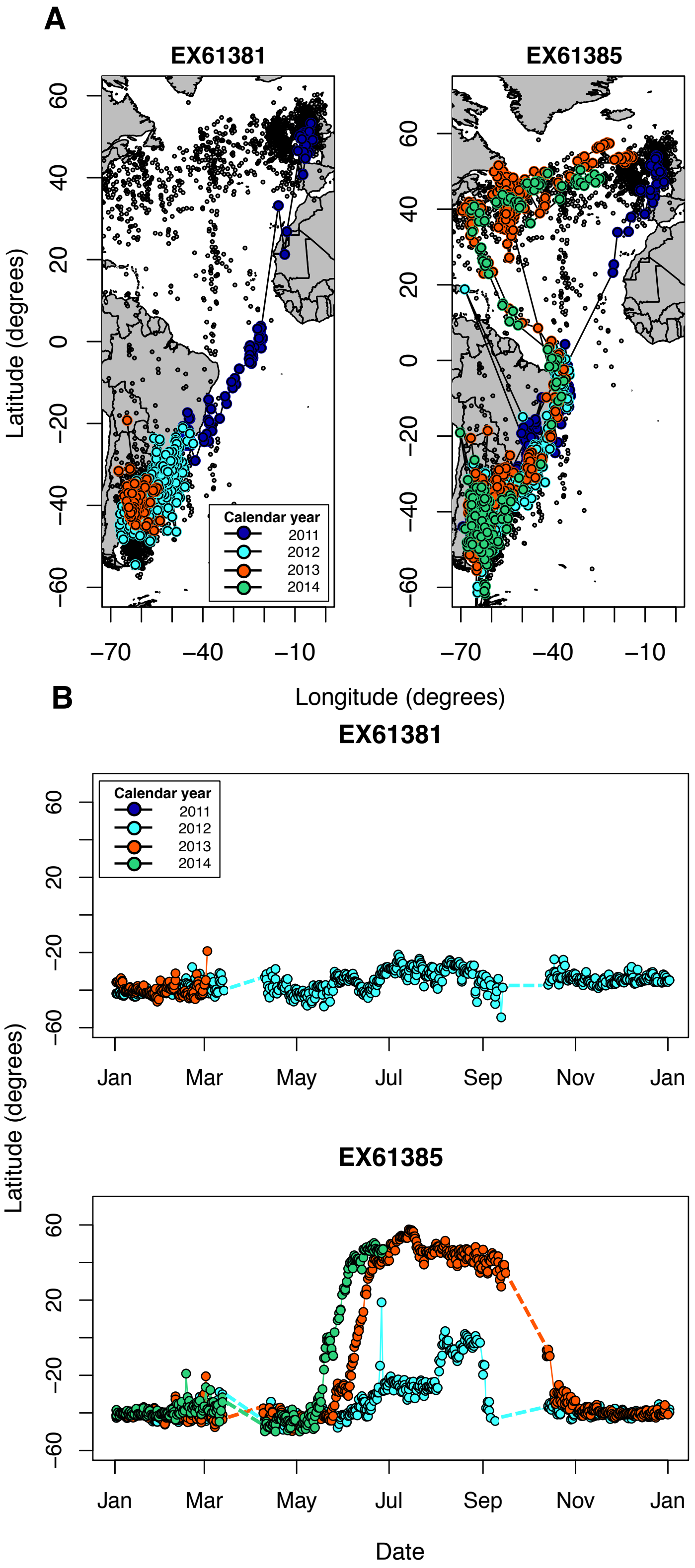

Figure 6.4: The development of return migration in Manx shearwaters. A) GLS positions for the two fledglings for which > 1 year's data were collected, coloured by year. B) The latitudinal position of the same birds over time, again coloured by year, with dotted lines showing estimated latitudinal position over equinox periods.

6.5 Discussion

Using a combination of loggers, we tracked the behaviour and movements of fledgling shearwaters from before fledging until, in one case, 3 years post-fledging. Based on these data, we below propose that social learning and cultural inheritance are of limited importance when considering both the outbound and return migration trajectories of Manx shearwaters, and instead that genetic inheritance and asocially learnt information inform their migration routes. We suggest, more generally, that this may be consistent across animals undertaking loop migrations independent of their parents.

RFID logging of juvenile shearwaters implied that the majority of birds had left their burrows and spent time on the surface at night prior to fledging. In turn, this implies that birds are not entirely naïve to visual cues prior to fledging, and it is possible that this pre-migratory period could allow for the use of learnt, navigational information. However, given that shearwaters are seemingly inattentive to cloud cover, we might suggest that if this period is used to learn how navigational cues inform on the migration trajectory then it is unlikely that the cues involved are celestial. In turn, this suggests that, unlike songbirds, shearwaters seemingly cannot be guaranteed access to a fully learnt rotational star compass at the point of fledging (Michalik et al., 2014).

RFID records also showed that parents visited their offspring for the last time around a week prior to fledging, with no parents recorded on the colony on the night of fledging or afterwards. This, combined with our finding that tracked fledglings were several hundred kilometres away from their parents, indicates that there is little if any sensory contact between fledglings and related adults. Whilst it is possible that first years follow non-related adults, this might seem unlikely given that fledglings seemingly follow a more direct route than all observed adults. Further, at-sea sightings data from the JNCC seabirds-at-sea survey ('JNCC SAS') suggests that the majority of Manx shearwaters, presumably including non-breeding individuals, have left Europe by the time fledging occurs (with only 5% of JNCC SAS sightings recorded after the 7th September; Camphuysen et al., 2004). This necessarily reduces the likelihood that cultural transmission from breeding adults influences migration route, consistent with other studies of procellariform migration (Yoda et al., 2017; Yoda et al., 2021). If the information used on first migration is unlikely to be learnt socially, it is therefore possible that it is inherited genetically or epigenetically, possibly as a vector. Indeed, the straight-line trajectory taken by fledglings, more direct than is seen in adults, is consistent with an inherited vector (as has been noted in procellariforms and avian taxa more generally; Hake et al., 2003; Yoda et al., 2017; Yoda et al., 2021).

The extent to which fledglings diverged is also notable (> 1,500km between 2 birds on the same day) before converging to winter in the same part of the Patagonian Shelf. Short of each bird inheriting a unique 'dog-leg' trajectory, which seems implausible for a genetically inherited mechanism, it would seem unlikely that such a pattern could be explained by an inherited vector. Therefore, it might be more parsimonious to suggest that shearwaters do not rely exclusively on vector navigation to reach the wintering site. Indeed, previous studies using autumn ringing recoveries suggest that vector-navigators accumulate error (Mouritsen, 1998) and, therefore, given how conserved an area both adult and fledgling shearwaters winter in, it would perhaps be unrealistic to assume that such accuracy could be achieved using only a genetic vector. What mechanism allows shearwaters to re-orient towards the wintering site in the second half of migration is unclear, particularly with such a small sample size, though a learnt ability to compensate for drift from the intended course has been noted in several seabird taxa (Goto et al., 2017; Wynn et al., 2020a). It is, therefore, possible that a similar system may allow juvenile shearwaters to adjust their course to target the wintering site following drift.

All 3 fledglings tracked on first migration also stopped for an extensive period on the equator, in 2/3 cases spending as long on the equator as they did reaching the equator. This could reflect the requirement of naïve birds for rest before continuing southwards, particularly since the winds encountered over the equator are typically stronger than those further north (Guilford et al., 2009). Alternatively, it is notable that compass orientation on the equator is extremely difficult using the majority of established avian compass mechanisms (magnetic inclination compass, time-compensated sun compass or rotational star compass; Berthold and Terrill, 1991; Wiltschko and Wiltschko, 1992). Given that compass orientation is an essential part of vector navigation such equatorial stopovers may, therefore, be a consequence of navigational uncertainty. A larger sample size is, however, necessary to investigate this further.

Whilst wintering in a similar area to their adult conspecifics, juvenile shearwaters exhibited very different return migratory behaviour. A key difference was the timing of northwards movement, with both juveniles for which we have complete second calendar year tracks starting northwards movement three to four months later than breeding adults. The differing phenology of adult and immature shearwaters implies that the route followed by immatures cannot be learnt by following breeding adults, and hence that social learning is unlikely to underlie the westerly trajectory into the Caribbean characteristic of the returning Manx shearwater's loop migration. Social learning of the northbound migration route involving non-breeding adults is possible, though this might seem unlikely given that such birds are present on the colony from mid-June (Harris, 1966; Perrins et al., 1973; Fayet et al., 2015). In turn, this implies that the loop migration structure is unlikely to be the result of cultural transmission. We might, therefore, suggest that the decision to take a different return migration route could be encoded genetically (Mouritsen, 2003). Alternatively, or additionally, the observed route taken may instead result from conditions in the West Atlantic rendering this route more efficient, with the favourable winds around the North Atlantic gyre reducing the likelihood of headwinds on return migration (Guilford et al., 2009; Fayet et al., 2020). This latter suggestion would be consistent with other loop migrants, where differences in trajectory have been attributed to differing environmental conditions (and different ecological requirements) on the return migration leg (e.g. Mellone et al., 2013; Lisovski et al., 2021).

Unlike southwards migration, the return migration route in Manx shearwaters appears to be built up iteratively over a series of years, with birds reaching greater latitudes in later years. We believe this is the first reported example of such age-related route extension. It is unclear whether this reflects younger birds limiting their migration as they don't need to return to the colony, or whether this instead implies a process whereby birds use information gathered on the previous leg of the iteration to inform navigation on the current leg. Such a process of iteratively refining the migration route over successive years would be consistent with the 'exploration-refinement' of migratory routes seen in other long-lived seabirds (Guilford et al., 2011; Campioni et al., 2020).

Between legs of this iterative process, the tracked juveniles returned to the wintering site via the West Atlantic, with the juvenile tracked into its third year returning to the wintering site via a route unseen in European adult shearwaters (see Figure 6.4). Differing southbound migration routes between adults and immatures implies that shearwaters do not simply store innate outbound and return migration trajectories and execute the relevant trajectory at the correct time of year. If this were the case, we would not expect such marked differences in birds of different ages. However, given the small sample size, it is unclear why the fledgling returned to the wintering site via the West Atlantic, especially given that the route selected would probably involve flying into a headwind (Guilford et al., 2009; Fayet et al., 2020) and is approximately 2,745km longer than if the immatures had extended its northbound migration to the natal site and then returned via the same trajectory it took in its first calendar year.

Taken together, our results imply that Manx shearwaters rely primarily on genetic inheritance to inform their outbound migration route. We further propose that, given the lack of opportunity for cultural inheritance, it is possible that a similar mechanism underlies return migration also and that the iterative construction of a return migration route may reflect 'exploration-refinement' in route selection. Whilst conclusions based on such small sample sizes must be necessarily taken with caution, and further study is essential, we suggest that our results inform on loop migration more generally and highlight the utility of a biologging approach when studying the early-life ontogeny of migratory behaviour.

6.6 Appendix

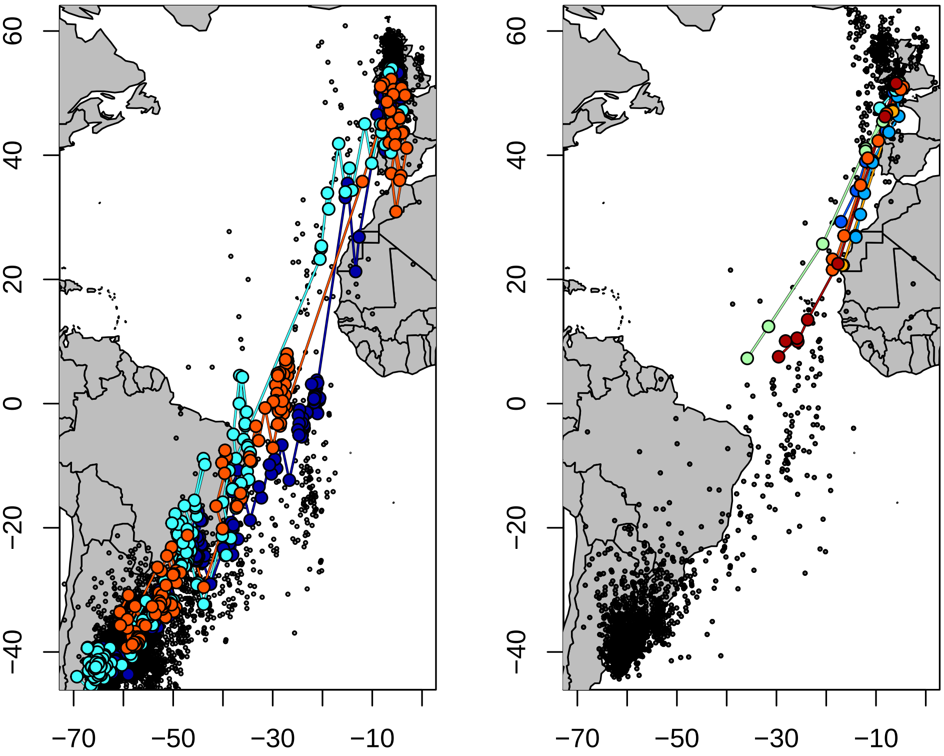

Figure 6.5: GLS and GPS-PTT position for all fledgling Manx shearwaters tracked in 2011 and 2019. (left) GLS-tracked fledgling Manx shearwaters tracked in 2011 from Lighthouse Island (Copeland), (right) PTT-GPS tracked fledgling Manx shearwaters moving in 2019 from Skomer Island (Pembrokeshire). Each bird is denoted by a different colour, with adults moving in the same year are shown as smaller black points.

