# Mechanisms of long-distance navigation and the time-compensated sun compass in wild shearwaters




Patrick Lewin

Merton & St Anne's Colleges

University of Oxford

Thesis submitted for the degree of

*Doctor of Philosophy*

Trinity Term 2025



*"I'm like a bird, I'll only fly away [... ] I don't know where my home is."*

Nelly Furtado, *I'm Like a Bird* (2000)



*"They make the most ungodly din ever created by birds."*

G. V. T. Matthews, in response to Captain W. R. Colbeck, R.N.R. at a joint meeting of the Institute and the Royal Geographical Society held on 5th January 1951.

Artwork by Rita Freely

# Abstract

Decades of research have shown that birds attend to the motions of our planet and distant stars to navigate across the earth. Yet how such cues contribute to guiding their natural movements remains largely a mystery because the animal navigation literature has relied heavily on captive or incarcerated birds, motivated to orient either by displacement or migratory restlessness. In this thesis, I utilise the growing body of tracking data from the free-ranging movements of wild shearwaters to investigate the sensory and cognitive mechanisms of a wild avian navigator. I achieve this by leveraging errors inherent in the constraints of putative navigational mechanisms or induced by sensory manipulation. First, I exploit the highly conserved mechanisms of circadian entrainment to predict that Manx shearwaters (*Puffinus puffinus*) might experience jet-lag-like time shifts during rapid longitudinal flights, causing errors in use of a time-compensated sun compass. These errors reveal that shearwaters use the sun compass to home after their natural foraging trips, apparently as the primary compass cue when out of sight of land, and integrate information from land when coast-following, perhaps by visual pilotage. Further, capitalising on this interaction between use of the sun compass and coast-following, which can be detected without *a priori* knowledge of the shearwater's goal, I show that shearwaters use the sun compass while commuting towards foraging grounds. I build on these findings using an artificially induced clock-shift, and show that the timing of shearwaters' foraging movements is influenced by their endogenous circadian clocks. I next find that shearwaters do not appear to rely on geomagnetic cues to calibrate their time-compensated sun compass, nor indeed for any part of their homing navigation. The last empirical chapter of this thesis investigates the spatial representations which facilitate distance estimation in the migration of Balearic shearwaters (*Puffinus mauretanicus*), and the contribution of this spatial cognition to individual migratory flexibility and population range shifts under climate change. Finally, I consider surprising parallels to the navigation of homing pigeons (*Columba livia*) and the implications for the evolution of navigational mechanisms; the value of data on the free-ranging movements of wild birds for investigating navigation, especially beyond homing and migration; and the potential this provides for studying the behavioural ecology of navigational and chronobiological mechanisms.

# Acknowledgements

This DPhil was made possible by the Leverhulme Trust, with additional funding from Merton and St Anne's Colleges, Oxford. I also have to acknowledge the British Trust for Ornithology for facilitating shearwater research and for first opening my eyes to the joys of working with wild birds, over ten years ago. In addition, the Islands Conservation Advisory Committee, the Wildlife Trust of South and West Wales, Skokholm Bird Observatory and the Northern Ireland Environment Agency allowed me to undertake my fieldwork and welcomed me to their islands. The greatest thanks in this regard must go to Copeland Bird Observatory, particularly those who have kept me company (and reminded me of my social skills) during three summers in my favourite place on earth. Of course, I couldn't have reached the island without Philip McNamara, nor would I have received numerous strange but invaluable deliveries.

The most important thanks have to go to Tim Guilford and Ollie Padget, my supervisors. Ollie, I'll come back to you soon. Tim, I have to recognise that much of my approach to biology and certainly my fascination with the navigation of shearwaters comes from your influence. You fostered my love of behavioural ecology (even if, at the time, I didn't realise what that was) and I couldn't have hoped for a mentor more willing to sit and ponder utterly hopeless questions about animal behaviour.

My supervisors haven't been my only mentors. To Maria Abbott, thank you for the Encyclopaedia that fuelled my love of animals and kept me enthralled for years. To Roger Booth and Tony Galsworthy, my first scientific role models: the depth of your natural history knowledge and your patient mentorship will be the standard I always aspire to. Joe Wynn, my third supervisor, you're incredibly generous with your time and my most excitable scientific accomplice. My best ideas are yours. And Joe Morford, ever since I first arrived at Merton, you've been my most constant and least excitable scientific accomplice. You occasionally injected some much-needed realism into my wild ideas but your wisdom and encouragement have been invaluable. I look forward to many more moments of inspiration over a pint.

My mentors are joined by my fieldwork companions. Lewis, my PhD twin – I will always be grateful for the effort you put into my mad experiments, even at the most difficult times, and into top-notch spa nights. Paris, my tutor in the ways of Copeland and Swedish numeracy: you made my first fieldwork season not only less daunting but so much fun. And, of course, you introduced me to the hardest-working shearwaters (thanks, Scotty and Alfie). Ollie, thank you for exposing me to a baffling array of both very good and very bad music and, of course, Buffy. My tastes will never be the same again. Steph, BB, I can't think of anything better than tipexing moths and laughing at tea towels. Let's all go back to Copeland next year. Although none of it made it into my thesis, I spent parts of three summers at the

Wytham Field Station. Dave, Allex, Helen and Lucy, thank you for welcoming me into morning coffees and never failing to make me laugh.

Other members of OxNav have also been a big part of my life for the last four years. Sarah, you've been a stalwart and level-headed help at all times – it's a miracle we're not still chatting outside the Obs. Trina, you handed me my first ever manxie and taught me the right kind of weird required for island life. Lucinda, my one and only housemate! Thanks for looking out for me and Olivia. Jonathan, my LaMB partner to the very end: good luck for the last push, your thesis will be incredible.

I'd like to extend thanks to Michael Flatley, not only for your artistry as a filmmaker and actor, but for bringing me the friends who've deepened the madness of the last years. Tom, thank you for some great acting and terrible slam jam poetry, Bil for bringing whimsy to my life and bringing so much joy to Olivia's while I was away, Daisy for introducing me to the wonders of New Zealand, Nat for hysteria worthy of extensive sea air, Alice for tempering Olivia's aversion to biology pub trips, and Will for many a tea break, considered discussion of experimental design, and truly terrible film.

I do have to have some people in my life capable of keeping me grounded, so thank you to Ollie and Lucy for enduring friendship and much-needed breaks in Wales. During the last couple of months, ringing has been my relaxation – thank you to the chiffchaffs of Burgess Field, Alex, Thomas and Alice for great CORG times.

Family has always been my chief source of support and I'm lucky now to have two. Thank you, Julie, Gower and William for welcoming me into yours and for accepting the Birdman, despite his strange obsession and dubious job prospects. Mark, you may not always have understood my hobbies but the genuine interest you've developed for my work means an awful lot. Mum and Dad, you are the longest-suffering victims of my obsession with birds and my longest-standing supporters. Encouraging me to pursue my interests can't have been easy when it involved crack-of-dawn lifts to QMR or 'holidays' timetabled to the minute, but you pushed me not to shy away from opportunities and find the work that makes me happy. To Teddie, a constant companion in my outdoor adventures: miss you.

Olivia, you deserve more than a paragraph but I promised myself I'd stick to two pages. Sorry. More than anyone, you've listened to me ramble on about navigation and get excited about utterly incomprehensible ideas. I promise I'll remember to explain what a beeline is next time. You've always supported my work, especially in the last months, even if in-person contributions to data collection were certainly out of the question. But more importantly, you've brought me the joy that has been the hallmark of the last four years. I'm not sure I would even have started this DPhil, let alone finished it, without you. Thank you for putting up with my long absences (not without complaint) and making me smile every day, whether you were 250 miles away or right by my side. I love you.

# Declaration and Author Contributions

All the work presented in this thesis is primarily my own – I led the conception and intellectual development of every chapter, conducted the analysis, interpreted the results and wrote the manuscripts. Thirty-seven other authors contributed to at least one chapter.

Tim Guilford and Oliver Padget contributed to the development of ideas throughout this thesis, guided the analysis and provided feedback on the written manuscripts. They also managed and took part in data collection for Chapters 2, 3 and 6.

Joe Wynn contributed to Chapters 2, 3, 5 and 6. In Chapter 6, his contributions were equal to those of my own. Other substantial contributions to the ideas in this thesis, particularly Chapters 2, 3, 5 and 6, were made by Lewis Lancaster-Reeves and Joe Morford.

A number of authors managed collection of the data used in Chapter 6: Maite Louzao, José Manuel Arcos, Miguel McMinn, David García, Henri Weimerskirch, Karine Delord and Thierry Micol.

Other authors contributed to data collection or processing in one or more chapters: Katrina Siddiqi-Davies, Sarah Bond, Ben Dean, Annette L. Fayet, Robin Freeman, Natasha Gillies, Stephanie M. Harris, Paris Jaggers, Holly Kirk, Lou Maurice, Akiko Shoji, Martyna Syposz, Melany de Boer, Patricia Pereira Serafini, Gwennan Hughes, Rhiannon E. Austin, Josephine Blagrove, Gemma Carrasco, Isobel Hawkins, Christian Kirk, Greg Morgan, Jason Moss, Elisa Miquel Riera, Ana Rodriguez, and Russell B. Wynn. Many of these authors also provided feedback on written drafts of the relevant chapters.

The writing and ideas presented in the General Introduction and General Discussion are my own. Consequently, in these chapters I have used singular pronouns, whereas in other chapters, I have used plural pronouns. The authors who contributed to each chapter are listed on the title page.

# Contents

**1** General Introduction.....1

**2** Jet-lagged birds: longitudinal flights cause clock-shift and sun compass error.....59

**3** Sun compass orientation during foraging commutes in shearwaters.....91

**4** Endogenous timing of foraging movements in free-living shearwaters.....115

**5** Free ranging shearwaters do not rely on magnetic maps or compasses.....143

**6** Climate change drives migratory range shift via individual plasticity.....173

**7** General Discussion.....209

# 1

# General Introduction

## Contents


**1.1** Introduction ..... 2

**1.2** An overview of animal navigation ..... 5

**1.2.1** Maps unlike our own ..... 9

**1.2.2** Compasses much like our own ..... 14

**1.2.3** Clocks inside us all ..... 19

**1.2.4** Pigeons – the established model of avian homing ..... 20

**1.3** General methods ..... 23

**1.3.1** Shearwaters as a model of avian navigation in the wild ..... 23

**1.3.2** Global Positioning System and light-level geolocation tracking ..... 26

**1.3.1** Methods of navigational inference ..... 28

**1.4** The aims of this thesis ..... 30


*"Every living thing has the same instinct: to come back home."*

The Doctor, *Doctor Who* (2018)

## 1.1 Introduction

In the 18th Century, European states faced a growing problem. The exigencies of global empire required that, for the first time, people be able to traverse the entire globe efficiently and en masse. Despite two thousand years of astronomical and navigational study, no one had yet decoded a practical means by which the earth or the sky might reveal one's longitudinal position while at sea (Major, 2014). This left mariners dangerously exposed to navigational error. Spurred on by the disastrous fate of Sir Cloudesley Shovell and two thousand sailors on the Western Rocks of Scilly in 1707, the British government, among others, launched a massive effort to solve the 'longitude problem' (Baker, 2025). For a brief time, the study of navigation became the chief concern and most hotly contested race in Western science.