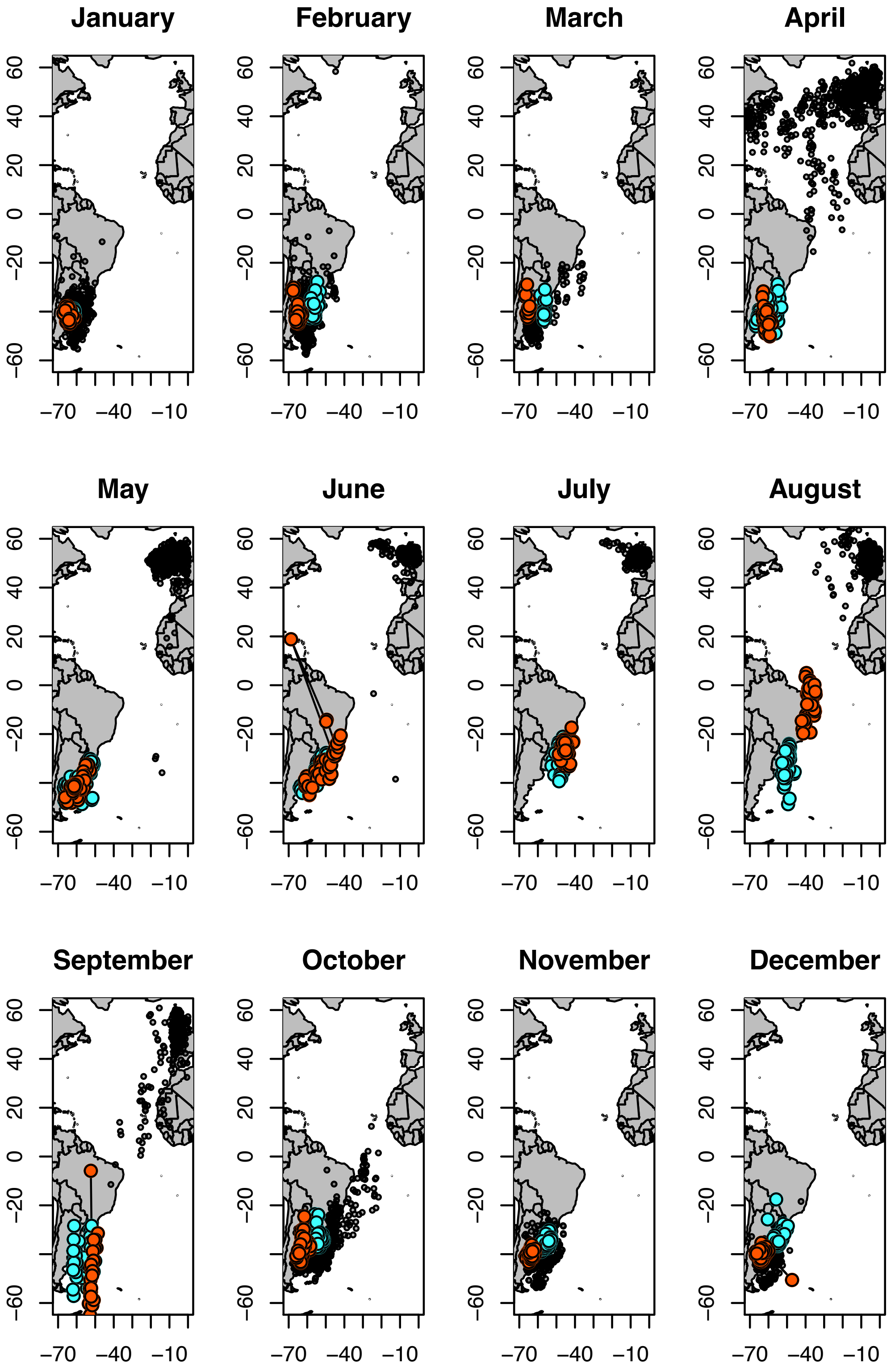

Figure 6.6: GLS position for shearwaters in their second calendar year. The non-equinox positions for the 2 fledglings for which position in the second calendar was discerned. Each fledgling is shown as coloured points, whilst adults moving in the same month are shown as smaller black points.

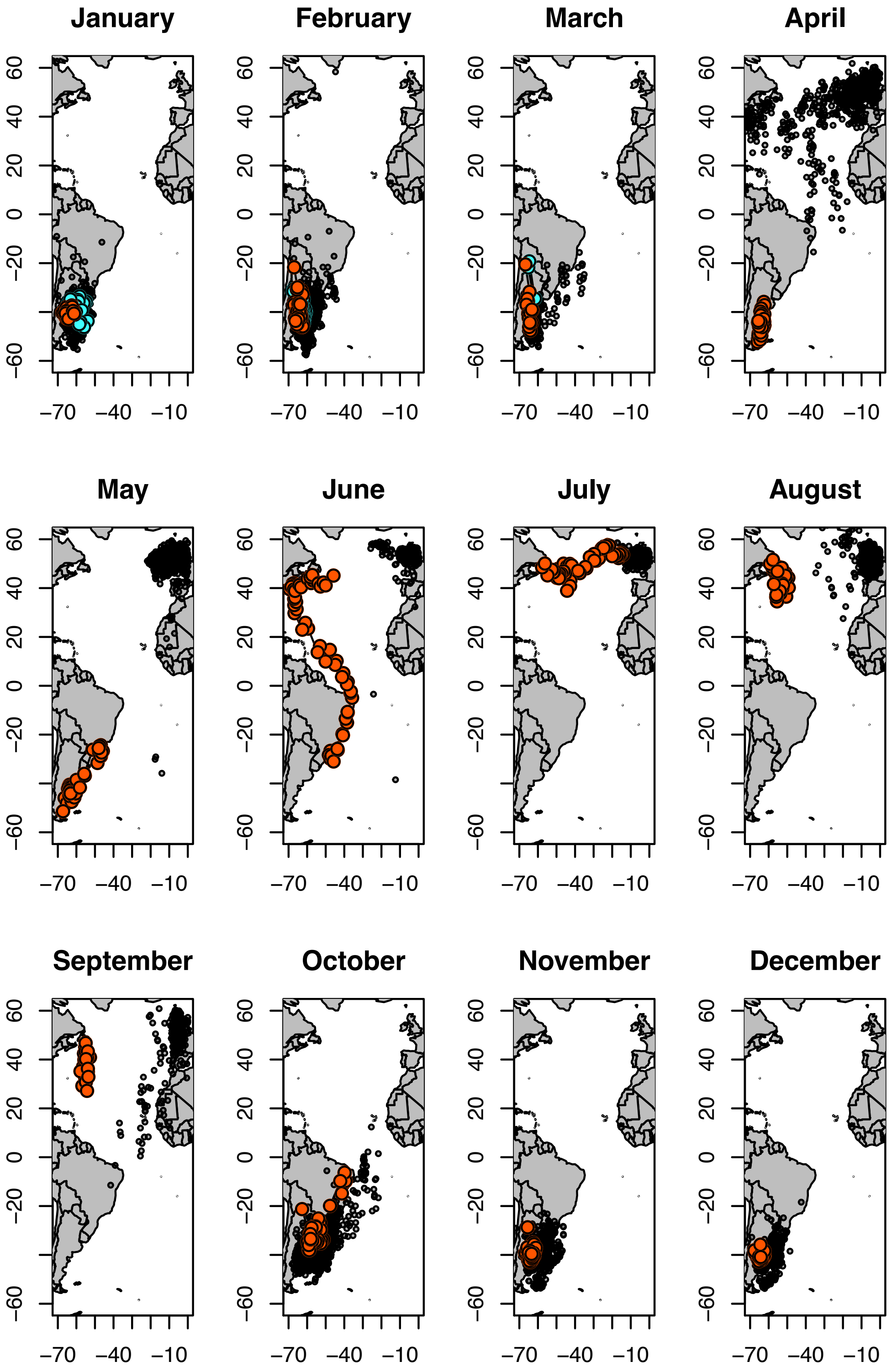

Figure 6.7: GLS position for shearwaters in their third calendar year. The non-equinox positions for the 2 fledglings for which position in the second calendar was discerned. Each fledgling is shown as coloured points, whilst adults moving in the same month are shown as smaller black points.

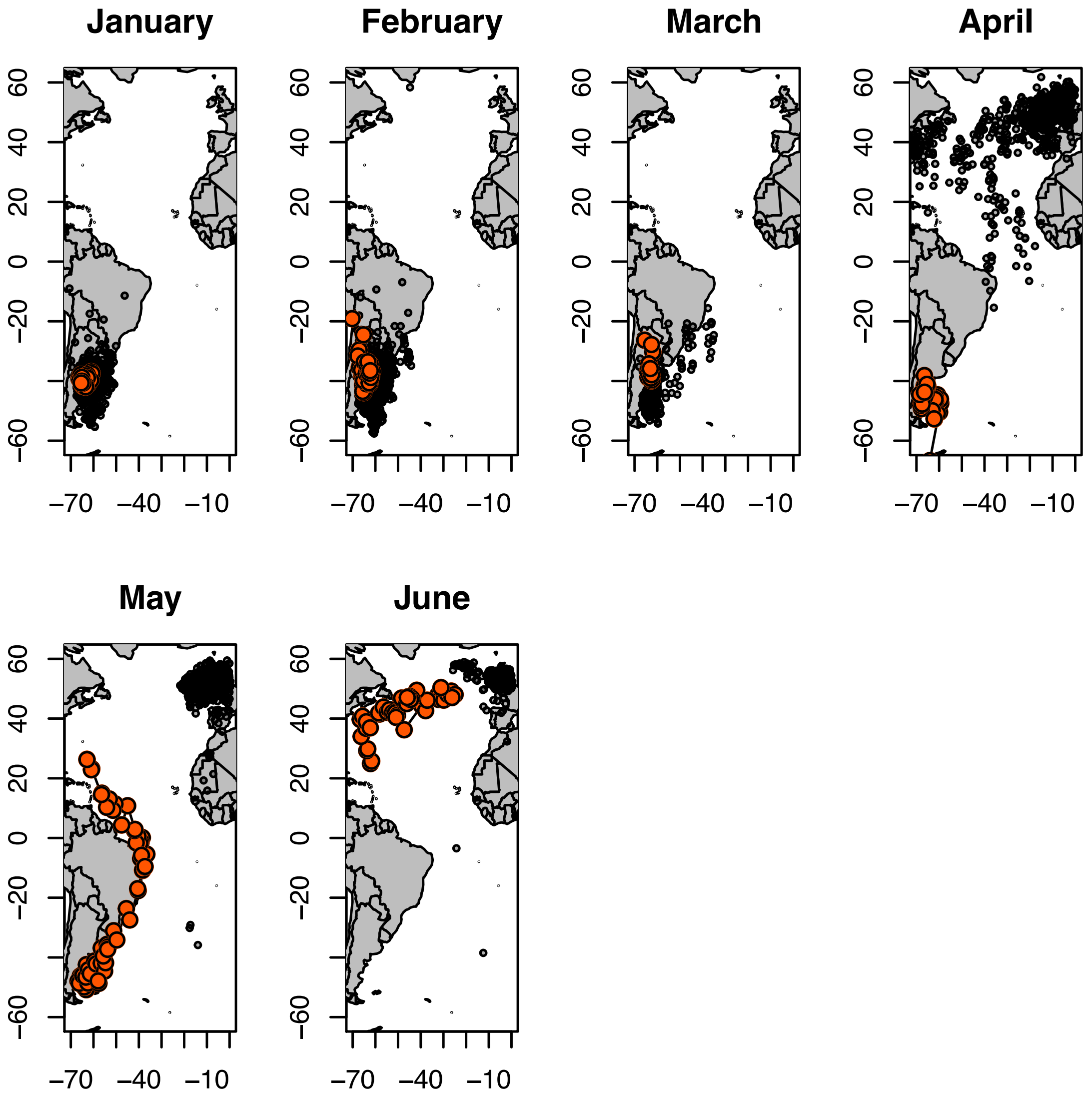

Figure 6.8: GLS position for a shearwater in it's fourth calendar year. The non-equinox positions for the fledgling for which position in the second calendar was discerned. Each fledgling is shown as coloured points, whilst adults moving in the same month are shown as smaller black points.

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7

How might secular variation impact philopatry?

Adapted from: Wynn, J., Padget, O., Morford, J., Jaggers, P., Davies, K., Borsier, E. and Guilford, T. 'How might secular variation impact philopatry?' In press, *Journal of Comparative Physiology A*.

Contents

7.1 Abstract

Philopatry, the act of returning to the natal/breeding site, is near ubiquitous amongst migratory birds. It has long been suggested that a magnetic ‘map’ could underpin such movements, though it is unclear how a magnetic map might be impacted by year-on-year movement in the Earth’s magnetic field (‘secular variation’). Here, using the International Geomagnetic Reference Field, we quantified how secular variation translates to movement in the implied positions at which combinations of different magnetic cues (inclination, declination and intensity) intersect, noting that the magnitude of such movements is determined by the acute intersection angle between the isolines in question, and the direction of one isoline’s movement relative to the other. We propose that magnetic parameters varying in a near-parallel arrangement are unlikely to be used during philopatry, but that birds could use near-orthogonal magnetic gradient cues to achieve philopatry if augmented with navigation using more local cues. We further suggest that the use of uni-coordinate magnetic information may provide a philopatry mechanism that is substantially less impacted by secular variation than a bi-coordinate ‘map’, and we propose that between-year shifts in the position of magnetic coordinates might provide testable *a priori* predictions for changes in the breeding sites of migratory birds.

> *“Real stupidity beats artificial intelligence every time.”*
>
> – Terry Pratchett, *Hogfather*

7.2 Introduction

Every year, many billions of migratory birds from across the avian phylogenetic tree return from their wintering sites, in doing so often pinpointing the location of their breeding site with remarkable accuracy (Newton & Brockie, 2008). Such migrations regularly cover thousands of kilometres (e.g. Delmore et al., 2020), are often trans-equatorial (e.g. Guilford et al., 2009) and sometimes involve migrating from one polar latitude to the other (e.g. Egevang et al., 2010). The sensory basis of such long-distance navigation is the source of some debate, with very long-distance gradient cues suggested as a potential mechanism by which birds could precisely return to their natal or breeding sites (a process known as 'philopatry'). Such cues could be learnt prior to departure and, subsequently, could be used to target the natal site over very long distances (Baker, 1978; Lohmann et al., 2008). The main candidates for such global navigational gradients are thought to be olfactory (for a review, see Gagliardo, 2013) or, alternatively, geomagnetic (for reviews, see Holland, 2014; Mouritsen, 2018).

Geomagnetic cues might, in principle, make excellent gradient cues owing to their supposedly ubiquitous availability and the very long distances over which they vary. There have been 3 components of the Earth's magnetic field that are considered to be navigationally useful in animals: inclination, the 'dip angle' between the Earth's magnetic field and the Earth's surface; declination, the angle between true and magnetic north; and intensity, the overall strength of the Earth's magnetic field vector (for reviews, see Holland, 2014; Mouritsen, 2018). There exists evidence for the use of such cues in both avian and non-avian taxa, notably sea turtles (Chelonioidae; Brothers and Lohmann, 2015), teleost fish (specifically the Salmoniformes; Putman et al., 2013; Putman et al., 2014; Naisbett-Jones et al., 2017), monarch butterflies (*Danaus plexippus*; Wan et al., 2021) and songbirds (Passeriformes; Chernetsov et al., 2017; Kishkinev et al., 2021). However, a single magnetic gradient cue positions a bird with respect to only one spatial dimension. In some taxa, for example sea turtles or pelagic seabirds, topographic constraints (e.g. the edge of a land mass) may allow for the use of a single coordinate system with topography providing the second dimension required for bi-coordinate positioning (Putman & Lohmann, 2008). Magnetic cues could, however, potentially provide both the longitude and latitude of a breeding site, with the intersect of 2 or more magnetic isolines denoting the 2-dimensional location of the breeding site. Such bi-coordinate magnetic 'maps' have been suggested to underlie navigation in certain avian taxa, specifically in songbirds (e.g. Chernetsov et al., 2017; Pakhomov et al., 2018; Kishkinev et al., 2021), and hence it is possible that similar mechanisms underlie philopatry specifically.

One of the primary limitations of magnetic cues regarding philopatry could be secular variation in magnetic cues (Putman & Lohmann, 2008); year-on-year variation in the Earth's magnetic field that causes the geographic position occupied by specific magnetic parameters to shift. The shifts in a given cue are very slight, typically a few kilometres per year (Putman & Lohmann, 2008). However, if the geographic location of the natal site were to be represented using bi-coordinate magnetic information, it is unclear what the cumulative effects of secular variation in two cues would mean for movement in the supposed position of the natal/breeding site.