One candidate solution (though admittedly not the one favoured by the scientific establishment of the time) was intricately tied to timekeeping. Due to the earth's eastwards rotation, solar noon occurs 4 minutes earlier for every degree of eastward longitude. Thus, if a sailor could use a clock synchronised to a reference location, the difference in time between their locally observed solar zenith and noon on the clock would reveal the difference in longitude. This was the concept of the marine chronometer: a clock capable of keeping time even after months at sea (Gould, 1921; Pogo, 1935). In 1759, this approach finally brought a tractable solution to the longitude problem in the form of John Harrison's Marine Timekeeper H4 (**Fig. 1.1**). This machine (his imaginatively named fourth prototype) was small enough to fit inside a desk drawer but could keep time through a violent Atlantic storm, the sweltering doldrums or a bitter Antarctic passage (Betts, 1993). H4 and its three predecessors can still be seen amidst iconic historic artefacts at the Royal Observatory in Greenwich, where they undertook their first testing almost three centuries ago.




Fig. 1.1. John Harrison's prototype H4 Marine Timekeeper, made in 1759. It was this watch and its subsequent copies which solved the longitude problem and transformed global navigation. Image reproduced without alteration courtesy of © National Maritime Museum, Greenwich, London. All rights reserved. CC-BY-NC-ND.

The beauty of these objects and other navigational instruments is not just in their physical manifestations but in their intricate tuning to the motions of planets and stars. Mariners used clocks to track the spinning of the earth on its axis and determine longitude (Gould, 1921), sextants to measure the altitude of the solar zenith and thus calculate their latitude (May, 1973), and, in antiquity, the azimuth of the sun and stars to find direction (Lewis et al., 1974; Sølver, 1953; see Fig. 1.2). Yet the greatest navigational instruments are found not in the hands of mariners but the in the bodies and minds of animals. Through relentless natural selection, animals evolved to solve these astronomical and navigational problems hundreds of millions of years ago. Indeed, the tuning of their sensory, cognitive and behavioural adaptations, not only to their immediate environment but to the motion of celestial bodies billions of years old and trillions of miles away, is arguably even more exquisite than that of H4. Inside every animal are endogenous clocks ticking away each day and each year, and an urge to read from the heavens the direction they should travel.

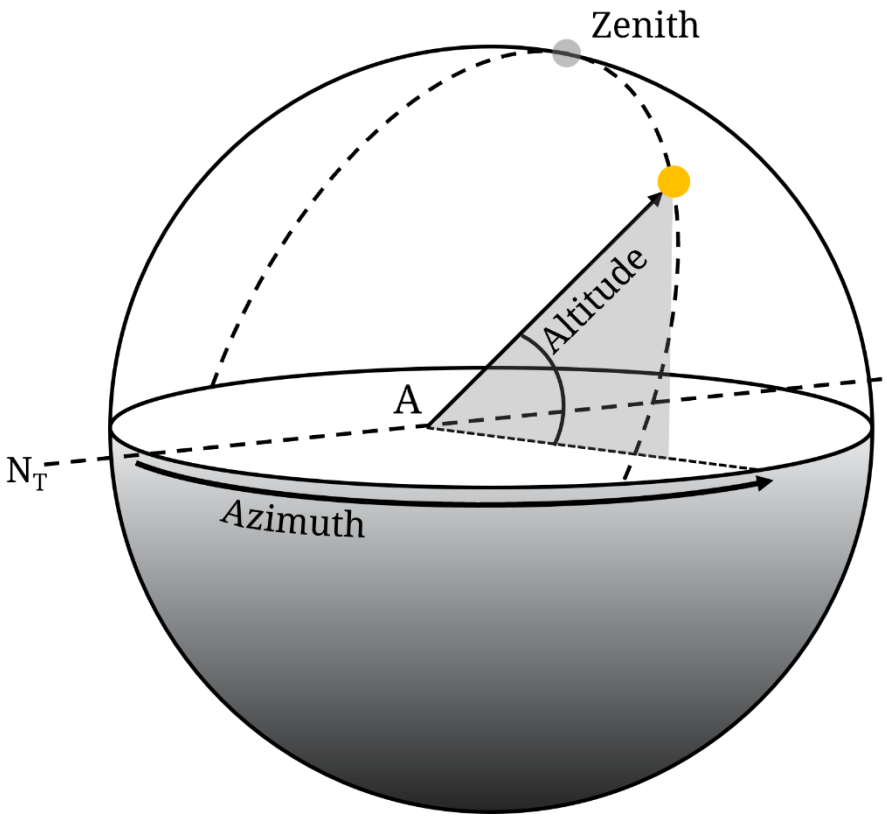



**Fig. 1.2. Parameters of the solar arc used for position- or direction-finding**, as viewed from position A, in the Northern Hemisphere. The vertical angle of the sun from the horizon is its **altitude**, which peaks each day at the **zenith**. The height of the zenith varies with season and latitude. The horizontal angle of the sun from true north ($N_T$) is its **azimuth**.

## 1.2 An overview of animal navigation

As any school student who has come across the acronym MRS GREN knows, movement is a hallmark of animal life. In most cases, however, movement alone is not sufficient. To be adaptive, movement must usually be organised towards a goal (Nathan et al., 2008; Wiener et al., 2011). This can be as simple and immediate as moving towards a directly perceptible food resource but also includes movement over thousands of kilometres towards an unfamiliar migratory destination (Nathan et al., 2008). The mechanisms by which animals direct their movement constitutes the central theme of animal navigation, and the manner in which space and direction are represented in the mind constitutes spatial cognition. This thesis will touch on both sensory and cognitive mechanisms of orientation, though is focused primarily on the former.

Animal navigation can be divided into a number of broad mechanistic categories. This categorisation comes with the substantial caveat that few, if any, real-world examples will fit neatly into a single category, and some navigational mechanisms blur the lines between them. A second but equally important caveat is that these mechanisms go by many names, and the purpose of this list is partly to make clear my own use of these terms.

Perhaps the simplest strategy is beaconing. Beaconing involves orienting to cues which emanate directly from the goal, e.g. use of olfactory plumes to travel towards a food resource using upwind surge (Svensson et al., 2014). Trail-following is somewhat similar, although in this case, the cues do not emanate directly from the goal but instead form a continuous path between the animal's current location and its goal. This mechanism is prominent in eusocial ants, where nestmates follow each other's pheromone trails to and from food resources (MacGregor & Thorpe, 1948) but might also have parallels in the following of linear visual features by homing pigeons (Lau et al., 2006). Pilotage involves a similar trail but here made up of a series of cues which, if beaconed towards in order, lead an animal to its goal. This mechanism is seen in the movements of individual ants along idiosyncratic foraging routes using memorised snapshots of the visual panorama to recapitulate an idiosyncratic route (Collett et al., 1992; Durier et al., 2003; Graham et al., 2003; Philippides et al., 2011). Trail-following and pilotage are somewhat more complex than beaconing to the goal in that the animal must form an association between the goal and not just cues which directly coincide with it but also intervening cues which are separated in time and space.

The strategies above are, in effect, blind to the direction and distance between locations – only the order in which they are encountered relative to the goal is important. This is not the case for vector navigation. Under this mechanism, animals travel in a given direction (memorised or innately programmed) for a given time or over a given distance (Åkesson et al., 2014; Bingman & Cheng, 2005).

In vector navigation, the animal's starting position is not estimated from local environmental cues but is implicit in the memorised or inherited vector. As a result, this mechanism allows animals to travel between relatively broad, fixed areas but has little flexibility and no capacity to correct for error. For instance, an animal could simply travel along a known vector to a foraging area before reversing that vector to return to its breeding location. Yet if that same animal were disturbed from its commute, continuing to rely on its vector orientation from the new starting location would fail to bring it to its goal (e.g. Müller & Wehner, 1988; Perdeck, 1958). Some of the most prominent examples of vector navigation are the migrations of naïve insects (Chapman et al., 2008; Chapman et al., 2015; Hawkes et al., 2022; Reppert & de Roode, 2018; Warrant et al., 2016) and juvenile passerine birds, which reach their unfamiliar migratory destinations without experienced conspecifics by travelling in an innate preferred compass direction for a certain amount of time (Berthold, 1984, 1990; Helbig, 1991). This is termed the 'clock-and-compass' model of navigation (Berthold, 1996).

One special case of vector navigation is called path integration. It is central to the well-studied navigation of Hymenopteran insects (Wehner & Srinivasan, 2003), though probably plays a role in a wide diversity of animals (Mittelstaedt & Mittelstaedt, 1980; Seyfarth & Barth, 1972; Sibeaux et al., 2024; von Saint Paul, 1981; Zeil, 1998) and may be a fundamental mechanism underpinning map learning (Collett & Collett, 2000; Morford, Wynn, et al., 2025; Müller & Wehner, 2010; Savelli & Knierim, 2019; Wang, 2016). Path integration requires that animals keep track of their own movements whilst travelling away from a central location. They may do this either through step-counting during transits and proprioception during turns (an idiothetic mechanism), or by monitoring their movements relative to environmental cues, e.g. via optic flow and compass cues (an allothetic strategy; Cheung & Vickerstaff, 2010; Heinze et al., 2018). The end result is that the animal can continuously sum the vectors of its movement away from the central location

and, at any time, reverse the resulting vector to return there (Wehner & Srinivasan, 2003).

The final major category is map-and-compass navigation. Although this is what might be considered navigation proper in human contexts, it was only formalised as an explanation for animal orientation by Gustav Kramer in the 1950s (Kramer, 1953). There are two steps to this process: first, an animal must determine its position relative to its goal and thus the direction towards the goal. Second, it must use a compass (or directional cue in the same frame of reference as the map) to align its heading with the goal direction and travel towards it. This has the marked advantage that it allows animals to orient towards precise goals by compensating for error; the animal must simply re-estimate its position every so often and it will eventually reach the goal. Although map-and-compass navigation is generally used to refer to large-scale, global orientation, it has mechanistic parallels in the well-studied small-scale 'cognitive maps' of rodents (O'Keefe & Nadel, 1978; Tolman, 1948), as noted by Morford, Wynn, et al. (2025) and discussed in more detail in section 1.2.1.