Here, we investigated how secular variation in magnetic cues translates into between-year variation in the geographic position occupied by specific cue values. We used the International Geomagnetic Reference Field (IGRF 12; Thebault et al., 2015), a mathematical model of the Earth's magnetic field over the last century, to quantify the distance between the site previously occupied by specific magnetic parameter values and the site subsequently occupied by the same values. Specifically, we looked at how the geographic points indicated by the intersect coordinates of inclination/intensity, inclination/declination and intensity/declination isolines varied between years in 3 parts of the globe suggested to be well-suited to magnetic navigation: central North America, Europe and Central Asia (Bostrom et al., 2012).

7.3 Methods

All statistics were calculated in R (R Core Team, 2017).

7.3.1 Sampling the International Geomagnetic Reference Field

Yearly magnetic values, averaged from 12 dates between May and August, were derived from the IGRF for each of inclination, intensity and declination for sites across North America, Europe and Asia at a spatial resolution of 0.05° x 0.05°. For North America, values were extracted from the IGRF across a latitudinal range of 25° to 65° and a longitudinal range of -10° to 40°; for Europe, values were extracted for a latitudinal range of 25° to 65° and a longitudinal range of -115° to -65°; and for Asia values were extracted for a latitudinal range of 40° to 80° and a longitudinal range of 65° to 115°.

For each of North America, Europe and Asia we selected 100 geographic positions at random where, over the years 1900-2020, yearly values for inclination, declination and intensity were calculated using the IGRF. Based on these values, between-year variation in the positions occupied by specific magnetic isolines could be calculated. To do this the magnetic parameter value representing a given site in a given year were extracted, and the isoline representing the same value was isolated in the next year. This was repeated for each of inclination, intensity and declination. For example, if a site had an inclination value of 65°, a declination value of 5° and an intensity value of 49,500nT, the geographic positions of the 65° inclination isoline, the 5° declination isoline and the 49,500nT intensity isoline would be isolated in the following year. Once the location of the isolines in the subsequent year have been established, the location of the intersect of these isolines in the next year was then calculated. Finally, the distance between the site previously occupied the intersect of specific parameter values and subsequently occupied by the same values was calculated. This is summarised in Figure 7.1.

7.3.2 Mathematical modeling of isoline movement

Additionally, we derived a model to predict the geographic distance moved by specific magnetic coordinates (i.e. the intersection between the isolines in two magnetic parameters; sensed/learnt at that geographic site the year previously) between years. This allowed us to investigate the extent to which this distance depended both on the acute angle at which the isolines intersected, and the distance/direction moved by each isoline. This model assumed that the magnetic field parameters vary along linear gradients, which was considered to be a good approximation at small spatial scales (i.e. < c500km; see Appendix diagrams for large-scale isolines patterns).

7.3.3 Investigating the effect of between-isoline angle on secular variation

In addition to modeling the effect of the acute angle between 2 isolines on the secular variation of bi-coordinate magnetic positions, we also sought to investigate whether the predictions made by such a model were borne out by data derived from the IGRF. To do this, we calculated the angle between isolines of inclination/declination, inclination/intensity and declination/intensity (expressed on a scale of 0^o-90^o), and regressed this angle against the bi-coordinate secular variation (see above) in a series of linear regressions.

7.4 Results

Using the IGRF, we quantified the extent to which the intersect of specific magnetic isolines moved between years. We found that the median geographic distance moved by the magnetic coordinate formed by inclination and declination between years was 11.0km (± 0.204km [bootstrapped 95% CI]). For a coordinate comprising declination and intensity measurements, the median geographic distance moved was 21.4km (± 0.211km) between years, and, finally, for a coordinate comprising inclination and intensity, a median of 28.4km (± 0.211km; see Figure 7.1; see Appendix for more information).

We attempted to explain the variation in the movement of different gradient intersect-defined positions by modelling the movement of the position denoted by the intersect of 2 isolines. In our theoretical model we made 3 assumptions: 1) that the curvature of Earth was of negligible importance (as the distance over which magnetic

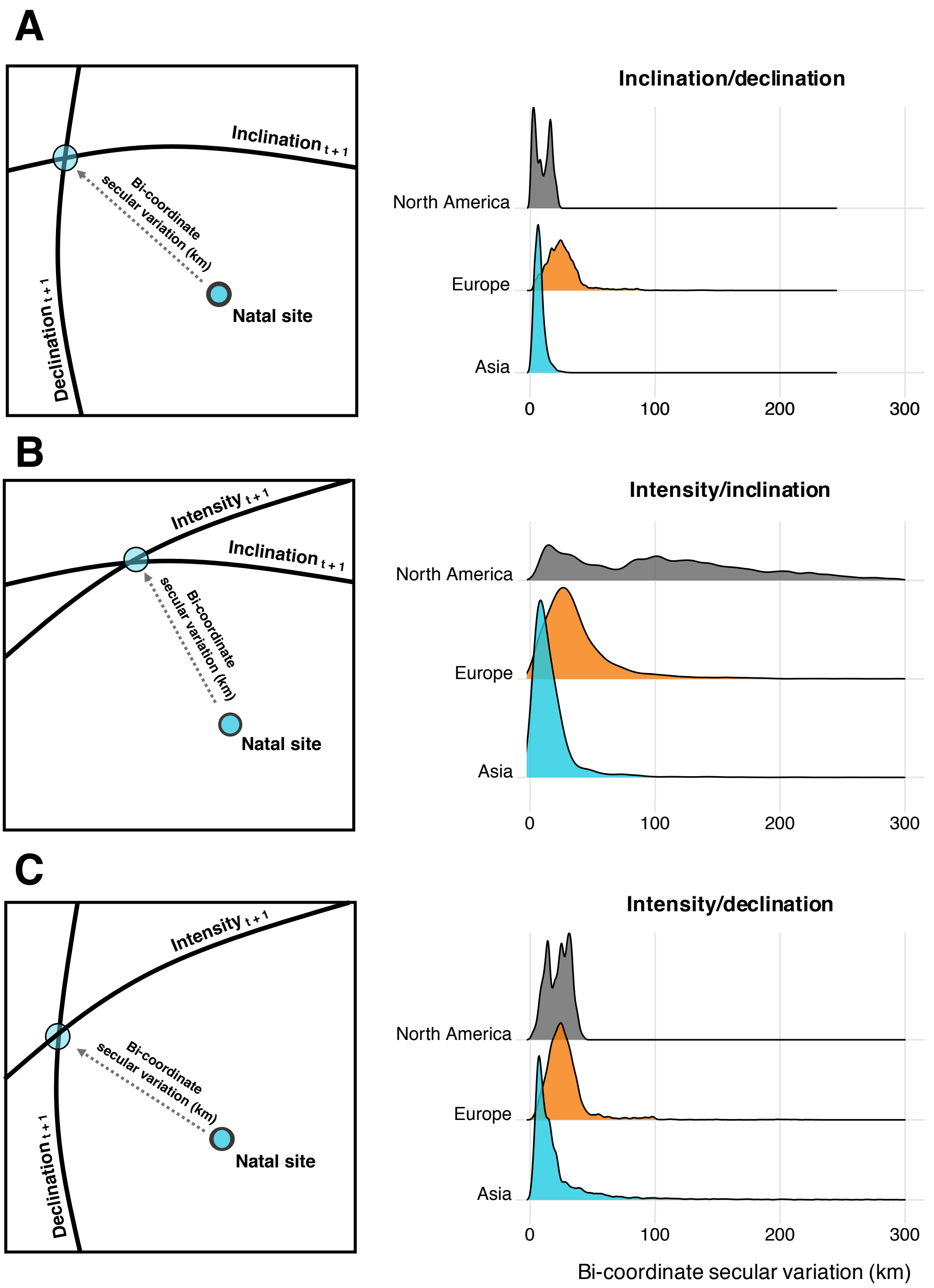


Figure 7.1: The effect of secular variation on the position of different isoline combinations. (left) An illustration of how the intersect of each pair of isolines can be located in successive years and (right) the distance moved by the intersect of 2 isolines ('Bi-coordinate secular variation') in successive years for each of A) inclination/declination, B) intensity/inclination and C) intensity/declination. For each set of isolines the distance moved is displayed as a density curve for each region (bandwidth = 10km).

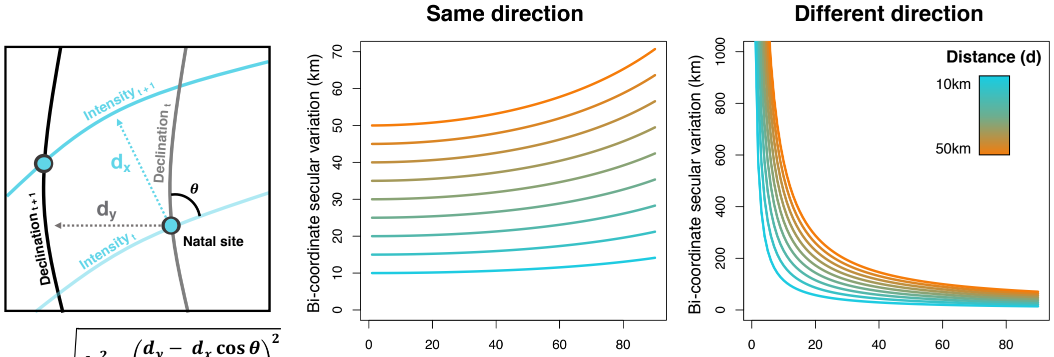
isolines moved was typically < 50km), 2) that the angle between 2 isolines did not change substantially between years and 3) that, over short distances, a given magnetic isoline could be approximated as a linear tangent of the overall contour. Pairs of magnetic field components define a Cartesian or non-orthogonal linear coordinate system, depending on the acute angle (θ) between the axes along which the cues vary. Secular variations in the magnetic field can be assumed to translate to coordinates such that $(x, y) \rightarrow (x + d_x + d_y)$ where d_x and d_y represent the magnitude of secular variation in 2 components of the Earth's magnetic field between successive years (see Figure 7.2). It therefore follows that the distance moved ($d_{overall}$) by a coordinate position owing to secular variation can be given as:

$$d_{overall} = \sqrt{d_x + (\frac{d_y - d_x \cos\theta}{\sin\theta})^2} \tag{7.1}$$

The sign of d_x and d_y can be set to denote whether isolines move in the same or different directions. For example, if a declination isoline moved north east and an intensity isoline moved south west, d_x would be signed positively and d_y would be signed negatively (or vice versa). Conversely, if an inclination isoline and an intensity isoline both moved south, d_x and d_y would either both be signed positively, or both be signed negatively. We can, therefore, vary the direction of movement for isolines in our model so as to investigate how the relative direction of isoline movement, caused by secular variation, impacts on the geographic position that would be arrived at if navigating to those magnetic coordinates (i.e. that intersection).

Using equation 1, we investigated how variation in the position denoted by the intersect of 2 isolines varies with a) the distance moved by the isolines in question (d_x and d_y) and b) the acute angle between these isolines (θ). We found that the effect of the angle between isolines was contingent on whether isolines were moving in the same or different directions. When isolines were moving in the same direction we found that smaller angles (i.e. near-parallel angles) reduced the effect of secular variation on the distance moved by the isoline intersect, with 10km of movement per isoline translating to 10km bi-coordinate movement when isolines were parallel and 14.4km bi-coordinate movement when isolines were perpendicular (see Figure 7.2). Conversely, we found that if isolines move in opposite directions then larger angles (i.e. near perpendicular angles) reduced the effect of secular variation, with 10km of isoline movement causing 1,146km of bi-coordinate movement when isolines were almost-parallel and 14.4km of bi-coordinate movement when isolines were perpendicular (see Figure 7.2). In all instances we found that the greater the movement of isolines, the greater the movement of their intersect position, though the isoline intersect's movement was greatest in instances where near-parallel isolines were moving in opposite directions (see Figure 7.2). This means that, on average, as the acute angle between isolines reduces, the distance moved by isoline intersects increases.

We might, therefore, make predictions about the movement of real isoline intersects based on our model. Specifically, we might expect that as the angle between magnetic isolines gets smaller, movement in the bi-coordinate position denoted by the intersect of 2 isolines becomes a) greater - given that the distance moved by isoline intersects on



$$d_{overall} = \sqrt{{d_x}^2 + \left(\frac{d_y - d_x \cos\theta}{\sin\theta}\right)^2}$$

Figure 7.2: Modelling the effects on bi-coordinate secular variation of distance moved by isolines and the angular difference between isolines. (left) schematic showing how the distance moved by 2 isolines (in this example intensity and declination) and angle between the same isolines are calculated, with the equation used to discern bi-coordinate movement in position based on this information shown below. (centre) The effect of the angle between 2 isolines on bi-coordinate secular variation for isolines moving the same direction, with colour denoting different magnitudes of isoline movement. (right) The effect of the angle between 2 isolines on bi-coordinate secular variation for isolines moving in different directions, with colour again denoting different magnitudes of isoline movement.

average increases as the angle between them narrows - and b) more variable - given the differing effects of the acute angle between isolines when isolines move in the same or different directions.

To test these predictions, we used the IGRF to investigate whether the angle between isolines explained variance in the distance moved by intersect positions between years. We found that the angle between 2 isolines was a significant predictor of the movement of the position denoted by the intersect of isolines for all pairs of cues investigated (inclination/intensity; LM, $F = 1{,}324$, $p < 0.00001$; inclination/declination; LM, $F = 671$, $p < 0.00001$; intensity/declination; $F = 1{,}640$, LM, $p < 0.00001$). For both inclination/intensity (gradient = -3.95 ± 0.22) and declination/intensity (gradient = -1.4 ± 0.068) we found that as isolines became closer to parallel (i.e. the angle between isolines decreased) the movement of the isoline intersect was greater. In contrast, we found that movement in the site denoted by the intersect of inclination/declination isolines reduced slightly as isolines were closer to parallel (gradient = 0.09 ± 0.0071; see Figure 7.3). We also found that differences in the angle between isolines could cause very large differences in the movements of isoline-intersect positions even within relatively small areas. For example, within Europe the positions denoted by inclination/intensity isolines intersects moved a median average of 95km in the UK but only a median average of 28km in Poland, meaning that in principle even within the breeding range of a single species (e.g. the Eurasian reed warbler; *Acrocephalus scirpaceus*) the effect of secular variation could vary greatly.

In addition to finding that the angle between isolines affected the distance between the geographic positions denoted by the shifting isoline intersect in consecutive years, we also found that as the angle between isolines reduced, the variance in the effect of secular variation increased. We found that, when the acute angle between intensity/inclination isolines was $< 20^{\circ}$, the standard deviation in the distance moved by the intersection was 613km whilst, when the acute angle between 2 isolines was $> 70^{\circ}$, the standard deviation in the distance moved was 5.96km (see Figure 7.3). We found that this was also the case when considering both intensity/declination (where a standard deviation of 606km was observed when the angle between isolines was < 20° and a standard deviation of 11.5km was observed when the angle was > 70°) and, to a lesser extent, inclination/declination (where a standard deviation of 17.2km was observed when the angle between isolines was < 20° and a standard deviation of 9.06km was observed when the angle was > 70°; see Figure 7.3). This implied that as the angle between isolines decreased, not only did the isoline intersect movement distance increase but, additionally, became more variable.