The most extraordinary form of map-and-compass navigation is so-called true navigation (Griffin, 1952; Keeton, 1974): the ability to orient towards a goal which is beyond direct sensory contact, from a novel location and without information from the outward journey (Holland, 2014). It is this ability for which the homing pigeon became a model species and which spurred the early navigational studies of Manx shearwaters by Ronald Lockley and Geoffrey Matthews (Lack & Lockley, 1938; Matthews, 1953a, 1964). Yet true navigation is not limited to these iconic navigators; a surprising range of animals seem capable of this feat (Boles & Lohmann, 2003; Lohmann et al., 2008; Matthews, 1951b; Perdeck, 1958; Tsoar et al., 2011; Wikelski et al., 2015; Willemoes et al., 2015). To explain this ability requires a special form of map – an extrapolated grid map – which will be

addressed in the following section. In every other respect, it follows the basic two-step map-and-compass paradigm.

### 1.2.1 Maps unlike our own

When we think of maps, we generally think of topographic representations with prominent visual landmarks arranged accurately in two-dimensional space. Many animals appear to possess similar maps by which they can recognise spatially separated locations and execute the correct direction of travel between them. These maps can be very simple with few locations and fixed orientation responses between them (e.g. Lohmann et al., 2001) but many animals travel between numerous locations, even taking novel shortcuts between familiar locations. These complex movements imply a dense map in which the geometric relations of all locations are encoded (Morford, Wynn, et al., 2025) and are the hallmark of the cognitive map (O'Keefe & Nadel, 1978; Tolman, 1948). Such maps have been intensively studied using maze tasks in rodents and their neurological basis is now well-understood (Hafting et al., 2005; McNaughton et al., 2006; O'Keefe & Nadel, 1978; Solstad et al., 2008; Taube et al., 1990; Whittington et al., 2022). Similar neural representations are found in birds (Hough & Bingman, 2004; Payne et al., 2021), with some parallels in insects (Basu & Nagel, 2024), and likely underlie the efficient and flexible routes taken by animals within complex but familiar resource landscapes (Lihoreau et al., 2010; Tello-Ramos et al., 2015; Thomson et al., 1997),

Although cognitive maps are generally studied on a very small spatial scale, they may underpin navigation over wider areas (Harten et al., 2020; Toledo et al., 2020). From the perspective of spatial cognition, small-scale cognitive maps might, in fact, be indistinguishable from map-and-compass navigation (Morford, Wynn, et al., 2025). The only clear difference is that small scale navigation at least sometimes relies on directional information from local cues, rather than global compass cues. Given that over such small scales even relatively local cues can provide apparently global direction, this affects only the directional frame of reference within which

the map is arranged and perhaps the sensory mechanisms involved in direction-finding. Indeed, similar neural representations of head direction to those used in small-scale navigation seem involved in global compass senses in birds (Takahashi et al., 2022) and insects (Dreyer et al., 2025), whilst many animals appear to rely on compass cues even at very small scales, when more local directional information is available (Chappell & Guilford, 1995; Duff et al., 1998; Kelly et al., 2019; Wiltschko & Balda, 1989; Zimmerman et al., 2009). Whatever the spatial scale in question, the central thread of these maps is that both the cues which define known locations and the spatial relationships between them must be learned through experience. In effect, they are 'familiar area' maps (Baker, 1982). This means that, unlike vector navigation, animals can correct their orientation after displacement but only as long as they remain within their familiar area. This limitation only to the area of prior experience means that these maps cannot explain true navigation.

The cues which might form the basis of familiar area maps are varied and even individual animals may use multiple sensory modalities within the same spatial representation. Visual cues are the most obvious, at least from a human perspective, and are used by a wide array of animals. Ants might learn to associate homeward vectors with familiar visual snapshots (Collett, 2010; Collett & Collett, 2009; Collett et al., 1998; Menzel et al., 1998; Müller & Wehner, 2010), homing pigeons visually recognise familiar release sites (Biro et al., 2003; Biro et al., 2002; Braithwaite, 1993; Braithwaite & Guilford, 1991) and rodents associate visual stimuli with geometry in maze tasks (Benhamou & Poucet, 1998; Greene & Cook, 1997). However, very unlike most human maps, animal familiar area maps might also be based on local patterns of olfactants (e.g. Fischler-Ruiz et al., 2021), auditory cues (Rossier et al., 2000; Werkhoven et al., 2014) or even magnetoreception (Lohmann et al., 2004; although whether any examples of magnetic maps represent a strictly familiar area map is unclear).

Although these maps are often represented as encoding discrete locations, and that may well be the case in many examples, maps might also allow for continuous location-finding by animals (Morford, Wynn, et al., 2025). This relies on the existence of non-parallel gradients in two or more environmental cues forming a grid in which each position is associated with a unique combination of cue values. This is termed a grid map. Atmospheric olfactants might vary in concentration or in ratio to other olfactants continuously and predictably through space (Wallraff, 2013; Zannoni et al., 2020), and various parameters of the earth's magnetic field vary in a similar manner (Lohmann et al., 2022). These parameters are total intensity, which is strongest near the poles and weakest at the magnetic equator, the field's inclination (vertical) angle from the earth's surface, which is vertical at the poles and gradually rotates to horizontal at the equator, and the declination (horizontal) angle between geographic north and geomagnetic north, which varies both longitudinally and latitudinally over different parts of the earth (Fig. 1.3). Various animals are known to be able to detect one or more of these cues (Boles & Lohmann, 2003; Chernetsov et al., 2017; Goforth et al., 2025; Keller et al., 2021; Lohmann & Catherine, 1993; Newton & Kajiura, 2020a, 2020b; Phillips, 1986; Phillips & Borland, 1992; Putman et al., 2013; Putman et al., 2020; Wiltschko & Wiltschko, 1972). Visual cues less obviously form gradients but resection, triangulation or trilateration (Johnson, 1970; Morford, Wynn, et al., 2025) from distant landmarks can provide continuous positional information over a surprisingly wide area and are thought to provide the sensory basis for the cognitive map of bats (Harten et al., 2020).

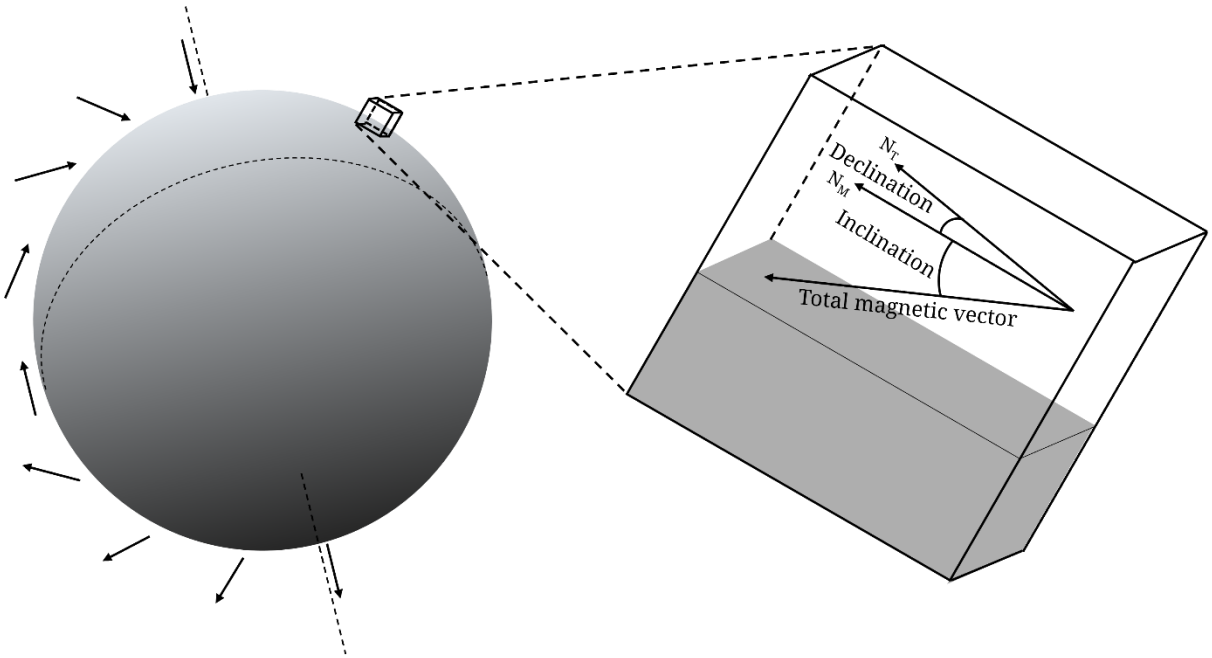



**Fig. 1.3. Parameters of the geomagnetic field.** At a given location, the total magnetic field vector is composed of a magnitude (geomagnetic **intensity**) and direction (**polarity**). The vertical angle from the earth's surface is geomagnetic **inclination**, which varies latitudinally in each hemisphere. The horizontal angle between magnetic ($N_M$) and true north ($N_T$) is the **declination** angle.

These continuous maps are the first step in explaining true navigation. In the mid-20th Century, mounting evidence that animals could compensate for displacement, not only within the familiar area but beyond it, generated contentious debate on the sensory basis of this ability (see the rather barbed comments of Matthews, 1951b, for example). Some sceptics, 'killjoys' in today's terminology (Shettleworth, 2010), posited that animals effectively path integrated their movements even when artificially displaced beyond even their entire species range (Barlow, 1964). A series of increasingly extreme experiments involving spinning pigeons during transport (Matthews, 1951a), anaesthesia (Kluijver, 1935; Walcott & Schmidt-Koenig, 1973) and section of the semicircular canal (Wallraff, 1965) provide evidence to the contrary. Less cynical authors realised that the explanation for true navigation must come in the form of cues which vary predictably through space across vast areas, well beyond any individual animal's familiar area.

Whilst Geoffrey Matthews, an early pioneer of navigation research with homing pigeons and Manx shearwaters, drew alluring comparisons between the position finding of mariners and the putative map mechanisms of birds, the sensory basis of true navigation in animals is, in fact, rather different from our own. Matthews' sun arc hypothesis (Matthews, 1953b) and the component double-clock mechanism (reliant on Matthews' 'physiological chronometer;' Kishkinev et al., 2010; Matthews, 1951b) are now numbered among other cues which have been considered and discarded (Ising, 1946; Wilkinson, 1949; Yeagley, 1951; Yeagley & Whitmore, 1947), or for which there remains little empirical evidence (Blaser et al., 2014; Dornfeldt, 1991; Hagstrum, 2000). Instead, evidence points to the same cues which might provide continuous familiar area maps, although with evidence for use of triangulation from distal landmarks in only one case (Tsoar et al., 2011). The proposed mechanism is that animals learn the predictable pattern of variation in these gradient cues within their familiar area but can extrapolate the patterns well beyond these limits. Effectively, if we consider the animals as completing some trigonometry to convert cue values in each gradient into a homeward vector, the same trigonometric function can be applied wherever the pattern of intersecting gradients remains stable. Such extrapolation need not be based on any complex cognition (Guilford & Burt de Perera, 2017; Morford, Lewin, et al., 2025). In these cases, animals are said to possess an extrapolated grid map.

Before we leave animal maps behind, it is necessary to consider a final interesting mechanism of location-finding which defies easy categorisation. There is a small but growing body of evidence that some animals use gradient cues not to form a continuous and extrapolated map but to identify discrete locations in continuous space, apparently without facilitating position-finding beyond these limited locations. Birds, sea turtles and salmon imprint on a geomagnetic signature of their natal location and use this signature as a 'stop sign' when recruiting to a breeding site (Brothers & Lohmann, 2015, 2018; Putman et al., 2013; Wynn et al., 2022; Wynn

et al., 2020). Salmon and turtles may use the imprinted signature as a goal within an integrated map (Lohmann et al., 2004; Putman et al., 2020) but this is not thought to the case in juvenile birds. However, some animals inherit responses to these discrete magnetic signatures genetically. Sea turtles, fish and birds respond appropriately to these location-specific signatures by changing their travel direction (Beck, 1984; Naisbett-Jones et al., 2017; Putman et al., 2014; Putman et al., 2020; Wiltschko & Wiltschko, 1992) or altering key physiological processes (Boström et al., 2010; Bulte et al., 2017; Fransson et al., 2001; Kullberg et al., 2003) during migration, even though they have never been to these places before. In effect, they have an inherited map, though it appears not to be continuous or extrapolated (Fuxjager et al., 2011; Henshaw et al., 2010).

### 1.2.2 Compasses much like our own

After an animal has determined the direction to its goal within the frame of reference of its map, it requires some mechanism by which to translate its heading into that same frame of reference. In small-scale navigation, the map may be arranged relative to some local directional cue, which acts as a heading indicator – cues which allow an animal to maintain a constant heading direction over a short time or distance, without giving global directional information (Guilford & Taylor, 2014). For global orientation, animals must rely on cues with origins sufficiently distant that to a reasonable approximation, the animal's heading relative to the origin changes only with rotational movement, not with translational movement. These are compass cues and provide directional information within a global frame of reference.

Animals are known to use three primary sources of compass information. The first and most familiar is the geomagnetic compass. A dynamo effect in the earth's molten core generates an electromagnetic field with an axis roughly (though variably) corresponding to the axis of rotation. Thus, sensitivity to the geomagnetic

field yields information on the direction of the magnetic poles, which lie close to the geographic poles.

Humans have used naturally occurring magnetite (lodestones) for technological magnetic compasses since at least 11th Century China (Shu-hua, 1954) but it was not until the 1960s that biological sensitivity to the earth's magnetic field was demonstrated in bacteria (Bellini, 1963). Later in the decade, studies of the migratory orientation of European robins (*Erithacus rubecula*) showed that they too were sensitive to the earth's magnetic field (Merkel & Wiltschko, 1965). The birds used this information as a compass sense, directing their migratory orientation relative to the geomagnetic vector. Geomagnetic compasses have since been demonstrated in insects, amphibians, fish, reptiles and non-passerine birds (Dreyer et al., 2018; Fleischmann et al., 2018; Grob et al., 2024; Guerra et al., 2014; Lohmann & Catherine, 1993; Phillips, 1986; Phillips & Borland, 1992; Zimmerman et al., 2009).

By the use of Helmholtz coils to flip the vertical and horizontal components of an artificial magnetic field independently, robins were shown to possess a compass sensitive only to the magnetic field's inclination angle, not its polarity (Wiltschko & Wiltschko, 1972). That is, they can detect the direction of the nearest pole but cannot distinguish the north pole from the south pole, thus necessitating a switch in orientation response for trans-equatorial migrants (Wiltschko & Wiltschko, 1992). The sensory basis of the avian inclination compass has been a source of considerable debate (Hore & Mouritsen, 2016; Mora et al., 2004; Nimpf et al., 2019; Nordmann et al., 2017; Ritz et al., 2000; Treiber et al., 2012; Walcott et al., 1979; Wiltschko & Wiltschko, 2013; Wiltschko & Wiltschko, 2019).

Unlike birds, other animals have been shown to possess a polarity compass (Fleischmann et al., 2018; Phillips, 1986), seemingly based on biogenic magnetite receptors in at least some taxa (Brassart et al., 1999; Diebel et al., 2000; Naisbett-Jones et al., 2020). Some species even possess two magnetoreceptors – one sensitive

to polarity and intensity, and the other sensitive to inclination (Goforth et al., 2025; Phillips, 1986). Though discovered late both by human navigators and human students of animal navigation, the use of the earth's magnetic field to orient is widespread and has become one of the most active areas of animal navigation research.

The remaining compass cues pertain to the closely linked celestial compasses. Due to the rotation of the earth on its axis, celestial bodies appear to move in arcs across the sky. These arcs are centred on two diametric fixed points in the celestial sphere corresponding to the axis of the earth's rotation; one lies directly above the North Pole and the other directly above the South Pole. Only one of these points is visible in each hemisphere due to the earth's curvature but individuals which can detect the horizontal direction of one of these points (or another point at a known azimuth offset, as achieved by Polynesian stellar navigators; Lewis et al., 1974) can orient relative to a north-south axis. However, this is not necessarily straight forward.

The starry sky is crowded and the ease of extracting directional information depends on where one looks. Dung beetles have been shown to use the stars, especially the bright line of the Milky Way, to orient but they do so in arbitrary directions and for short periods (Dacke et al., 2013), effectively using the stars as a heading indicator, rather than a true compass. Outside human navigators, only Bogong moths (*Agrotis infusa*) and night-migratory passerine birds have been shown to use the stars as a compass (Dreyer et al., 2025; Emlen, 1967a, 1967b, 1975). In the absence of the geomagnetic field, Bogong moths rely on an accurate arrangement of stars in the night sky to orient in a seasonally appropriate migratory direction, via directionally sensitive visual neurons (Dreyer et al., 2025). However, the exact manner in which these moths extract directional information from the pattern of stars is unclear.

In contrast, the mechanism of stellar orientation and its ontogeny in birds has been studied since the mid-20th Century. Stars close to the celestial poles, those fixed points, remain relatively static over the night. In the northern hemisphere, the North Star lies almost directly at the centre of rotation, whilst in the southern hemisphere, the Southern Cross lies nearby. To extract directional information from other stars would require a mechanism of tracking their arc over time. In contrast, direction can be extracted instantaneously from constellations near the centre of rotation. In a remarkable series of experiments using nestling indigo buntings (*Passerina cyanea*) raised under an artificial night sky, Emlen showed that these birds use the pattern of rotation to find the centre and learn to recognise the North Star and nearby constellations. Subsequently, when orienting in cages during first migration, they disregarded the pattern of rotation, relying only on the learned constellations. Indeed, if the artificial sky was made to rotate around another star during the imprinting period, the birds subsequently oriented as if that star pointed north (Emlen, 1975).

The sun compass, by contrast, is very much dependent on timekeeping. During the day there are no fixed markers near the centre of rotation. Instead, the sun is the only salient cue as it traces its arc across the sky from east to west, via south at midday in the northern hemisphere, and north at midday in the southern hemisphere. As a result, any animal using solar azimuth as a compass outside of a limited and fixed time of day, must be able to anticipate these changes, and update their expectations over the seasons or when moving across latitudes (Schmidt-Koenig, 1990). The mechanisms by which this time-compensation is possible will be explained in the next section. Despite its complexity, use of the sun as a compass is remarkably widespread in animals, making it one of the most ubiquitous of all known navigational cues (Guilford & Taylor, 2014).

Orientation by the sun was demonstrated in starlings (*Sturnus vulgaris*) by the use of mirrors to change the apparent direction of the sun within an orientation cage

(Kramer, 1950) and the time-compensation programme necessary for use of the sun as a true compass was revealed shortly after. Using artificial light-dark cycles, Hoffmann (1954) successfully fast-shifted starlings' internal clocks by six hours, causing a corresponding shift in the birds' orientation, as if they expected the sun to be six hours later in its arc. Since these first observations, use of a time-compensated sun compass has been demonstrated in crustaceans, insects, fish, amphibians, reptiles, mammals and other birds (Adler & Phillips, 1985; DeRosa & Taylor, 1978; Duff et al., 1998; Emlen & Penney, 1964; Fluharty et al., 1976; Graham et al., 1996; Haigh, 1979; Kelly et al., 2019; Landreth & Ferguson, 1968; Mouritsen et al., 2013; Pardi & Grassi, 1955; Penney & Emlen, 1967; Perez et al., 1997; Schmidt-Koenig, 1958; Ugolini et al., 1999; Wiltschko & Balda, 1989; Zimmerman et al., 2009), including via use of polarisation cues in some taxa (Muheim, 2011; Wehner, 1984). In fact, this cue is so apparently universal that some animals seem to rely on sun compass orientation even over very short distances when numerous time-independent cues are available (Chappell & Guilford, 1995; DeRosa & Taylor, 1978; Duff et al., 1998; Fluharty et al., 1976; Kelly et al., 2019; Pardi & Grassi, 1955; Ugolini et al., 1999; Wiltschko & Balda, 1989; Zimmerman et al., 2009) or when they have direct sensory contact with their goal (Armstrong et al., 2013; Graue, 1963). There is something remarkably pervasive about the time-compensated sun compass in the movement of diurnal animals, despite its intricacies.

Many animals are known to use more than one compass cue. Some advantages of compass redundancy are intuitively clear; the sun is not visible at night but the stars are, and when clouds obscure the sky, the geomagnetic field remains available. However, use of both celestial and geomagnetic compasses potentially creates as many issues as it solves. The geomagnetic compass allows for orientation within the geomagnetic reference frame, whereas celestial compass cues form a geographic reference frame. Animals using only celestial or magnetic compasses could simply organise their movements entirely within one reference frame but

any animal switching between celestial and magnetic compasses will take an inefficient path, especially if they move near the poles, where the discrepancies are largest. Some passerine birds (and perhaps Manx shearwaters; Wynn et al., 2021) are able to account for these discrepancies by calibrating one compass against the other, using the correspondence between solar azimuth and geomagnetic north at dawn or dusk to bring both compasses into a unified reference frame (Able, 1993; Muheim et al., 2006; Sjöberg & Muheim, 2016). This unified reference frame is a reasonable approximation only within a small area, breaking down as the declination between magnetic and geographic north varies through space. As a result, these birds likely recalibrate their compasses each day during migration (Cochran et al., 2004). Comparison of celestial and geomagnetic compass cues is also important during ontogeny but in all forms of compass calibration the hierarchy of different cues is unclear (Muheim et al., 2006; Pakhomov & Chernetsov, 2020). Only in ants is the ontogeny of redundant compass systems relatively well-understood. During initial learning walks outside the nest, naïve workers of *Cataglyphis fortis* use a geomagnetic compass to learn the seasonal solar ephemeris (Fleischmann et al., 2018; Grob et al., 2017). Subsequently, they rely entirely on a solar azimuth compass to execute their path integration (Wehner & Srinivasan, 2003).