7.5 Discussion

Using the IGRF we found measurable between-year movements in position as denoted using the intersect of isolines of inclination/declination, intensity/declination and inclination/intensity across all areas sampled. We found that the extent to which magnetic coordinates moved over geographic space was dependent on the angle between isolines, the extent to which isolines moved and whether isolines were moving in the same or different directions. We further found that variance in the extent to which isoline-intersects moved also changed with the angle between isolines. Below, we outline

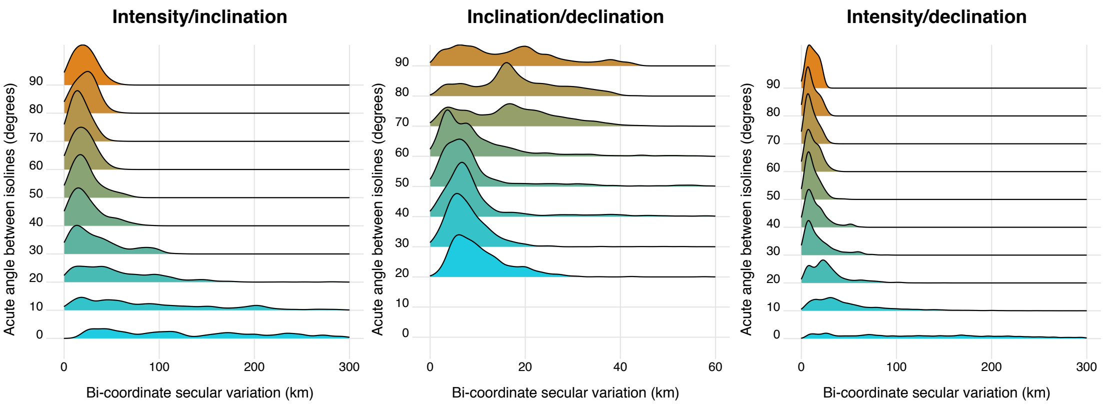


Figure 7.3: The observed effect of the angle between isolines on bi-coordinate secular variation in different coordinate systems. The effect of the angle between isolines on bi-coordinate secular variation (from left) intensity/inclination, inclination/declination and intensity/declination. Values for the angle between isolines have been rounded to the nearest 10 degrees and presented as a density curve (bandwidth = 5km), with larger peaks in the curve denoting greater frequency amongst the observed data.

why near-parallel isolines have seemingly limited utility during philopatry, and propose mechanisms by which migratory animals might counter the effects of secular variation. We further suggest that the empirical comparison of the between-year movements of migratory birds to those predicted under a model of magnetic bi-coordinate navigation may be informative when investigating mechanisms of philopatry.

Near-parallel gradient cues have been suggested to be of limited navigational use to animals for a variety of reasons, most notably owing to the necessarily high resolution with which cues would have to be discerned in order to be useful (Akesson & Alerstam, 1998; Bostrom et al., 2012). Additionally, it has been questioned whether near-parallel gradient cues could be used by animals during straight-line orientation if animals were constrained to cognitive processing that interpreted cues as if they were perpendicular (Benhamou, 2003). However, even if an animal were able to able to detect magnetic cues with perfect accuracy, and process them correctly, it would seem that secular variation makes near-parallel magnetic gradients extremely difficult to use for precise natal homing. This is owing not only to large between-year movement in the position denoted by the intercept but also owing to the large year-on-year variance in the distance moved by isoline intercept positions. This variance, caused by the differing effects of the angle between isolines when isolines move in the same or different directions, makes field movement erratic and seemingly difficult to account for. We suggest, therefore, that it is unlikely that birds could rely on pairs of magnetic cues that vary through space along near-parallel gradients as a bi-coordinate position when re-locating a natal/breeding site.

Isolines of inclination/intensity and declination/intensity are non-orthogonal across our sample areas (see Appendix for isoline maps) and we might, therefore, predict that they are of limited use during philopatry. This is borne out in predictions made by the IGRF, which suggest large and erratic between-year movements across each area sampled. Further, the extent to which bi-coordinate position moved even within a relatively constrained area was pronounced (see Appendix), further suggesting that inclination/intensity and declination/intensity are imperfect cues when considering philopatry. However, we found that, in most parts of the globe, inclination and declination formed a more perpendicular grid. Further, movement in the inclination/declination reduced as they became closer to parallel, hence even as isolines became near-parallel the effect of secular variation was limited (see Figure 7.2). Of the candidate bi-coordinate navigation hypotheses inclination/declination has, therefore, perhaps the greatest overall utility when indicating a geographic position.

However, we found that even within near-perpendicular cues there are movements in the position of specific magnetic coordinates owing to secular variation, with such movements likely large enough to require augmentation from other navigational mechanisms. Such movements, whilst an order of magnitude smaller than the movement of near-parallel cues (< 100km), could nonetheless impact philopatry amongst birds. For example, random movements of the geographic location of an isoline intersect of a magnitude between 0km and 20km could mean that the intersect value could occur anywhere within a 1,256km^2 area $(a = \pi \times r^2)$. It would seem, therefore, unlikely that magnetic parameters alone are sufficient to perform faithful philopatry. It has been suggested that return migration might comprise several fairly distinct 'phases', with long-distance navigation underpinned by spatial gradient cues and locale specific landmark cues thought to underpin precise local-scale homing (for a review, see Mouritsen, 2018). Birds could, therefore, counter the effects of secular variation by having a sufficiently large familiar area. Indeed there is some evidence that prior to first migration young songbirds make night-time forays away from their natal site (e.g. Baker, 1978; Mukhin et al., 2005), and such trips could be used to parameterise an appropriately large familiar area map.

Additionally, or alternatively, birds could use magnetic cues to determine position in only one dimension, relying on other cues to give the second. This would, necessarily, limit the multiplicative effects of secular variation on multiple cues used as a bi-coordinate position. One mechanism by which birds could limit their exposure to secular variation would be to, as is seemingly the case in sea turtles, use topographic barriers (alongside uni-coordinate magnetic information) in order to position themselves with regards to both longitude and latitude (Putman & Lohmann, 2008; Brothers & Lohmann, 2015). For example, animals breeding on the edge of a continent could use the coastline alongside a magnetic gradient to inform on position. However, such a mechanism is unlikely to work independent of topographic barriers to signal the end of migration. As an alternative, it has been suggested that single gradient cues could be used to inform on the position of the natal site by serving as a 'stop sign' on an otherwise pre-determined migratory bearing (Mouritsen, 2003; Holland, 2014). As with topography, using magnetic cues as a 'stop sign' on a migratory bearing would limit the impact of secular variation on the presumed position of the natal site and both could, therefore, be seen as a viable alternative to bi-coordinate information when considering the cues underlying philopatry.

Taken together, we believe our analyses not only outline the effects that secular variation could have on avian philopatry, but also make predictions as to where migratory birds should (or shouldn't) return to if relying on magnetic information during natal/breeding site philopatry. We suggest, therefore, that the comparison of empirical data (e.g. ringing or tracking data) to predictions made using the IGRF may be of some considerable use when investigating philopatry. As with any simulation-led study, it is necessarily possible that our navigational models are too abstract to reflect the precise mechanisms by which birds navigate. Nonetheless, we believe our results may be informative when considering both the advantages and the drawbacks of using different magnetic cues during avian philopatry.

7.6 Appendix

Variance in secular variation between regions

Using the IGRF, we found that the sites represented by the intersect of specific magnetic isolines moved measurably between years. We found that the position denoted by the intersect of inclination/declination isolines moved a median average of 11.0km (± 0.204km [bootstrapped 95% CI]) between years, breaking down into a median distance of 9.17km (0.317km) for points in North America, 6.58km (0.0692km) in Asia and 24.2km (0.236km) in Europe (see Figure 7.1). We found that the site represented by the intersect of specific declination/intensity isolines moved a median average of 21.4km (± 0.211km) between years, with points moving a median distance of 23.7km (0.221km) in North America, a median distance of 13.3km (0.375km) in Asia and a median distance of 25.0km (0.0692km) in Europe. Finally, we found that the site represented by the intersect of specific inclination/intensity isolines moved a median average of 28.4km (± 0.211km), breaking down into a median distance of 106.0km (1.67km) for points in North America, a median distance of 11.4km (0.323km) for points in Asia and a median distance of 30.9km (0.432km) for points in Europe (see Figure 7.1).

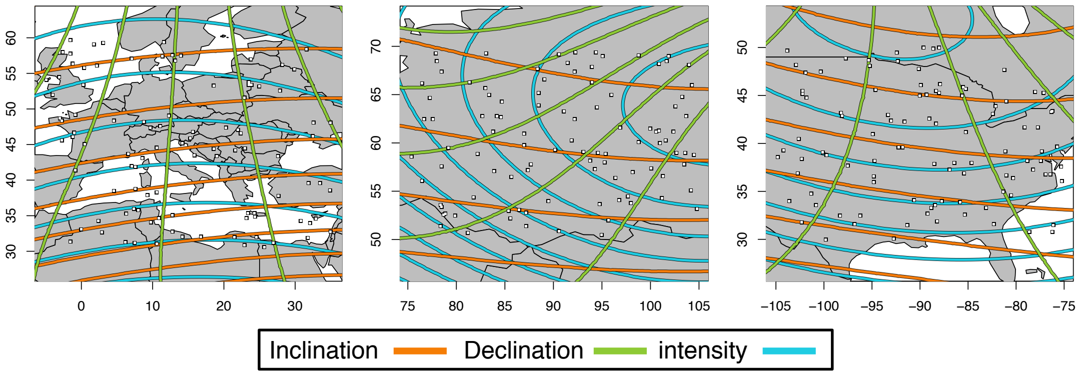


Figure 7.4: Isoline positions for each of inclination, declination and intensity in the year 1900. Isolines for focal magnetic parameters in (from left) Europe, Asia and North America. Points on the map represent randomly selected locations at which isolines were sampled for use in our analyis. Specific isoline values are included in Figures 7.6-7.8.

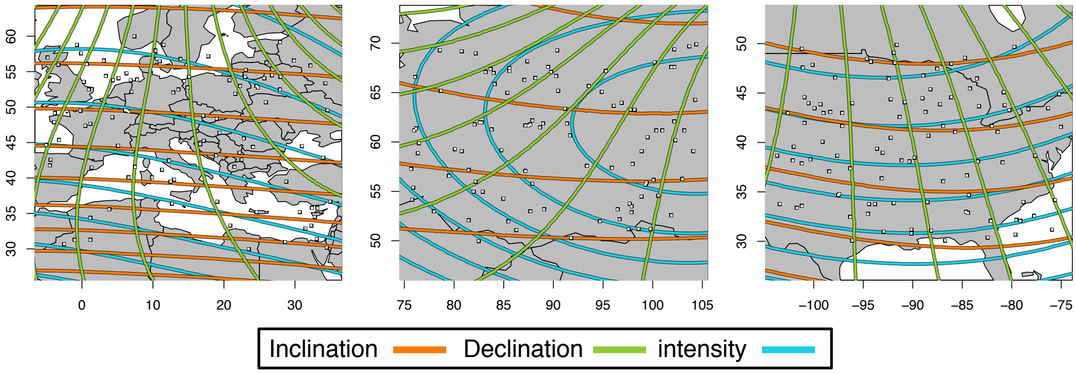


Figure 7.5: Isoline positions for each of inclination, declination and intensity in the year 2000. Isolines for focal magnetic parameters in (from left) Europe, Asia and North America. Points on the map represent randomly selected locations at which isolines were sampled for use in our analyis. Specific isoline values are included in Figures 7.6-7.8.

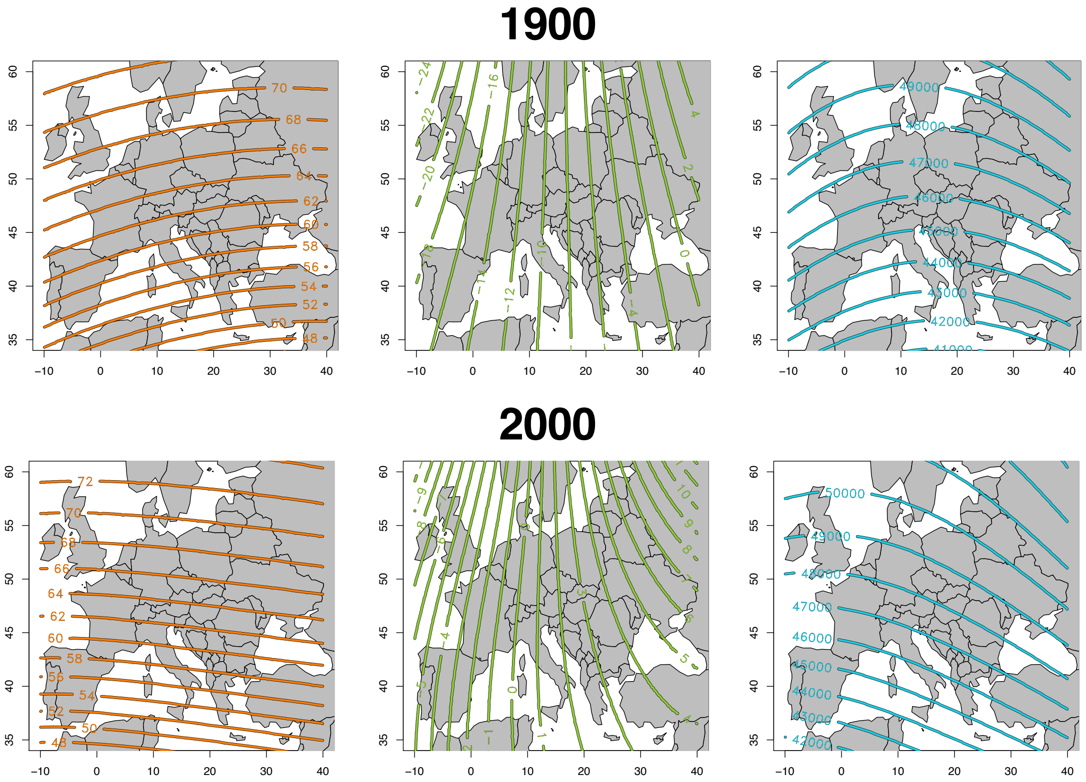
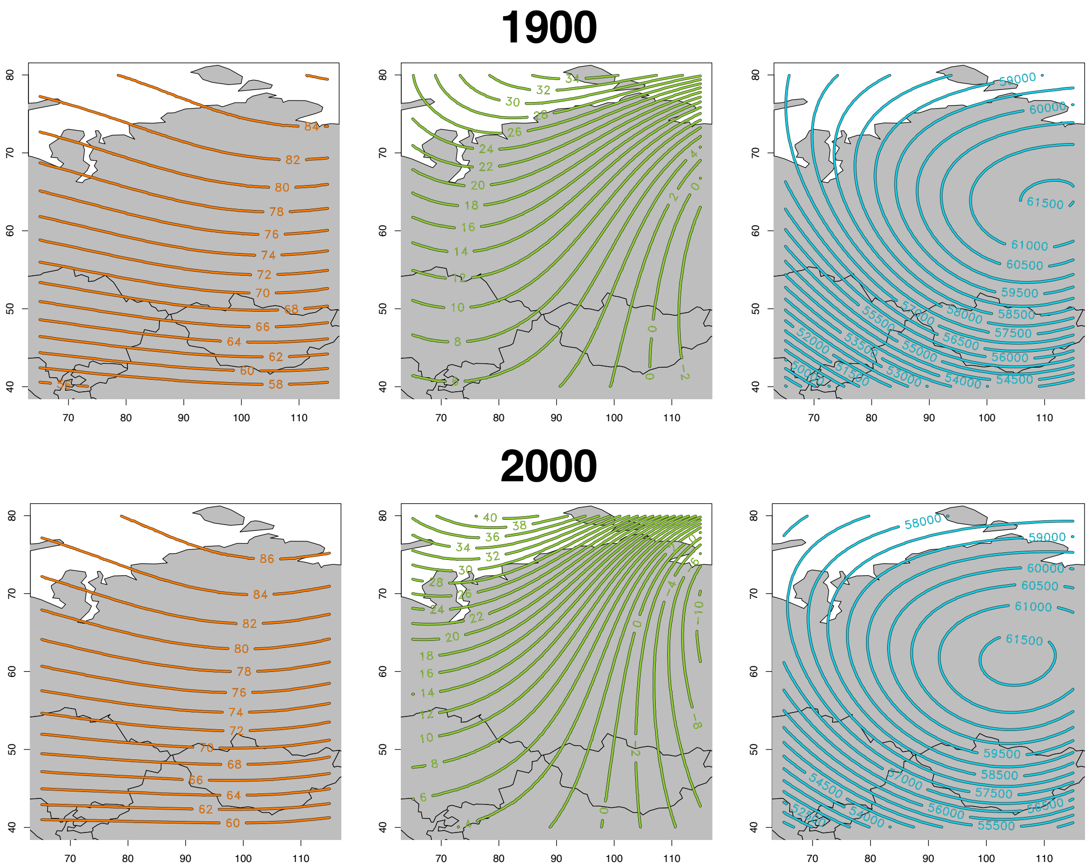


Figure 7.6: Isoline positions for each of inclination, declination and intensity in the years 1900 and 2000 in Europe. Isolines are shown for inclination (left), declination (centre) and intensity (right) , with the labels on each isoline denoting the value the isoline in question isoline represents.



1900

2000

Figure 7.7: Isoline positions for each of inclination, declination and intensity in the years 1900 and 2000 in Asia. Isolines are shown for inclination (left), declination (centre) and intensity (right) , with the labels on each isoline denoting the value the isoline in question isoline represents.

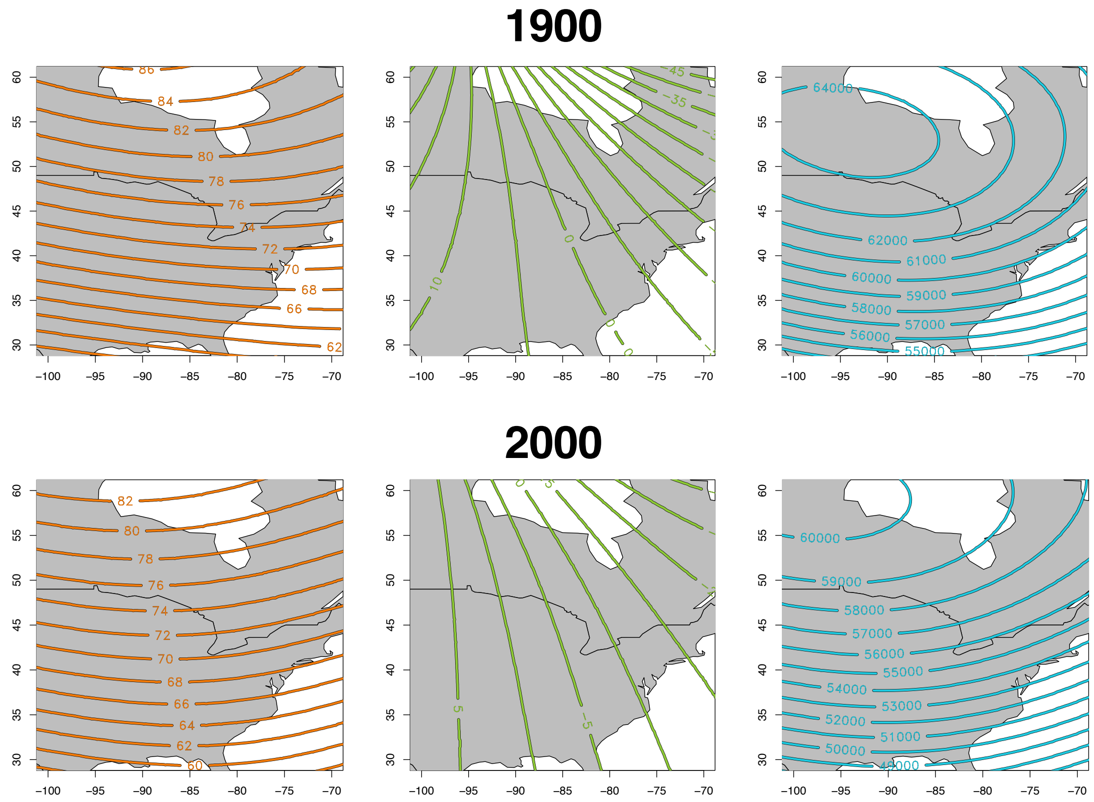


Figure 7.8: Isoline positions for each of inclination, declination and intensity in the years 1900 and 2000 in Europe. Isolines are shown for inclination (left), declination (centre) and intensity (right) , with the labels on each isoline denoting the value the isoline in question isoline represents.

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8

Discussion

Contents

"The secret to a happy ending is knowing when to roll the credits,

Better roll 'em now before something else goes wrong."

– Drive-By Truckers, *A World Of Hurt*

The mechanisms that underpin long-distance, inter-continental avian migration are both remarkable and unresolved. Throughout this thesis I have attempted to investigate both how birds navigate, and how this ability changes and develops through their lifespan. I have, further, focused on how birds achieve specific navigation feats, most notably the first outbound and return migration.

In **Chapters 2 and 3** I investigated the sensory and cognitive basis of philopatry; how birds return with considerable accuracy to the same site year-on-year. Using historic ringing records, I found in both seabirds and songbirds evidence for the use of magnetic inclination as a spatial cue when returning to the natal site. Further, I found evidence in songbirds that a similar mechanism might persist in adult birds too, and again in songbirds found evidence that magnetic inclination may be used as a uni-coordinate 'stop sign' during philopatry. This would suggest that birds do not recall the position of their breeding site as a bi-coordinate, but instead use a single uni-cooordinate position alongside a migratory bearing.

In **Chapter 4** I found evidence for magnetic compass orientation in a seabird. Using a twilight calibration paradigm, I found that the instantaneous deflection of Manx shearwaters (*Puffinus puffinus*) was predicted by the applied magnetic field, with the magnitude of this deflection in turn predicted by discrepancies between the inclination experienced during the experimental magnetic treatment and the inclination of the normal magnetic field. This is seemingly consistent with the use of a magnetic inclination compass, as is used in songbirds (Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1992; Schwarze et al., 2016).

In **Chapter 5** I investigated the development of orientation in a fluid medium, finding that the ability to compensate for wind drift in frigatebirds a) developed with experience and b) was improved by access to visual landmark cues. In **Chapter 6** I continued the investigation of the role of learning in navigation, assessing the relative contributions of learnt and inherited information on the outbound and return migratory trajectories of Manx shearwaters. By tracking both fledglings and their parents I concluded that it is unlikely that either the outbound or return migration trajectory is learnt socially, that the outbound trajectory is likely inherited genetically and the return trajectory is informed by a either genetic information or environmental conditions (or both). I further proposed that the return migratory trajectory might be iteratively extended through ‘exploration refinement’ (Guilford et al., 2011), with information learnt on each leg used to inform the next.

Lastly, in **Chapter 7** I investigated the effect of magnetic secular variation on the position denoted by a magnetic bi-coordinate. I found that even small magnetic field shifts can have large and unpredictable effects on the position denoted by the intersect of 2 magnetic isolines, with the the largest and most unpredictable effects seen in near-parallel isolines. Based on this, I suggest that a) magnetic cues varying in a near-perpendicular arrangement likely make for the most suitable ‘maps’, and b) that uni-coordinate magnetic information presents an alternative navigation system substantially less exposed to secular variation.

In this final chapter, I will integrate the results from each of the last 6 chapters, and discuss the wider implications of the findings. I will discuss what information shapes and informs long-distance migration, as well as investigating the evolutionary origins of avian navigation mechanisms and commenting specifically on the special case of philopatry. Finally, I will discuss future directions in the study of animal navigation that this thesis brings to light, and suggest the next empirical steps required to validate some of the findings presented here.

8.1 Synthesis

8.1.1 The ontogeny of outbound navigation: learning, genetics and culture

The early life development of navigation is, necessarily, difficult to study *in situ*. This is - first - because mortality amongst young birds is high, meaning that collecting large quantities of data is challenging (even when working with long-lived birds). Second, using archival tags to study navigational ontogeny is a inevitably a selective process:

unsuccessful individuals are not included in the study. The alternative is to use remote-download tags, the likes of which rely on more novel (and hence are less reliable) technology.

Nonetheless, in this thesis I present 2 *in situ* biologging studies aimed at investigating the development of long-distance navigation. In 2019 I tracked a cohort of 10 immature Manx shearwaters alongside their parents, tracking fledglings with remote-download GPS nearly to the equator and tracking adults with geolocators the complete distance to the Patagonian Shelf. In spite of garnering only incomplete immature tracks it was apparent that fledglings were not accompanied by their parents on first migration and, further, travelled via a different and more direct migratory route. This makes cultural inheritance from parents unlikely, whilst the different route (and slower migration) observed may make cultural inheritance from non-related individuals similarly improbable. I suggest, therefore, that genetic inheritance is key in the first migration of Manx shearwaters. This is consistent with other studies conducted in procellariforms, where birds were also observed to take different routes to their parents (Yoda et al., 2017; Yoda et al., 2021).

However, in the complete first Manx shearwater outbound migrations recorded using GLS in 2011, the extent to which birds diverged and subsequently converged is remarkable. Specifically, I note that birds diverged to a maximum separation of 1,612km on the equator, before converging to winter in the same part of the South Atlantic as both each other and their parents (Chapter 6, Figure 6.2). Theory, and indeed empirical observation using ringing data (Mouritsen, 1998; Mouritsen & Mouritsen, 2000), would suggest that error should accumulate with time in birds orienting along an inherited vector (such as the proposed clock and compass), hence it is perhaps surprising that shearwaters do not continue to diverge as they progress southwards. Consequently, despite the small sample size, the convergent migration of shearwaters perhaps requires some explanation.

It is possible that the convergence of shearwaters in the second half of migration simply reflects the reticence of birds to fly over land, with the African continent forcing birds westwards and the South American continent providing a similar eastwards barrier.

Likewise, one must consider the possibility that convergence in the migratory route of vector-orienting shearwaters reflects the prevailing wind forcing individuals together. This could well be the case in Manx shearwaters, with strong, predictable equatorial winds bringing birds together (Guilford et al., 2009; Fayet et al., 2020). Alternatively, or additionally, convergent migratory routes in shearwaters might reflect course correction towards the goal following displacement from the trajectory. Such an ability could be underpinned by an inherited navigational map, as seen in teleost fish and sea turtles (e.g. Lohmann et al., 2012; Putman et al., 2014b; Naisbett-Jones et al., 2017), or alternatively could be considered to represent a learnt ability to compensate drift, which I discuss and find evidence for in Chapter 5.

What 'drift compensation', or 'wind drift compensation', means is unclear. It has been suggested that wind drift compensation could utilise optic flow cues to minimise drift from the intended course, and indeed the use of optic flow to minimise drift has been proposed in other avian taxa and animals more generally (Esch et al., 2001; Bhagavatula et al., 2011; Hedenstrom & Akesson, 2017). Such 'instantaneous' wind drift compensation would not necessarily allow birds to compensate post-hoc for deviation from the intended migratory trajectory. It has, however, been suggested that improvement in wind drift compensation could instead reflect the parameterisation of a gradient map (Goto et al., 2017). As discussed in Chapter 5, a higher resolution gradient map would allow a navigator to reorient at a greater rate, in turn reducing drift (see Figure 8.1). Such a system could in principle be of some considerable use to birds moving over featureless expanses, given the lack of salient visual information, and could also explain why shearwaters converge in the second half of migration. Indeed, migratory birds more generally could compensate for departure from the intended course, despite inheriting a vector orientation system, using a recently parameterised gradient map. Such *en route* map development is not typically considered, with the distinction between 'experienced' and 'inexperienced' navigators often drawn after first migration (e.g. Perdeck, 1958). However, navigational ability could develop extremely rapidly, with the results presented in Chapter 5 certainly suggesting so, and in turn this might explain why some studies suggest that first-year migrants can

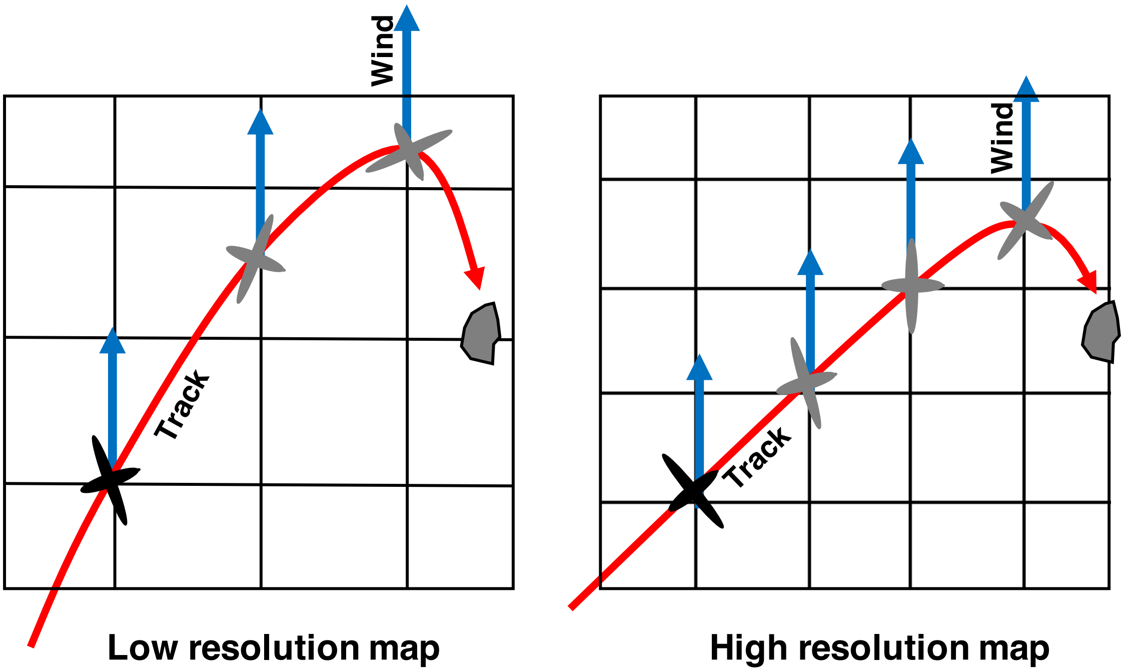

Figure 8.1: Wind drift compensation as a function of gradient map navigation. In principle, a highly resolute gradient map could be used to reduce wind drift. By increasing the rate at which position is accurately determined, and hence the rate at which heading is adjusted, wind drift is reduced. The development of wind drift compensation could, therefore, reflect the development of bi-coordinate navigation.

navigate (e.g. Thorup et al., 2011; Thorup et al., 2020), whilst others find that they can't (e.g.Mouritsen and Larsen, 1998; Thorup et al., 2007; see Figure 8.1).