### 1.2.3 Clocks inside us all

As noted above, use of the sun as a reliable compass cue across the day requires accurate time-compensation. The endogenous origins of organisms' circadian rhythms were confirmed by the continued physiological and behavioural cycles of plants and animals held in sealed laboratories – or even space (Sulzman et al., 1984) – under constant conditions (de Mairan, 1729). Hoffman's early experiments on solar orientation in starlings revealed an adaptive, flexible clock entrained on the light-dark cycle (Hoffmann, 1954). In effect, the clock is synchronised to the very environmental cycle – the rotation of the earth – that it has evolved to predict. Far

from being redundant, though, the utility of the clock lies in organising the timing of behaviour even when environmental time cues are hard to come by or might be ambiguous (Helm et al., 2017). The clock, therefore, lies at the heart of temporal organisation of a vast array of physiological pathways and behavioural outputs (Mistlberger & Rusak, 2021). Environmental cues indicating the time of day which are used to entrain or reset the endogenous circadian clock are termed *zeitgebers* (from German, meaning 'time-givers;' Aschoff, 1951, 1954). Whilst some animals are able to use accessory zeitgebers such as temperature or social cues (Chen et al., 2015; Fuchikawa et al., 2016), dawn and dusk almost always dominate entrainment (Hirschie Johnson et al., 2003). Though animals might reasonably be expected to use solar elevation to interpret the geographic direction of solar azimuth, this appears not to be the case, at least in birds (Schmidt-Koenig, 1990). Instead, animals are entirely reliant on their endogenous clocks for time-compensated use of the sun compass. As a result, Hoffman's approach – shifting the endogenous clock to generate predictable orientation errors – remains the key method in detecting and investigating use of the sun compass.

### 1.2.4 Pigeons – the established model of avian homing

So far, I have tried to provide a comprehensive, if necessarily rather shallow summary of the academic understanding of animal navigation. Now, I will turn towards my study taxon, by way of the homing pigeon. There are two major paradigms in avian navigation research: the orientation of migratory passerines held captive in Emlen funnels during periods of migratory restlessness (*zugunruhe*), and the homing navigation of birds artificially displaced by translocation. Although these paradigms are sometimes blended, for instance in the simulated magnetic displacements used to reveal the extrapolated magnetic maps of adult reed warblers (*Acrocephalus scirpaceus*; Chernetsov et al., 2017; Kishkinev et al., 2015; Kishkinev et al., 2021), they have remained largely separate and emphasise different navigational mechanisms. Most passerines are night migratory whereas

homing pigeons, the birds most commonly used in displacement experiments, navigate back to their home lofts during daylight. Manx shearwaters, which form the main focus of this thesis, face similar navigational challenges. They breed on coastal islands but forage far out at sea, sometimes hundreds or even thousands of kilometres away (Dean et al., 2015; Padget et al., 2019). After foraging, they navigate during daylight back to their colonies to resume incubation of their egg or feed their chick. Consequently, homing pigeons appear likely to provide the most relevant model for shearwater navigation.

In contrast to the focus on geomagnetic navigation in night-migratory passerines (Wiltschko & Wiltschko, 2003), the evidence for use of magnetic cues by homing pigeons is at best mixed (Beacon et al., 1997; Gordon, 1948; Holland et al., 2013; Jandačka et al., 2022; Keeton et al., 1974; Lednor & Walcott, 1983; Matthews, 1951a; Schiffner & Wiltschko, 2011; Walcott et al., 1979; Wallraff et al., 1986; Wiltschko et al., 2009; Yeagley & Whitmore, 1947). Nonetheless, pigeons are able to home from well beyond their familiar area, even with little prior experience outside their natal loft (Matthews, 1951a). Decades of research conceived at the University of Pisa and taken up elsewhere suggests that pigeons learn the association between wind direction and atmospheric olfactants carried into their loft (Baldaccini et al., 1975; Ioalè, 1980; Ioalè et al., 1990; Ioalè et al., 1978; Papi et al., 1972; Papi et al., 1974) during a sensitive period after fledging (Gagliardo et al., 2001). By associating a given wind direction with the odours it carries, pigeons are able to build a map of the concentration gradients of different olfactants in the area around their loft. When subsequently displaced to distant locations, the local concentration of various odours provides information on the relative direction of the loft (Benvenuti & Gagliardo, 1996; Benvenuti et al., 1992; Benvenuti & Wallraff, 1985; Guilford et al., 1998; Papi & Casini, 1990; Papi et al., 1971; Wallraff & Foà, 1981). Whether pigeons are able to estimate the distance from the loft based on the magnitude of the difference in odour concentration is unclear (Gagliardo, 2013).

Numerous clock-shifting experiments demonstrate that, once the direction of the loft is established from a novel site, pigeons use a time-compensated sun compass to orient in the homeward direction (Schmidt-Koenig, 1961; Schmidt-Koenig, 1969; Schmidt-Koenig, 1972; Schmidt-Koenig, 1958; Walcott, 1972; Walcott & Michener, 1971). The time-compensation programme of pigeons appears to match local ephemerides very closely (Wiltschko et al., 2000), if with a slight time lag (Schmidt-Koenig et al., 1991), facilitating accurate perception of solar azimuth to around 3° (Ganzhorn et al., 1989; Ranvaud et al., 1988; Schmidt-Koenig, 1990). This time-compensation programme relies on observations of the sun's arc during a sensitive period in young pigeons (Gagliardo et al., 2001; Wiltschko & Wiltschko, 1981; Wiltschko et al., 1976).

Whilst this combination of olfactory map and sun compass is sufficient to explain pigeons' true navigation abilities, most animals are not regularly faced with the challenge of orienting from an unknown location. From the mid-1990s, work by the Oxford Navigation Group focused on the navigation of homing pigeons within their familiar area. Early work demonstrated that, through repeated release at the same site, pigeons learned the visual features of the site and used these to home more efficiently (Biro et al., 2003; Biro et al., 2002; Braithwaite, 1993; Braithwaite & Guilford, 1991). Development of Global Positioning Systems (GPS) revealed that each pigeon learned an idiosyncratic homing route, which increased in both homewards efficiency and fidelity over successive releases, before eventually reaching a plateau (Meade et al., 2005). Once familiar with a route, pigeons appeared mostly to navigate by beaconing towards prominent visual landmarks and by following linear visual features (Guilford & Biro, 2014; Lau et al., 2006; Mann et al., 2011; Mora et al., 2012). These landmarks were apparently so salient that pigeons released more than a kilometre off route would beacon towards them before taking up the homeward direction, even though they were presumably capable of orienting more directly towards the loft (Biro et al., 2004). Visual cues

are now recognised as a commonplace part of animal navigation strategies (see section 1.2.1).

To determine whether pigeons' routes are based on map-and-compass navigation between memorised landmarks or compass-independent pilotage, Biro et al. (2007) clock-shifted pigeons before releasing them at familiar sites. The effect of clock-shifting diminished with increasing familiarity, providing formal evidence for pilotage that mirrored earlier findings (Gagliardo et al., 2005; Wiltschko et al., 1994). However, a quirk of the pigeon navigation system became clear; even when pigeons are highly familiar with a simple route along a linear feature, they still attend to their sun compass, with clock manipulations producing small lateral shifts in pigeons' routes (Biro et al., 2007). In fact, even when pigeons are released within clear sight of their home loft, they still show these small but predictable errors (Armstrong et al., 2013; Graue, 1963). These findings mirror the surprising ubiquity of compass-based orientation, even over small scales (see section 1.2.2). This perhaps reflects some kind of weighting between a map-and-compass system which facilitates novel navigational tasks and a separate visual pilotage system, with the weighting slowly but never completely shifting to the latter with increasing familiarity. A control theoretic model of such a system, with parallels to neural control of behaviour, is conceivable.

## 1.3 General methods

The methodological basis of each chapter will be detailed therein; here, I provide only the broad rationale and methods common to every chapter.

### 1.3.1 Shearwaters as a model of avian navigation in the wild

Studies of two species are presented in this thesis: the Manx and Balearic shearwaters, both Procellariiform seabirds of the genus *Puffinus*. Although a great deal could be said about their life history, ecology and conservation, others have already covered these topics in detail (Brooke, 1990) and I will provide an overview only of those aspects relevant to their navigation. They are long-lived birds which

breed in colonies on coastal islands, predominantly across the western coasts of the UK, and exclusively within the Balearic Archipelago, respectively. Manx shearwaters nest in burrows, whilst Balearic shearwaters use rocky crevices and caves (Aguilar, 1997; Harris, 1966). Both species lay just one egg each year and the socially monogamous partners alternate incubation duties whilst the other embarks on a long-distance foraging trip of up to two weeks. Once the chick has hatched after roughly 50-60 days (Aguilar, 1997; Harris, 1966), both parents feed the chick, although in a similar alternating pattern (with one partner making short, near-daily trips, whilst the other embarks on a longer self-provisioning trip), termed dual foraging (Weimerskirch et al., 1993). In Manx shearwaters, these trips can range up to around 1,500 kilometres into the Atlantic. Shearwaters are only active on the colony at night, remaining at sea or underground during daylight. Parents depart on migration before their chicks, which fledge at about 70 days old (Aguilar, 1997; Harris, 1966). Manx shearwaters migrate 12-13,000 kilometres to the Patagonian Shelf (Guilford et al., 2009; Siddiqi-Davies et al., 2024), whilst Balearic shearwaters show a shorter migration (less than 3,000 km) to the North-East Atlantic which is much more variable in phenology, extent and duration (Austin et al., 2019; Guilford et al., 2012).

The migratory navigation of shearwaters shows parallels to migratory songbirds, for instance in clock-and-compass navigation during first migration (Yoda et al., 2021; Yoda et al., 2017) and mechanisms of natal philopatry (Wynn et al., 2020). Chapter 6 relates to the movement ecology and navigation of Balearic shearwaters exclusively during their post-breeding migration. However, this thesis otherwise focuses on mechanisms of navigation during foraging trips in adult Manx shearwaters, and it is in this area that I will provide a more thorough background.