The inheritance of vector navigation information in a fluid medium, however, presents another interesting question: how does vector orientation function when birds are liable to drift with the wind? As discussed above, a rapidly learnt ability to compensate for wind drift (by whatever mechanism) would allow birds to keep on course. An alternative, perhaps simpler solution would be for birds to inherit a migratory vector *relative* to the prevailing wind. In such a system bird would inherit a migratory bearing that takes them into the average wind field, so as their overall track taken (i.e. the vector sum of wind drift and the inherited vector) is in the 'correct' direction (see Figure 8.2). Such a system would not be predicated upon any learnt ability, and instead would reflect the fact that natural selection sees and acts upon the realised movement of birds and not their inherited vectors. In turn this would lead to the a vector that does not take into account the average wind field being sub-optimal, and hence that the inherited vector takes into account the average wind field over evolutionary time. As such, it is apparent that a learnt ability to compensate for wind drift is not necessarily required for first-time migration, and it is therefore unclear whether the results I find in frigatebirds are generalisable to other bird species.

Nonetheless, the straight-line trajectories of immature shearwaters, taken independent of their parents, are broadly consistent with the genetic inheritance of a navigational vector, as seen in other taxa (Perdeck, 1958; Mouritsen, 1998; Thorup et al., 2007; Yoda et al., 2017; Yoda et al., 2021). However, given the evidence discussed in this thesis it is extremely unlikely that an inherited vector is the only factor influencing the outbound migration trajectory, both in shearwaters and birds more generally. Specifically, as discussed above the evidence in frigatebirds for a rapidly learnt ability to counter drift suggests that a learnt ability to compensate for displacement from the beeline during first migration is possible. In turn, it is therefore possible that learnt information plays a role in navigation along the outbound migratory trajectory. Similarly, it is possible that outbound migration is also influenced by both topography and the wind, and that the

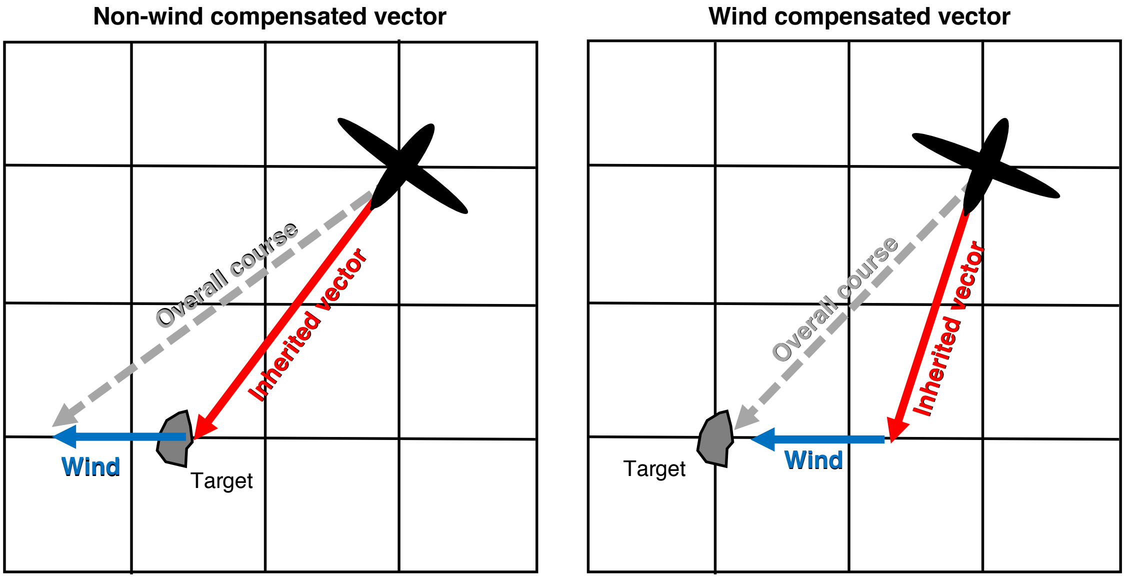

Figure 8.2: Wind-compensated vector orientation. The problem of wind drift might be overcome through evolutionary time via the selection of routes relative to the mean wind field, meaning that the vector sum of the inherited vector and the mean wind over evolutionary time leads an individual to the intended wintering destination (right). If this is not the case, an individual may overshoot the target (left).

selective processes shaping the inherited outbound trajectory should in principle take both into account. More generally, I suggest that this provides a generalised paradigm within which to consider outbound migration: an initially vector-oriented migratory program, inherited relative to the prevailing wind field and topography, which in turn is augmented by a learnt, flexible system of drift compensation. Within such a framework the relative inputs of these processes would likely reflect the ecology of the species in question, and the specific navigational tasks required. It is, alternatively, possible that birds do not inherit a vector and, instead, inherit map-like information (Thorup et al., 2020) as is thought to be the case in sea turtles (e.g. Fuxjager et al., 2014). It is, however, difficult to reconcile an inherited map with the repeated mis-orientation of displaced naïve birds (e.g. Perdeck, 1958; Mouritsen and Larsen, 1998; Thorup et al., 2007), and hence I suggest that rapid-onset learning is a more parsimonious explanation.

8.1.2 Could learnt, uni-coordinate magnetic information guide return migration?

Whilst vector orientation is a possible solution to the problem of outbound migration, it is unlikely that it underlies return migration also (Baker, 1978). This is because of the extraordinarily high fidelity which the majority of migratory birds return to the natal/breeding site ('philopatry'; Newton and Brockie, 2008). The exact function of philopatry is unclear, though it could reflect either local adaptation to a specific climatic/habitat niche, locale-specific learning leading to increased fitness, or even both (Waser & Jones, 1983). Nonetheless, the precision with which philopatry is achieved has been suggested to require some form of learning process (Baker, 1978; Paradis et al., 1998).

As discussed in both Chapters 2 and 3, it has repeatedly been suggested that sensory gradients might provide the cues that underpin extremely long-distance navigation (Baker, 1978; Lohmann et al., 2008). Such cues would have to be targetable over long distances, whilst also being stable enough through time to represent approximately the same site between years. Olfactory and magnetic cues have been suggested as some of the few gradient cues suitable for navigation, with both seen to vary over long enough distances whilst displaying the requisite stability through time for between-year targeting (for reviews, see Gagliardo, 2013; Mouritsen, 2018). Olfactory cues have been suggested to be of some use in pigeon (Papi et al., 1971; Benvenuti & Wallraff, 1985) and procellariform navigation (Gagliardo, 2013; Pollonara et al., 2015; Padget et al., 2017), whilst some evidence exists for olfactory navigation in songbirds also (Holland et al., 2009), whilst magnetic cues have been suggested to be useful in the navigation of migratory songbirds (Fransson et al., 2001; Chernetsov et al., 2017). However, neither magnetic or olfactory gradients have been specifically implicated in the philopatry of any species of bird.

In this thesis, I present a novel method whereby historical ringing records arw used to investigate whether magnetic cues might be used during philopatry. By measuring changes in position between ringing and recovery, and seeing whether slight (but measurable) 'secular' variation in the Earth's magnetic field predicts these changes, I attempted to investigate the sensory basis of philopatry. Using this technique, I found evidence for the use of magnetic inclination, but not intensity, in the natal philopatry of Manx shearwaters (see Chapter 2). In chapter 3, I similarly implicated inclination as a spatial cue used in the philopatry of both adult and first-year Eurasian reed warblers (*Acrocephalus scirpaceus*; 'reed warblers'). Taken together, these results suggest that magnetic inclination could underpin philopatry in birds and, given the phylogenetic distance and ecological differences between the 2 species investigated, I suggest that such a mechanism might be generalisable across avian taxa (see Section 8.1.3). This is perhaps unsurprising, given that magnetic inclination a) is both stable enough through time to represent a specific geographic position (Putman & Lohmann, 2008) and b) has been suggested to underlie return migration in both salmonid fish (Putman et al., 2013; Putman et al., 2014a; Putman et al., 2015) and sea turtles (Brothers & Lohmann, 2015). That a similar sensory mechanism might explain return migration in birds also might, therefore, make sense.

However, inclination gives position relative to only 1 dimension and, as such, there are many places around the world that share the same inclination value. The prevailing view

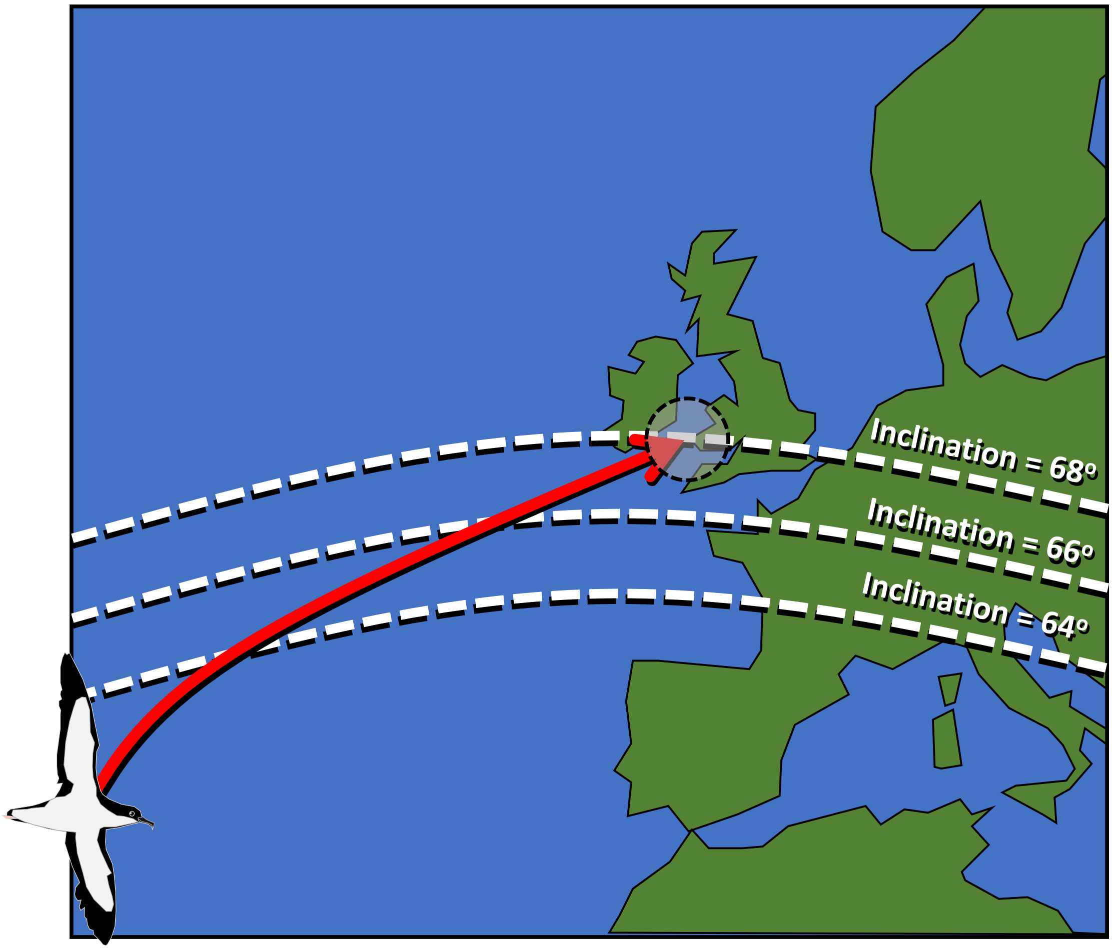

Figure 8.3: Using inclination and a coastline to determine position. In principle, a bird returning from the wintering site, here a Manx shearwater breeding in southwest Wales, could recall the location of their breeding sites (here a translucent white circle) using a single gradient cue (e.g. magnetic inclination; represented here by the white dotted line) if it were used in conjunction with the coastline.

in animal behaviour is that a second cue must be used to discern bi-coordinate position (for reviews, see Holland, 2014; Mouritsen, 2018). As discussed in Chapter 2, it is extremely difficult to examine what this second cue might be in Manx shearwaters, since there is very little longitudinal variation in their range. Indeed in shearwaters a second cue need not necessarily be utilised, since the coastline of Europe could be used to provide the longitude at which birds should breed (as has been suggested in sea turtles; Putman and Lohmann, 2008; Brothers and Lohmann, 2015; see Figure 8.3). However, in terrestrial birds where well defined well-defined topographic boundaries are less common, this strategy may be considerably more difficult to execute. As discussed in Chapter 3, there is considerable variation in both longitude and latitude at which reed warblers breed (see Chapter 1, Figure 1.4) and hence I sought to investigate what cues allowed them to return to a precise bi-coordinate position. Despite the predictions made by previous studies (Chernetsov et al., 2017; Pakhomov et al., 2018; Kishkinev et al., 2021), I found no evidence for the use of either magnetic declination or magnetic intensity in reed warbler philopatry. Instead, I found that the most parsimonious use of inclination was as a ‘stop sign’ on an *a priori* defined migratory trajectory (Mouritsen, 2003); in principle, birds might need to know position relative to only one cue gradient when locating the natal site if they are already travelling along a known bearing (see Figure 8.4).

At first glance the findings of our analyses may seem incongruous, especially given the existing evidence for both avian ‘true navigation’ amongst experienced individuals (Perdeck, 1958; Thorup et al., 2007; Chernetsov et al., 2008; Willemoes et al., 2015) and the apparent use of magnetic declination by reed warblers specifically (Chernetsov et al., 2017; Pakhomov et al., 2018; Kishkinev et al., 2021). However, I believe that our results can be reconciled with the extant literature. First, previous studies have used extremely long distance displacements (or virtual displacements) to test whether birds can orient in the correct direction from novel locations. Such experiments therefore seek to ask what cues might be available to birds displaced during migration, rather than asking precisely which cues inform philopatry (which is, navigationally speaking, a very different task). Indeed, it could be suggested that compensation for artificial displacement is more akin to the drift compensation discussed in Chapter 5 than the philopatry examined in Chapters 2 and 3. As such, I suggest that return migration might comprise 2 distinct tasks: minimising drift relative to the intended course, and knowing when to stop moving. The first of these tasks could well make use of bi-coordinate information, perhaps on a coarse spatial scale, and I speculate that it is such a drift compensation mechanism that is responsible for the apparent ability of experienced birds to compensate for long-distance displacement (e.g. Perdeck, 1958; Thorup et al., 2007; Chernetsov et al., 2008; Willemoes et al., 2015).

However, I suggest that bi-coodinate magnetic information is an imperfect mechanism when precisely targeting the natal site. This is because of the effect secular variation has

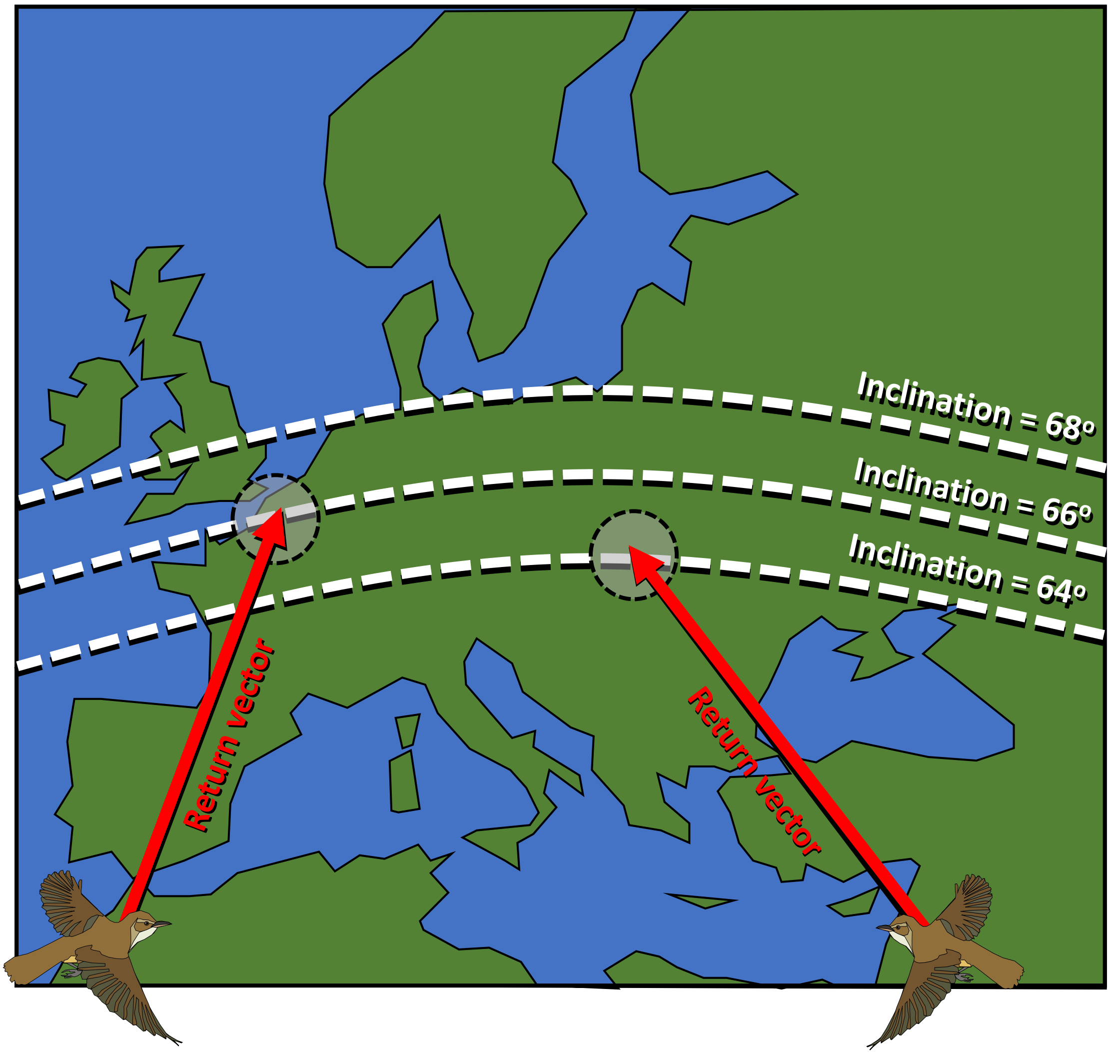

Figure 8.4: The magnetic 'stop sign' hypothesis. In principle, birds returning from the wintering site (here 2 reed warblers returning via the eastern and western European flyways) could recall the location of their breeding sites (here a translucent white circle) using a single gradient cue (represented here by the white dotted line) if it was used in conjunction with an *a priori* defined migratory bearing (here the solid red arrow).

on bi-coordinate magnetic information, as discussed in Chapter 7. Using the International Geomagnetic Reference Field I found that the position denoted by each bi-coorinate combination of magnetic inclination, declination and intensity moved measurably between years, with the extent and predictability of this movement in turn predicted by the acute angle between magnetic isolines. Specifically, I found that magnetic cues varying along near-parallel axes could move massive distances between years (> 100km), but that such movements were erratic owing to the differing effects of isolines moving in the same or different directions. Indeed, even when considering isolines varying along near-perpendicular axes there was some considerable movement between years (> 20km). Though smaller, such movements could still prove problematic to birds with very little pre-migratory experience of the local area. In contrast, as discussed in Chapter 3, the movement of a uni-coordinate inclination stop-sign is typically < 5km. Since within-year drift compensation is unaffected by between-year secular variation, the movement of magnetically-defined bi-coordinate positions has little effect on the use of multiple magnetic cues as a drift compensator. As such, I suggest that the most adaptively advantageous use of magnetic cues might be to use a single magnetic cue to denote the natal site, and other magnetic cues to ensure that variation about a migratory bearing is minimised.

I have thus far considered both the sensory modality of the information that underlies philopatry, and how this information might be used. However, it is also important to consider how this information is learnt. Previous studies in other animal taxa have considered natal philopatry to be distinct from philopatry more generally, with early-life ‘imprinting’ to spatial cues allowing naïve individuals to return faithfully to the natal site (Baker, 1978; Lohmann et al., 2008). Unlike in classical associative learning, imprinting is thought to occur at a specific point in an individual’s life, typically very early in life, and over time it has been speculated that experienced birds replace or augment the imprinted information over successive migration attempts (Baker, 1978; Mouritsen, 2018). In Chapter 2 we find that the between-year fidelity of adult shearwaters is very high, far higher than in immatures, with only 6 birds recorded at a second colony once being recorded at another as an adult (compared to 109 immatures). As discussed in Chapter 2, this is consistent with imprinted information underlying return amongst immature birds, and other information informing return migration in adults. Similarly, in Chapter 3 we find that adult reed warblers have a higher degree of philopatry than immatures (moving an average of 4.88km between years when compared to the 11.51km moved by immatures), which in turn would be consistent with other cues being used in philopatry. However, these increases in the likelihood of recovery at the breeding site might reflect greater incentives for doing so: it’s not that juveniles can’t return faithfully to the breeding sites, it's just that adults may have greater benefit (and hence motivation) to do so. This could stem from having established nests/territories/mates, which in turn may disincentivise deviation from the breeding site to a greater extent than would be observed in immatures.

So far, this is consistent with an imprinted magnetic cue being augmented with additional information through time. However, in reed warblers we find that, even when considered separately to immatures, adults are still susceptible to between-year changes in magnetic inclination. In turn, this implies that the magnetic target used by reed warblers is updated year-on-year and, seemingly unlike sea turtles and salmonids, that reed warblers might not imprint to a magnetic inclination value early in development and might, instead, repeatedly re-learn magnetic cues throughout their life. It has been suggest that associative stimulus-response ('SR') learning could underpin various facets of navigation (Guilford & Burt de Perera, 2017), and it is possible that reed warblers utilise an SR paradigm to recall magnetic values associated with the breeding site. This is especially plausible given their repeated nocturnal forays away from the breeding site, which are in principle long-distance enough that changes in magnetic inclination may provide salient information that could be associated with returns to the breeding site (Mukhin et al., 2005). In principle such flights could therefore allow birds to associate magnetic values with the natal site, in turn allowing for repeated re-learning of the breeding-site inclination without imprinting. Such a mechanism might even underpin learning in Manx shearwaters, where pre-fledging experience is extremely limited, given their pre-breeding exploration of the area adjacent to their burrows (as discussed in Chapter 6) may provide a suitable paradigm for associative learning of cues associated with the natal site. However, such nocturnal forays are over such short distances that it is difficult to imagine how magnetic inclination might vary enough to give salient navigational information. It is, therefore, unclear precisely how magnetic information is learnt prior to first migration.

Irrespective of the precise mechanism by which magnetic information is learnt, I suggest that the use of uni-coordinate magnetic inclination is not only consistent with the results presented in this thesis, but also makes sense given the apparent shortcomings of bi-coordinate navigation. I further propose that the use of magnetic inclination could in principle be widespread in avian taxa, given the divergent ecological and phylogenetic contexts within which we report the use of magnetic inclination in this thesis. However, as discussed in Chapter 2, the utility of magnetic information in avian navigation has a chequered and controversial history. This I will address in the next section, when I discuss the extent to which magnetic navigation pervades the avian clade.

8.1.3 The ecological and phylogenetic extent of magneoreception in avian taxa

As discussed in Section 8.1.2, magnetoreception has been shown to be of some importance in songbirds (passerines), particularly amongst those migrating at night (Mouritsen, 2018). Night-migrating songbirds are found across the globe in a variety of ecological contexts, within which species have been repeatedly shown to utilise magnetic cues for both orientation (e.g. Wiltschko and Wiltschko, 1972; Schwarze et al., 2016) and, seemingly, for spatial positional information (e.g. Wiltschko et al., 1998; Chernetsov et al., 2017). Evidence for magnetoreception in other avian clades is, however, surprisingly equivocal.

Magnetic information could inform orientation in racing pigeons (*Columba livia*), with some studies reporting changes in orientation either with the deployment of bird-borne magnets (Keeton, 1971) or in the presence of natural magnetic anomalies (Dennis et al., 2007; Wiltschko et al., 2009). Indeed, a putative magnetite-based receptor was thought to have been isolated in the beak of pigeons, which in principle would transfer magnetic spatial information via the trigeminal nerve to the brain (Fleissner et al., 2003; Falkenberg et al., 2010; Pakhomov et al., 2018). However, the putative pigeon magnetoreceptor is now widely considered to be a structure comprising mostly macrophages (Treiber et al., 2012), hence it is unclear how pigeons would sense the Earth's magnetic field. Similarly, whilst some empirical evidence exists that pigeons can seemingly learn magnetic cues in the context of conditional choice trials (Bookman, 1978; Mora et al., 2004), a specifically navigational response in pigeons to magnetic manipulation has proven difficult to replicate empirically (Gagliardo et al., 2006; Gagliardo et al., 2008, 2009; Holland et al., 2013). Moreover, there exists good evidence that spatial position is, in pigeons, largely informed by olfactory cues (for a review, see Gagliardo, 2013), whilst a sun compass has been implicated in pigeon orientation multiple times (Schmidt-Koenig, 1961; Biro et al., 2007; Armstrong et al., 2013). Evidence for the use of magnetic cues in pigeon navigation is, therefore, highly equivocal. Magnetic information has also been shown to be unlikely to underpin homing behaviour in procellariform seabirds, with both displaced (Gagliardo et al., 2013; Pollonara et al., 2015) and free-flying (Benhamou et al., 2003; Mouritsen et al., 2003; Bonadonna et al., 2005; Padget et al., 2017) birds seemingly unaffected by the presence of bird-borne magnets. As in pigeons, homing in procellariforms is instead seemingly predicated upon olfactory information (Gagliardo et al., 2013; Padget et al., 2017), augmented with visual cues (Pollonara et al., 2015), whilst orientation has been shown to utilise a time-compensated sun compass (Padget et al., 2018).

One of the few non-passerines in which empirical evidence for magnetoreception exists is the sanderling (*Calidris alba*; Gudmundsson and Sandberg, 2000), where migrating adults have been shown to reorient when placed in an altered magnetic field. As such, there appears a paucity of evidence for magnetoreception outside of songbirds. Therefore, given the apparently equivocal evidence for non-passerine magneotreception and, specifically, the apparent lack of any evidence for procllariform magnetoreception, the results presented in Chapters 2 and 4 therefore require some explanation.

In Chapter 2 I present evidence for the use of magnetic spatial information in Manx shearwaters, with immature shearwaters seemingly using magnetic cues to target the natal site. As mentioned previously, extant studies have used bird-mounted strong magnets to artificially change the direction and intensity of the experienced magnetic field, something to which procellariforms are seeimingly unresponsive. However, (somewhat) analogous anosmia treatments severely limit the homing capacity of both displaced and free-flying birds. Taken together, these results suggest that, at least during homing behaviour in the breeding season, olfactory cues are the primary gradient cues used in navigation (Gagliardo et al., 2013; Pollonara et al., 2015; Padget et al., 2017). It would seem that the findings presented in Chapter 6 are, then, slightly incongruous, which we believe could reflect differences in the scale of navigation between the above studies and the birds examined in Chapter 2. Previous studies of procellariform gradient map navigation have been conducted at or near the colony, with birds rarely reaching > 500km from the breeding site. Given the scale over which procellariform seabirds forage, experimental birds are therefore likely to be at least partially familiar with the area within which such experiments took place. This is, however, unlikely to be true of the immature birds considered in Chapter 2, since fledglings seemingly do not return to even the same hemisphere as their natal site until several years post-fledging (as discussed in Chapter 6). As such, the fledglings discussed in Chapter 2 are not only moving much greater distances than the procellariforms considered in previous studies, but are also much less familiar with the speicifc navigational task. Therefore, is is possible that whilst it appears olfactory cues predominate procellariform navigation during the breeding season, consistent with studies conducted in pigeons (Gagliardo, 2013), magnetic cues might underpin migratory procellariform navigation on a global scale.

In Chapter 4 I also consider magnetoreception in Manx shearwaters, focusing this time not on spatial position but instead on compass orientation. We believe that our results are consistent with the use of a magnetic inclination compass, representing not only the first evidence for a magnetic compass in a seabird but the first experimental evidence for seabird magnetoreception more generally. Previous studies into shearwater orientation have shown that a time-compensated sun compass is essential for orientation (Padget et al., 2018). This means that if a magnetic compass were to be used in addition, it would necessarily provide redundant information. Indeed, as discussed in Chapter 4 we might expect a degree of redundancy in the compass systems utilised given the various inaccuracies present in the various compass systems. Since multiple compass systems might be used simultaneously, it is not necessarily to be expected that birds are disoriented when the sensory input to one compass system is scrambled. Hence, one would not necessarily expect the addition of a rare-Earth magnet to affect orientation, since birds could be selectively inattentive to clearly erroneous magnetic information and focus instead on other compass systems that are providing reliable information. This is certainly what is reported in Chapter 4, where birds are seemingly only attentive to magnetic fields similar to the normal geomagnetic field of Earth. As such, seabirds, and perhaps birds more generally, might be expected to react more strongly to magnetic reorientation experiments (such as compass manipulations) when compared to magnetic disorientation experiments (such as magnet deployments) owing to redundancy in compass information. I suggest, therefore, that it is this redundancy that explains the lack of effect in jostling magnet experiments when compared to the compass manipulation presented in Chapter 4 (Packmor et al., 2021).