The homing navigation systems of Procellariiform seabirds are the best studied of any wild bird. In the 1950s Ronald Lockley and Geoffrey Matthews recognised the remarkable true navigational proficiency of Manx shearwaters. They displaced

shearwaters from Skokholm Bird Observatory across the UK, mainland Europe and even the United States, recording the remarkable fidelity and speed with which these birds reached home, as well as their accurate initial orientation at locations far from any prior experience (Lack & Lockley, 1938; Matthews, 1953a, 1964). These findings imply that shearwaters possess an extrapolated grid map. Modern analysis of shearwaters' GPS-tracked homing trajectories has provided support for this hypothesis and some of the only direct evidence for an explicitly extrapolated map structure. There is good evidence that shearwaters can estimate their distance from the colony and thus allocate appropriate time to homing before dusk (Padget et al., 2017; Padget et al., 2019; Shiomi et al., 2012). However, shearwaters avoid flying over land so must take detours to avoid landmasses (Padget et al., 2022; Padget et al., 2019). Padget et al. (2019) showed that they fail to anticipate landmasses which block their homeward trajectory, instead orienting on the homeward beeline and allocating time to homing according to the beeline distance. Given that decades-old shearwaters must be familiar with the obstacles near their colony, this implies that their position-finding when out of sight of land is not based on direct familiarity. Instead, they have likely extrapolated their position-finding mechanism from a smaller area, failing to account for obstacles encountered further afield.

Numerous experiments have been conducted to investigate the sensory basis of Procellariiform maps. Application of treatments designed to disrupt geomagnetic information suggest that Procellariiforms do not rely on a magnetic map (Bonadonna et al., 2005; Bonadonna et al., 2003; Gagliardo et al., 2013; Massa et al., 1991; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015). However, there is evidence that Manx shearwaters use magnetic cues in natal philopatry (Wynn et al., 2020), streaked shearwaters (*Calonectris leucomelas*) might possess a magnetic compass (Takahashi et al., 2022), and Manx shearwaters might calibrate a sun compass against a magnetic compass (Wynn et al., 2021).

The map-and-compass systems of shearwaters in fact bear remarkable resemblance to those of homing pigeons. Whilst magnetic cues appear to have little importance, ablation of olfactory receptors causes almost complete disorientation (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015), without non-specific effects on other behaviour (Padget et al., 2017). During these experiments, anosmic birds compensated for disorientation at sea by following coastlines in the homewards direction much like a homing pigeon follows a road (Padget et al., 2017; Pollonara et al., 2015). This suggests use of visual cues along the coast either for map-and-compass navigation based on memorised landmarks or pilotage along the linear visual feature. In addition, Manx shearwaters are uniquely suited among birds to clock-shifting experiments due to their long incubation stints in enclosed burrows. Padget et al. (2018) exploited this to conduct the first clock-shift of a free-flying wild bird and show that shearwaters, like pigeons, use a time-compensated sun compass to home after displacement. Whilst the cues used by shearwaters to navigate – olfactory maps, coastal features, geomagnetic and solar compasses – are now relatively well-studied among wild birds, the question of *how* shearwaters use these cues, especially in combination with each other, remains open. To answer this question requires close analysis of shearwater movement under natural conditions or sensory manipulation.

### 1.3.2 Global Positioning System and light-level geolocation tracking

Although there is a long tradition of collecting data on the movements of shearwaters, early work was limited to ringing recoveries after natural movements or vanishing bearings and homing times after experimental displacement (Lack & Lockley, 1938; Matthews, 1953a, 1964). These methods impose severe limitations on the depth and scope of navigational inference, particularly through survivorship bias, site-specific orientation effects and the lack of information on movements between release and recapture. Due to the pelagic lifestyle of shearwaters, this impediment was only overcome with the advent of modern

biologging technology. In 1989, wandering albatross (*Diomedia exulans*) were first tracked using Satellite Telemetry (Jouventin & Weimerskirch, 1990) and miniaturisation of GPS loggers soon allowed tracking of smaller birds, first in captivity (Steiner et al., 2000; von Hünerbein et al., 2000), then in the wild (e.g. Guilford et al., 2008). Every year since 2004, the foraging trips of Manx shearwaters breeding on various islands around the UK have been tracked by the Oxford Navigation Group using temporary dorsal attachment of GPS loggers, as laid out in Guilford et al. (2008). This dataset now comprises over 2,000 GPS tracks and improvements in technology have allowed for further miniaturisation (from almost 20 g to 11 g), increased temporal resolution over full foraging trips (from 2 hours to 30 seconds), and incorporation of additional data streams such as accelerometry, magnetometry and saltwater immersion. These data now allow for the interrogation of the detailed behaviour of shearwaters at sea to answer precise navigational questions, as demonstrated in Chapters 2 to 5.

Shortly after the miniaturisation of GPS devices, far smaller (1-3 g) light-level geolocator devices became available. Through the timing and duration of day and night, light data can be used to estimate longitude and latitude, respectively. The average positional error of these estimates is in the order of hundreds of kilometres, compared to only metres for GPS (Fudickar et al., 2012; Halpin et al., 2021; Lisovski et al., 2012; Phillips et al., 2004; Shaffer et al., 2005). Nonetheless, their smaller size and much lower power requirements make them suitable for tracking migratory movements of birds – movement on a scale where such error becomes almost negligible. Light-level geolocation data have been used to track the migrations of both Manx and Balearic shearwaters (Austin et al., 2019; Guilford et al., 2008; Guilford et al., 2012; Siddiqi-Davies et al., 2024) and are used in Chapter 6.

### 1.3.1 Methods of navigational inference

The basic approach we have taken throughout this thesis is to identify a diagnostic pattern of errors expected to result from a candidate navigational mechanism. These errors might be inherent in the constraints of that mechanism (see Chapter 6), generated by an interaction between those constraints and the bird's own behaviour (see Chapters 2 and 3) or induced by some sensory manipulation (see Chapters 4 and 5). This is the general approach traditionally underlying much of the navigation literature (Matthews, 1951b) but here, we put particular emphasis on observational interpretation of errors resulting from navigational constraints in tracks of unmanipulated birds. As for the sensory manipulations experimentally induced in the studies presented here, we use two well-established approaches: clock-shifting and the use of disruptive neodymium magnets.

Before the navigational performance of a free-ranging bird can be quantified, its motivation must first be established. In shearwaters, this generally corresponds to the identification of homing behaviour. In general, this is a relatively easy task; after a period of foraging at some distance from the colony, a clear switch occurs; the bird rapidly and monotonically moves closer to the colony (Padget et al., 2019; Shiomi et al., 2012). However, as with any natural behaviour, there are numerous complications: sometimes shearwaters home over multiple days, resting overnight; sometimes they must orient away from the colony to detour around an obstacle, sometimes they forage en route and when homing from close to the colony they may do so only slowly and intermittently. To generate robust and repeatable identification of homing across all the behavioural variability seen in 20 years' worth of tracking data and various experiments, we have advanced algorithmic methods of homing identification in Chapters 2, 4 and 5. In Chapters 3 and 4 we apply similar approaches to identify outbound commuting bouts. The approach first involves identification of periods of persistent travel using a rolling mean speed over a relatively long time window, rather than merely flight between fixes,

which may happen in fits and starts. The direction of travel, relative to the colony, the proportional change in distance from the colony and the starting distance of each bout of travel can then be calculated. These metrics generally show multimodal distributions, which can be used to identify those bouts most likely to represent outward commuting or homing behaviour. In the case of Balearic shearwater migration, the start of return migration is analogous to the initiation of homing.

After the relevant behaviours are identified, measurement of navigational ability takes two key forms: orientation error and the allocation of time to homing. The former is the most common in studies of animal navigation and uses the central tendency and spread of movement directions, relative to an assumed goal. These behavioural metrics can be easily extracted from GPS tracking data by comparing the geographic bearing between fixes to the geographic bearing towards the colony (giving the instantaneous angular deflection). With a temporal resolution between 5 and 30 minutes, shearwater orientation shows high autocorrelation so, to avoid pseudoreplication, the (circular) mean deflection or mean absolute deflection is taken for each homing bout or trip.

Allocation of time to homing is a more unusual approach but is possible to assess in shearwaters because they feed during the day and return to the colony at night, leading to an optimal time of return around dusk. Multiple studies have shown that the timing of homing initiation relates strongly to shearwaters' distance from the colony at the start of homing, indicating distance estimation (Padget et al., 2017; Padget et al., 2019; Shiomi et al., 2012). This approach is used in Chapter 5 and, with a modification to use the speed of travel during initial return migration, in Chapter 6.

## 1.4 The aims of this thesis

In general, the navigational mechanisms of wild, free-ranging animals have only been widely studied in the last three decades, and the broad aim of this thesis is to advance understanding of shearwater navigation, as a model taxon for avian navigation in the wild. Especially through the analysis of movement data from free-ranging birds, I aim to elucidate the sensory and cognitive mechanisms by which birds navigate over vast tracts of ocean. This stands in contrast to the majority of avian navigation research, which has relied on migratory restlessness in caged birds or artificial displacement to generate an orientation response, and thus offers limited insight into navigation within the complexities of the real world.

Although some chapters address (to a greater or lesser extent) the spatial cognition and map sense of shearwaters, most of the work presented here pertains to the use of a time-compensated sun compass, sometimes in combination with a geomagnetic compass. Despite the long history and great volume of work on the sun compass of captive birds and other animals (Guilford & Taylor, 2014; Schmidt-Koenig, 1990), very few studies have theoretically (Alerstam & Pettersson, 1991), circumstantially (Alerstam et al., 2008; Alerstam et al., 2001) or directly (Emlen & Penney, 1964; Padget et al., 2018; Penney & Emlen, 1967) provided evidence for use of the sun compass by wild animals outside eusocial Hymenoptera (Wehner, 1984). This has precluded detailed understanding of how free-ranging animals use the sun compass to navigate, except by inference from captive models. This thesis addresses both the navigational and chronobiological aspects of this deficiency.

In Chapters 2 and 3, we use the discovery of a novel chronobiological phenomenon – jet lag resulting from rapid longitudinal flights – to investigate how shearwaters use the sun compass during natural foraging trips, including on the outward journey, a form of navigation that cannot be investigated via traditional displacement experiments. We also show that jet-lagged shearwaters are weakly deflected when following the coast, implying some combination of pilotage and

map-and-compass mechanisms, in another remarkable parallel of pigeon navigation (Biro et al., 2007).