Indeed, the relative effectiveness of disorientation vs. reorientation experimental paradigms may partially explain the extent to which magnetoreception is reported in avian taxa. For example, one of the workhorse reorientation paradigms of animal navigation, the Emlen funnel (Emlen & Emlen, 1966), requires that birds scratch the inside of a funnel to express an orientation preference. Emlen funnels permit complete control of the cues accessed by a test subject, allowing not only for reorientation of the cues of interest, but also for a the establishment of a ‘sensory vacuum’ within which test subjects are deprived of all navigational cues aside those of interest. It is notable that the vast majority of birds seemingly capable of geomagnetic orientation do so either in Emlen funnels (e.g. Gudmundsson and Sandberg, 2000; Fischer et al., 2003; Schwarze et al., 2016) or in reorientation experiments (e.g. Cochran et al., 2004), and that disorientation experiments seemingly only work when other cues are absent (Packmor et al., 2021). As such, I make 2 assertions. First, that the apparent lack of magnetic compass orientation outside of songbirds may be exacerbated (or even completely caused) by a confound in the methods used to investigate orientation (since non-passerines are not readily experimented upon in an Emlen funnel). Second, that such a confound could be potentially alleviated through the use of *in situ* reorientation experiments, possibly using the twilight calibration paradigm presented in Chapter 4.

Further, as discussed above, the scales over which passerine navigation and non-passerine navigation are considered are often very different. Passerine navigation is typically investigated within the context of trans-continental migration, which is characterised by both the extremely long distances travelled and the lack of familiarity with the route. Other taxa are typically considered during homing behaviour, which in contrast takes place over shorter distances with a greater degree of familiarity. I propose, therefore, that this difference in scale may at least partially explain why magnetic spatial information is found more readily in passerines: since they are more likely to be considered in the context of long-distance migration. Indeed, magnetic cues might predominate in very long-distance navigation since, as discussed in Chapter 7, year-on-year movement in the Earth's magnetic field might make it less amenable to short-distance movement and, instead, better suited to long-distance navigation. Further, whilst inter-hemisphere sensory gradients have been suggested for magnetic cues (e.g. inclination), there is not yet a candidate olfactory gradient that varies over the same scale (although short distance gradients are well documented; Wallraff and Andreae, 2000; Zannoni et al., 2020, and some experiments have suggested that long-distance navigation could be affected by anosmia; Holland et al., 2009; Wikelski et al., 2015). As such, I suggest that in order to ascertain whether magnetoreception is limited to songbirds the empirical paradigm with which magnetoreception is assessed must be taken into account, alongside the specific navigational task which is being completed.

Based on the above discussion, one might therefore ask the following: is magnetoreception likely ubiquitous across avian taxa? If the above speculation is correct, then it follows that it is presently extremely difficult to know just how widespread avian magnetoreception is owing to several confounding factors. However, within this thesis I present evidence, both experimental and correlative, for magnetoreception in both a songbird and a seabird. These are not only phylogenetically distinct taxa, but are also ecologically very different with very different life histories. The fact that evidence exists for magnetoreception in both might suggest that the use of magnetic information in migratory birds is more common that has previously been suggested, and may even be basal amongst avian taxa. However, investigating whether this is the case necessarily requires further information and study, which is something I shall focus on in the next and final section.

8.2 Future directions

As with many of the papers cited throughout this thesis, the chapters enclosed within perhaps prompt more questions than answers. Further, the methods presented within this thesis may also warrant additional refinement into the future. Specifically, refining the use of historic ringing data when considering avian philopatry could be of some considerable use when considering both the use of specific navigational cues, but also potential environmental drivers of the sites to which birds return. More generally, I will below pick out several themes from this thesis that are both of interest and also can be taken forward in the next few years, either using ringing-data analysis, correlative analysis more generally or experimental manipulation.

The role of learning in determining first migratory trajectory

Through the course of this thesis I have discussed the possibility that learnt navigational abilities, such as true navigation, could arise surprisingly early in development. Such early-life development of navigation could explain disparities between studies purporting to show navigation in naïve individuals (e.g. Thorup et al., 2020) and those that don't (e.g. Mouritsen and Larsen, 1998; Thorup et al., 2007). It would, therefore, be of some interest to investigate whether migratory birds might show age-dependent navigational ability even within the first migratory trajectory.

This would, necessarily, require experimentation on migratory birds for which navigational experience is either known (as is the case in Chapter 5) or could be estimated. Knowing the precise navigational experience of actively migrating birds might prove impractical outside of the laboratory, as known-age cohorts of migratory birds would probably spread out along migration (as is the case in Chapter 6) and hence experimentation mid-migration would prove challenging. However, birds could in principle be intercepted *en route* and their experience calculated retrospectively. For example, birds could be captured at an established migratory stopover site, outside of the breeding range, and the navigational capacity of the birds in question could be tested (through displacement or virtual displacement, for example). Assay response could then be compared to the migratory distance already travelled by birds, which could be calculated by estimating a breeding latitude through isotopic analysis (e.g. Jong et al., 2019), or through using birds ringed at the natal site and subsequently recovered on migration. If experience predicted navigational ability, we would expect that birds that have travelled further would have a greater probability of reorienting in response to displacement.

The effects of topography and weather on naïve migrants

Whilst the roles of genetic and cultural inheritance are by-now well understood when considering first outbound migration, it is still not entirely clear how these inputs interact with abiotic factors to produce the observed migratory trajectory. Studying the interaction of migrant species with the environment is likely extremely difficult in the laboratory, hence *in situ* experimentation would likely prove a more successful approach. Specifically, I suggest that this thesis raises 2 questions which might be of interest. First, as speculated upon in Chapter 8, is the migratory vector inherited by birds relative to the prevailing wind field? Predictable wind patterns prevail across much of the globe (e.g. Guilford et al., 2009), consistent enough that we might expect over evolutionary time they exert selection pressures on migratory birds. Specifically, we might expect birds to inherit a migratory trajectory that takes into account the prevailing wind direction (as shown in Figure 8.2). If this were the case, we might make 2 predictions: a) that birds are ‘blown’ off course by strong winds from unusual directions, but also b) that birds are ‘sucked’ off course by weaker-than-expected winds from the prevailing wind direction. This could be readily assessed using remotely-sensed wind data (for example the NOAA Global Forecast System, as used in Chapter 5) and remote-download GPS devices.

As my second proposal, I suggest investigating whether inherited trajectories take into account account the topography of the migration route. Vector navigation is apparently limited in the complexity of the inherited trajectory that can be inherited, leading to seemingly maladaptive migratory routes (Yoda et al., 2017; Yoda et al., 2021). However, more complex (and less maladaptive) trajectories could result from the application of simple rules. For example, for terrestrial species a reticence to fly over mountains or long distances over open water might reduce mortality. Similarly, amongst pelagic species we might expect birds to 'pinball' off coastlines towards the destination. Understanding whether this is the case is of interest for 2 reasons. First, a flexible system of obstacle avoidance is inconsistent with simple orientation, and could imply a navigational ability not typically attributed to naïve individuals. Second, if first-time migrants were attentive to the topography, this must necessarily be taken into account in studies into the inheritance of navigational information. For example, correlative studies examining the genetic basis of migration typically utilise the overall direction between the breeding and wintering sites as a response variable (e.g. Delmore et al., 2020). Hence, if this direction were strongly influenced by abiotic factors, this would need to be taken into account. As such, we suggest that investigating the effect of topography on migratory orientation may be of some interest.

Experimental verification of avian geomagnetic imprinting

In Chapter 3 I speculate that birds might recall the location of their breeding site relative to a single uni-coordinate magnetic cue, and that the ability to 'true navigate' posited in previous studies might instead reflect a mechanism by which birds reduce drift during return migration. As such, I submit that it is impossible to use long-distance displacement to test whether birds use bi-coordinate magnetic information when specifically recalling the location of the natal site. This is because it is impossible to distinguish natal site recollection from drift compensation. Further, many studies of long-distance navigation focus on orientation in the autumn, hence are not particularly relevant when considering philopatry.

I believe that experimental verification of my proposed mechanism is essential, especially given that the study presented in this thesis is correlative and hence could be driven by confounding variables (however unlikely this would seem). This could be achieved *in situ*, by scrambling magnetic information early in the development of migratory birds and recording the rate of philopatry when compared to a control. This would, however, likely require an extremely large sample size given the disorientation paradigm, and could be considered unnecessarily unethical. Alternatively, magnetic imprinting could be tested in the laboratory where a requisite increase in physical control would allow for precise *a priori* predictions to be made. For example, a migratory bird could be raised in an artificial magnetic field with either an increased or decreased inclination. In the winter, birds could be kept in a magnetic field representative of the wintering site, at which point the magnetic field might be slowly returned to that representitive of the breeding site (as in Bulte et al., 2017). In such a process, inclination would slowly increase to simulate northwards movement (assuming a northern hemisphere migrant is used as a model organism). If the *zugunruhe* of birds were measured, we would expect birds raised in a lower inclination field to arrest their restlessness prematurely, whilst birds raised in a field with larger inclination values would remain restless until the inclination exceeds that of the real natal site. This could then, in principle, be repeated for each magnetic parameter and each set of magnetic parameters, allowing for the exploration of which cues underpin philopatry. Such an experiment would be time-consuming, but would allow for the disentanglement of cues used during return migration more generally from those used specifically during philopatry.

Compass calibration in short-distance navigators

In this thesis I present evidence that the direction of information flow within a compass calibration system might differ between breeding Manx shearwaters and the high-latitude songbirds migrants examined in previous studies. I suggest that this disparity might reflect differences in the navigational challenges faced by Manx shearwaters and trans-continental songbird migrants, though there are few studies in the extant literature of compass calibration in birds moving ‘shorter’ distances (< 1,000km per day). In order to further investigate the flexibility of compass calibration, I therefore suggest an experimental investigation into the compass calibration of very short-distance avian navigators. Specifically, I suggest that investigating whether familiarity with local visual cues interacts with compass cue accuracy when determining the direction of information flow within compass calibration systems.

An ideal candidate for such a study would be homing pigeons, not only because of the well developed experimental paradigms within which they can be used, but also because familiarity with a given locale can be experimentally manipulated. Given the extremely short distances over which pigeons typically navigate (< 50km) we would expect shifts in magnetic declination to be extremely minimal, and hence we would predict that pigeons, as with the Manx shearwaters discussed in Chapter 4, would calibrate their sun compass to a magnetic compass if they had minimal access to visual cues. In contrast, if access to visual cues was allowed we might expect pigeons, as with bats (Holland et al., 2010), might calibrate instead calibrate their magnetic compass using a sun compass. This would be of interest not only because it could provide empirical evidence for magnetic compass orientation in pigeons, something which has previously been found to be highly equivocal, but would lend credence to the idea that compass calibration is a flexible system that reflects the specific ecology of the species in question. As such, I submit that investigations into the compass calibration of short-distance avian navigators might be of interest.

How widespread is avian magnetoreception?

Given the results presented in Chapter 4, and the above discussion, I suggest that it is unclear how widespread avian magneoreception is. I suggest that this could be the subject of further study, both when considering the ecological predictors of navigational mechanism and how basal the magnetic sense is within the avian phylogenetic tree. Recent studies into the mechanistic basis of the songbird magnetic sense suggest that 3 point mutations on a single protein (Cryptochrome 4a) predict much of a bird's magnetosensitivity (Xu et al., 2021), meaning that there are relatively few evolutionary steps between magnetoreception and non-magnetoreceptive individuals. As such, the ability of birds to sense the Earth's magnetic field could perhaps be lost to genetic drift or gained through natural selection.

De novo experimentation could likely prove too large an undertaking when tackling a question such as this, given the sheer number of species required. Instead, I propose that an alternative approach would be to utilise ringing data as described in Chapter 3. Using the ringing data derived from migratory birds from both all over the globe and across the avian phylogenetic tree, I propose that the likelihood of magnetoreceptive could be determined through comparison of where birds home to following long distance migration and where we would expect them to home to under a magnetic model of navigation. As such, I believe that testing the extent of avian magnetoreception is an attainable goal when using ringing data alongside data pertaining to magnetic secular variation.

8.3 Concluding remarks

Throughout this thesis I have sought to investigate both the mechanisms that allow birds to complete some of nature's most remarkable navigational feats, as well as the ontogeny of these mechanisms. To that end I suggest that the first migration of birds is likely to rely in part on genetically inherited material, with birds possibly following an inherited vector course. I suggest that this could be augmented early in development with learnt navigational abilities, such as the ability to compensate for drift. Such drift compensation could rely on optic flow cues, but in principle could function using some form of gradient map. If the latter was true, this mechanism could form a generalisable solution to multiple different navigational tasks, even allowing birds to correct their course following displacement (either artificially or via strong winds). Other studies have shown outbound migration to also utilise cultural information socially learnt from experienced conspecifics (e.g Mueller et al., 2013), though this is unlikely to be ubiquitous across avian taxa given the results presented in this thesis.

Unlike outbound migration, I suggest that return migration requires precise return to a specific site and, as such, the mechanisms that allow precise natal philopatry are unlikely to be entirely based on a clock and compass. I find evidence that both seabirds and songbirds might utilise learnt, magnetic information during natal homing, specifically using magnetic inclination to give an indication of latitude. I also find that, in songbirds, inclination appears to be used as a uni-coordinate 'stop sign' on a return migratory vector. Further, this mechanism might indeed make navigational sense, given it's limited exposure to between-year secular variation in the Earth's magnetic field. Additionally, given the results of Chapter 4, I suggest that the magnetic compass observed in songbirds may also underpin orientation decisions in seabirds, and may be used to calibrate a time-compensated sun compass to limit the effects of solar declination caused by day-to-day changes in the sun's arc through the sky.

More generally, I propose that there may be no generalisable solution to the problem of long-distance migration. In the introduction to this thesis I posited the idea of an 'ideal migratory bird', a bird which typifies the navigational capacity and development of all birds. In the introduction it was suggested that such a bird does not exist, and through my investigations over the last 4 years this has seemingly been borne out. I suggest that the mechanisms of navigation are shaped by both the ecology of the individual in question, which defines the navigational problem that need solving, alongside the evolutionary lineage from which the individual hails. As such, it is therefore essential that avian navigation is studied in as wide a number of ecological and phylogenetic contexts as possible.

Humans have been interested in animal navigation, and specifically avian navigation, since the beginning of recorded history. I suggest, however, that there is no better time to study birds. In this thesis I find that novel technologies (such as remote-download GPS and variable-current Helmholtz coils) have broadened the range of methods available to the ornithologist, particularly when considering the movements of wild birds *in situ*. However, it is perhaps in the recontextualisation of historic data within modern, computationally-intensive, non-parametric statistics and remotely-sensed environmental/physical data where the greatest analytical power is perhaps to be found. Such analyses have the capacity to answer some fundamental but unanswered questions in animal navigation, from it's sensory basis to it's cognitive underpinnings and evolutionary history. I hope, therefore, that such analyses become a mainstay of ornithology in years to come: it has never been more exciting a time to watch birds for a living.

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