In Chapter 4, we build on the clock-shifting procedure developed by Padget et al. (2018) to address experimentally the question of how shearwaters orient towards food resources. As a corollary, we provide some of the first evidence that the endogenous clock controls foraging movements in wild animals and, by circumventing many of the practical difficulties associated with chronobiological studies of free-living animals (Helm et al., 2017), provide a new avenue for the study of the endogenous clock in the wild.

In Chapter 5, we extend work on geomagnetic navigation in shearwaters, addressing the methodological flaws and tantalising marginal effects of previous experiments, as well as the possibility that shearwaters might rely on calibration for accurate sun compass orientation.

In the final empirical chapter, we link spatial cognition and navigation in the wild to its wider ecological consequences. In an investigation of climate impacts on the migration of Balearic shearwaters, we demonstrate that the shearwaters' post-breeding migratory area is shifting north with rising temperatures. We find that this range shift arises from reversible individual flexibility in migratory destination among adult shearwaters, yielding insights into the individual-level processes underlying climate-driven range shifts. There is growing evidence that such processes may be important determinants of distributional shifts in long-lived animals (Andrade et al., 2025; Keith & Bull, 2017; Linssen et al., 2023; Siddiqi-Davies et al., 2024; Verhoeven et al., 2018; Wrensford et al., 2025) and we show that spatial cognition – namely distance estimation via route learning – has the potential to shape these shifts via impacts on the flexibility of migratory behaviour.

Finally, in Chapter 7, I synthesise the findings of this thesis and discuss how they relate to existing literature. I consider how they advance the understanding of

avian navigation and identify some questions still be addressed, suggesting a number of potential approaches.

## References

Able, K. P. (1993). Orientation cues used by migratory birds: A review of cue-conflict experiments. *Trends in Ecology & Evolution*, *8*(10), 367-371. https://doi.org/10.1016/0169-5347(93)90221-A

Adler, K., & Phillips, J. B. (1985). Orientation in a desert lizard (*Uma notata*): time-compensated compass movement and polarotaxis. *Journal of Comparative Physiology A*, *156*(4), 547-552. https://doi.org/10.1007/BF00613978

Aguilar, J. (1997). Biología y conservación de la pardela balear Puffinus mauretanicus. *Documents Tècnics de Conservació, II$^{a}$ època*.

Åkesson, S., Boström, J., Liedvogel, M., Muheim, R., Hansson, L.-A., & Akesson, S. (2014). Animal navigation. In *Animal movement across scales*. Oxford University Press, United Kingdom. https://doi.org/10.1093/acprof:oso/9780199677184.003.0009, ISBN: 0199677182

Alerstam, T., Bäckman, J., Strandberg, R., Gudmundsson, G. A., Hedenström, A., Henningsson, S. S., Karlsson, H., & Rosén, M. (2008). Great-circle migration of Arctic passerines. *The Auk*, *125*(4), 831-838. https://doi.org/10.1525/auk.2008.07142

Alerstam, T., Gudmundsson, G. A., Green, M., & Hedenstrom, A. (2001). Migration along orthodromic sun compass routes by arctic birds. *Science*, *291*(5502), 300-303. https://doi.org/10.1126/science.291.5502.300.

Alerstam, T., & Pettersson, S.-G. (1991). Orientation along great circles by migrating birds using a sun compass. *Journal of Theoretical Biology*, *152*(2), 191-202. https://doi.org/10.1016/S0022-5193(05)80452-7

Andrade, P., Franco, A. M., Acácio, M., Afonso, S., Marques, C. I., Moreira, F., Carneiro, M., & Catry, I. (2025). Mechanisms underlying the loss of migratory behaviour in a long-lived bird. *Journal of Animal Ecology*, *94*(5), 1061-1075. https://doi.org/10.1111/1365-2656.70035

Armstrong, C., Wilkinson, H., Meade, J., Biro, D., Freeman, R., & Guilford, T. (2013). Homing pigeons respond to time-compensated solar cues even in sight of the loft. *PLoS One*, *8*(5), e63130. https://doi.org/10.1371/journal.pone.0063130

Aschoff, J. (1951). Die 24-Stunden-Periodik der maus unter konstanten umgebungsbedingungen. *Naturwissenschaften*, *38*(21), 506-507. https://doi.org/10.1007/BF00628863

Aschoff, J. (1954). Zeitgeber der tierischen Tagesperiodik. *Naturwissenschaften*, *41*(3), 49-56. https://doi.org/10.1007/BF00634164

Austin, R. E., Wynn, R. B., Votier, S. C., Trueman, C., McMinn, M., Rodríguez, A., Suberg, L., Maurice, L., Newton, J., Genovart, M., Péron, C., Grémillet, D., & Guilford, T. (2019). Patterns of at-sea behaviour at a hybrid zone between two threatened seabirds. *Scientific Reports*, *9*(1), 14720. https://doi.org/10.1038/s41598-019-51188-8

Baker, A. (2025). Launching the Eighteenth-Century Search for Longitude. In A. Baker, R. Dunn, R. Higgitt, S. Schaffer, & S. Waring (Eds.), *The Board of Longitude: Science, Innovation and Empire* (pp. 39-64). Cambridge University Press, Cambridge. https://doi.org/10.1017/9781009602556.003, ISBN: 9781009602501

Baker, R. R. (1982). *Migration: paths through time and space*. Hodder & Stoughton Educational, London. ISBN: 0340260793

Baldaccini, N. E., Benvenuti, S., Fiaschi, V., & Papi, F. (1975). Pigeon navigation: Effects of wind deflection at home cage on homing behaviour. *Journal of comparative physiology*, *99*(3), 177-186. https://doi.org/10.1007/BF00613834

Barlow, J. S. (1964). Inertial navigation as a basis for animal navigation. *Journal of Theoretical Biology*, *6*(1), 76-117. https://doi.org/10.1016/0022-5193(64)90067-0

Basu, J., & Nagel, K. (2024). Neural circuits for goal-directed navigation across species. *Trends in Neurosciences*, *47*(11), 904-917. https://doi.org/10.1016/j.tins.2024.09.005

Beacon, R. C., Wiltschko, R., & Wiltschko, W. (1997). Pigeon Homing: Effects of Magnetic Pulses on Initial Orientation. *The Auk*, *114*(3), 405-415. https://doi.org/10.2307/4089242

Beck, W. (1984). The Influence of the Earth Magnetic Field to the Migratory Behaviour of Pied Flycatchers (*Ficedula hypoleuca pallas*). In D. Varjú & H. U. Schnitzler (Eds.), *Localization and Orientation in Biology and Engineering* (pp. 357-359). 1984, Springer Berlin Heidelberg, Berlin, Germany. https://doi.org/10.1007/978-3-642-69308-3_62

Bellini, S. (1963). Su di un particolare comportamento di batteri d'acqua dolce (On a unique behavior of freshwater bacteria). *Institute of Microbiology, University of Pavia, Italy*.

Benhamou, S., & Poucet, B. (1998). Landmark use by navigating rats (*Rattus norvegicus*) contrasting geometric and featural information. *Journal of Comparative Psychology*, *112*(3), 317-322. https://doi.org/10.1037/0735-7036.112.3.317

Benvenuti, S., & Gagliardo, A. (1996). Homing Behaviour of Pigeons Subjected to Unilateral Zinc Sulphate Treatment of Their Olfactory Mucosa. *Journal of Experimental Biology*, *199*(11), 2531-2535. https://doi.org/10.1242/jeb.199.11.2531

Benvenuti, S., Ioalè, P., Gagliardo, A., & Bonadonna, F. (1992). Effects of zinc sulphate-induced anosmia on homing behaviour of pigeons. *Comparative Biochemistry and Physiology Part A: Physiology*, *103*(3), 519-526. https://doi.org/10.1016/0300-9629(92)90281-T

Benvenuti, S., & Wallraff, H. G. (1985). Pigeon navigation: Site simulation by means of atmospheric odours. *Journal of Comparative Physiology A*, *156*(6), 737-746. https://doi.org/10.1007/BF00610827

Berthold, P. (1984). The endogenous control of bird migration: a survey of experimental evidence. *Bird Study*, *31*(1), 19-27. https://doi.org/10.1080/00063658409476810

Berthold, P. (1990). Spatiotemporal programs and genetics of orientation. *Experientia*, *46*(4), 363-371. https://doi.org/10.1007/BF01952169

Berthold, P. (1996). *Control of bird migration*. Chapman & Hall, London. ISBN: 0412363801

Betts, J. (1993). John Harrison: inventor of the precision timekeeper. *Endeavour*, *17*(4), 160-167. https://doi.org/10.1016/0160-9327(93)90056-9

Bingman, V. P., & Cheng, K. (2005). Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethology Ecology & Evolution*, *17*(4), 295-318. https://doi.org/10.1080/08927014.2005.9522584

Biro, D., Freeman, R., Meade, J., Roberts, S., & Guilford, T. (2007). Pigeons combine compass and landmark guidance in familiar route navigation. *Proceedings of the National Academy of Sciences*, *104*(18), 7471-7476. https://doi.org/10.1073/pnas.0701575104

Biro, D., Guilford, T., & Dawkins, M. S. (2003). Mechanisms of visually mediated site recognition by the homing pigeon. *Animal Behaviour*, *65*(1), 115-122. https://doi.org/10.1006/anbe.2002.2014

Biro, D., Guilford, T., Dell'Omo, G., & Lipp, H.-P. (2002). How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking. *Journal of Experimental Biology*, *205*(24), 3833-3844. https://doi.org/10.1242/jeb.205.24.3833

Biro, D., Meade, J., & Guilford, T. (2004). Familiar route loyalty implies visual pilotage in the homing pigeon. *Proceedings of the National Academy of Sciences*, *101*(50), 17440-17443. https://doi.org/10.1073/pnas.040698410

Blaser, N., Guskov, S. I., Entin, V. A., Wolfer, D. P., Kanevskyi, V. A., & Lipp, H.-P. (2014). Gravity anomalies without geomagnetic disturbances interfere with pigeon homing – a GPS tracking study. *Journal of Experimental Biology*, *217*(22), 4057-4067. https://doi.org/10.1242/jeb.108670

Boles, L., & Lohmann, K. (2003). True Navigation and Magnetic Maps in Spiny Lobsters. *Nature*, *421*, 60-63. https://doi.org/10.1038/nature01226

Bonadonna, F., Bajzak, C., Benhamou, S., Igloi, K., Jouventin, P., Lipp, H.-P., & Dell'Omo, G. (2005). Orientation in the wandering albatross: Interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *272*, 489-495. https://doi.org/10.1098/rspb.2004.2984

Bonadonna, F., Chamaillé-Jammes, S., Pinaud, D., & Weimerskirch, H. (2003). Magnetic cues: are they important in Black-browed Albatross *Diomedea melanophris* orientation? *Ibis*, *145*(1), 152-155. https://doi.org/10.1046/j.1474-919X.2003.00117.x

Boström, J. E., Fransson, T., Henshaw, I., Jakobsson, S., Kullberg, C., & Åkesson, S. (2010). Autumn migratory fuelling: a response to simulated magnetic displacements in juvenile wheatears, *Oenanthe oenanthe*. *Behavioral Ecology and Sociobiology*, *64*(11), 1725-1732. https://doi.org/10.1007/s00265-010-0985-1

Braithwaite, V. A. (1993). When Does Previewing the Landscape Affect Pigeon Homing? *Ethology*, *95*(2), 141-151. https://doi.org/10.1111/j.1439-0310.1993.tb00464.x

Braithwaite, V. A., & Guilford, T. (1991). Viewing familiar landscapes affects pigeon homing. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *245*(1314), 183-186. https://doi.org/10.1098/rspb.1991.0107

Brassart, J., Kirschvink, J. L., Phillips, J. B., & Borland, S. C. (1999). Ferromagnetic material in the eastern red-spotted newt *Notophthalmus viridescens*. *Journal of Experimental Biology*, *202*(22), 3155-3160. https://doi.org/10.1242/jeb.202.22.3155

Brooke, M. (1990). *The Manx Shearwater*. T. & A. D. Poyser, London, United Kingdom. ISBN: 9780856610578

Brothers, J. R., & Lohmann, K. J. (2015). Evidence for Geomagnetic Imprinting and Magnetic Navigation in the Natal Homing of Sea Turtles. *Current Biology*, *25*(3), 392-396. https://doi.org/10.1016/j.cub.2014.12.035

Brothers, J. R., & Lohmann, K. J. (2018). Evidence that Magnetic Navigation and Geomagnetic Imprinting Shape Spatial Genetic Variation in Sea Turtles. *Current Biology*, *28*(8), 1325-1329.e1322. https://doi.org/10.1016/j.cub.2018.03.022

Bulte, M., Heyers, D., Mouritsen, H., & Bairlein, F. (2017). Geomagnetic information modulates nocturnal migratory restlessness but not fueling in a long distance migratory songbird. *Journal of Avian Biology*, *48*(1), 75-82. https://doi.org/10.1111/jav.01285

Chapman, J. W., Reynolds, D. R., Hill, J. K., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008). A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology*, *18*(19), R908-R909. https://doi.org/10.1016/j.cub.2008.08.014

Chapman, J. W., Reynolds, D. R., & Wilson, K. (2015). Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters*, *18*(3), 287-302. https://doi.org/10.1111/ele.12407

Chappell, J., & Guilford, T. (1995). Homing pigeons primarily use the sun compass rather than fixed directional visual cues in an open-field arena food-searching task. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *260*(1357), 59-63. https://doi.org/10.1098/rspb.1995.0059

Chen, C., Buhl, E., Xu, M., Croset, V., Rees, J. S., Lilley, K. S., Benton, R., Hodge, J. J. L., & Stanewsky, R. (2015). *Drosophila* Ionotropic Receptor 25a mediates

circadian clock resetting by temperature. *Nature*, *527*(7579), 516-520. https://doi.org/10.1038/nature16148

Chernetsov, N., Pakhomov, A., Kobylkov, D., Kishkinev, D., Holland, R. A., & Mouritsen, H. (2017). Migratory Eurasian Reed Warblers Can Use Magnetic Declination to Solve the Longitude Problem. *Current Biology*, *27*(17), 2647-2651.e2642. https://doi.org/10.1016/j.cub.2017.07.024

Cheung, A., & Vickerstaff, R. (2010). Finding the Way with a Noisy Brain. *PLoS computational biology*, *6*(11), e1000992. https://doi.org/10.1371/journal.pcbi.1000992

Cochran, W. W., Mouritsen, H., & Wikelski, M. (2004). Migrating Songbirds Recalibrate Their Magnetic Compass Daily from Twilight Cues. *Science*, *304*(5669), 405-408. https://doi.org/10.1126/science.1095844

Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proceedings of the National Academy of Sciences*, *107*(25), 11638-11643. https://doi.org/10.1073/pnas.1001401107

Collett, M., & Collett, T. S. (2000). How do insects use path integration for their navigation? *Biological Cybernetics*, *83*(3), 245-259. https://doi.org/10.1007/s004220000168

Collett, M., & Collett, T. S. (2009). The learning and maintenance of local vectors in desert ant navigation. *Journal of Experimental Biology*, *212*(7), 895-900. https://doi.org/10.1242/jeb.024521

Collett, M., Collett, T. S., Bisch, S., & Wehner, R. (1998). Local and global vectors in desert ant navigation. *Nature*, *394*(6690), 269-272. https://doi.org/10.1038/28378

Collett, T. S., Dillmann, E., Giger, A., & Wehner, R. (1992). Visual landmarks and route following in desert ants. *Journal of Comparative Physiology A*, *170*(4), 435-442. https://doi.org/10.1007/BF00191460

Dacke, M., Baird, E., Byrne, M., Scholtz, Clarke H., & Warrant, Eric J. (2013). Dung Beetles Use the Milky Way for Orientation. *Current Biology*, *23*(4), 298-300. https://doi.org/10.1016/j.cub.2012.12.034

de Mairan, J. J. (1729). Observation botanique. Histoire de l'Academie Royale des Sciences. *Des Sciences (1729)*.

Dean, B., Kirk, H., Fayet, A., Shoji, A., Freeman, R., Leonard, K., Perrins, C. M., & Guilford, T. (2015). Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area. *Marine Ecology Progress Series*, *538*, 239-248. https://doi.org/10.3354/meps11443

DeRosa, C. T., & Taylor, D. H. (1978). Sun-Compass Orientation in the Painted Turtle, *Chrysemys picta* (Reptilia, Testudines, Testudinidae). *Journal of Herpetology*, *12*(1), 25-28. https://doi.org/10.2307/1563498

Diebel, C. E., Proksch, R., Green, C. R., Neilson, P., & Walker, M. M. (2000). Magnetite defines a vertebrate magnetoreceptor. *Nature*, *406*(6793), 299-302. https://doi.org/10.1038/35018561

Dornfeldt, K. (1991). Pigeon homing in relation to geomagnetic, gravitational, topographical, and meteorological conditions. *Behavioral Ecology and Sociobiology*, *28*(2), 107-123. https://doi.org/10.1007/BF00180988

Dreyer, D., Adden, A., Chen, H., Frost, B., Mouritsen, H., Xu, J., Green, K., Whitehouse, M., Chahl, J., Wallace, J., Hu, G., Foster, J., Heinze, S., & Warrant, E. (2025). Bogong moths use a stellar compass for long-distance navigation at night. *Nature*, *643*(8073), 994-1000. https://doi.org/10.1038/s41586-025-09135-3

Dreyer, D., Frost, B., Mouritsen, H., Günther, A., Green, K., Whitehouse, M., Johnsen, S., Heinze, S., & Warrant, E. (2018). The Earth's Magnetic Field and Visual Landmarks Steer Migratory Flight Behavior in the Nocturnal Australian Bogong Moth. *Current Biology*, *28*(13), 2160-2166.e2165. https://doi.org/10.1016/j.cub.2018.05.030

Duff, S. J., Brownlie, L. A., Sherry, D. F., & Sangster, M. (1998). Sun compass and landmark orientation by black-capped chickadees (*Parus atricapillus*). *Journal of Experimental Psychology: Animal Behavior Processes*, *24*(3), 243-253. https://doi.org/10.1037/0097-7403.24.3.243

Durier, V., Graham, P., & Collett, T. S. (2003). Snapshot Memories and Landmark Guidance in Wood Ants. *Current Biology*, *13*(18), 1614-1618. https://doi.org/10.1016/j.cub.2003.08.024

Emlen, J. T., & Penney, R. L. (1964). Distance navigation in the Adelie Penguin. *Ibis*, *106*(4), 417-431. https://doi.org/10.1111/j.1474-919X.1964.tb03724.x

Emlen, S. T. (1967a). Migratory orientation in the Indigo Bunting, *Passerina cyanea*. Part II: Mechanism of celestial orientation. *The Auk*, *84*(4), 463-489. https://doi.org/10.2307/4083330

Emlen, S. T. (1967b). Migratory Orientation in the Indigo Bunting, *Passerina cyanea*: Part I: Evidence for Use of Celestial Cues. *The Auk*, *84*(3), 309-342. https://doi.org/10.2307/4083084

Emlen, S. T. (1975). The stellar-orientation system of a migratory bird. *Scientific American*, *233*(2), 102-111. https://doi.org/10.1038/scientificamerican0875-102

Fischler-Ruiz, W., Clark, D. G., Joshi, N. R., Devi-Chou, V., Kitch, L., Schnitzer, M., Abbott, L. F., & Axel, R. (2021). Olfactory landmarks and path integration converge to form a cognitive spatial map. *Neuron*, *109*(24), 4036-4049.e4035. https://doi.org/10.1016/j.neuron.2021.09.055

Fleischmann, P. N., Grob, R., Müller, V. L., Wehner, R., & Rössler, W. (2018). The Geomagnetic Field Is a Compass Cue in *Cataglyphis* Ant Navigation. *Current Biology*, *28*(9), 1440-1444.e1442. https://doi.org/10.1016/j.cub.2018.03.043

Fluharty, S. L., Taylor, D. H., & Barrett, G. W. (1976). Sun-Compass Orientation in the Meadow Vole, *Microtus pennsylvanicus*. *Journal of Mammalogy*, *57*(1), 1-9. https://doi.org/10.2307/1379508

Fransson, T., Jakobsson, S., Johansson, P., Kullberg, C., Lind, J., & Vallin, A. (2001). Magnetic cues trigger extensive refuelling. *Nature, 414*(6859), 35-36. https://doi.org/10.1038/35102115

Fuchikawa, T., Eban-Rothschild, A., Nagari, M., Shemesh, Y., & Bloch, G. (2016). Potent social synchronization can override photic entrainment of circadian rhythms. *Nature Communications*, *7*(1), 11662. https://doi.org/10.1038/ncomms11662

Fudickar, A. M., Wikelski, M., & Partecke, J. (2012). Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution*, *3*(1), 47-52. https://doi.org/10.1111/j.2041-210X.2011.00136.x

Fuxjager, M. J., Eastwood, B. S., & Lohmann, K. J. (2011). Orientation of hatchling loggerhead sea turtles to regional magnetic fields along a transoceanic migratory pathway. *The Journal of Experimental Biology*, *214*(15), 2504-2508. https://doi.org/10.1242/jeb.055921

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *The Journal of Experimental Biology*, *216*(12), 2165-2171. https://doi.org/10.1242/jeb.070250

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *The Journal of Experimental Biology*, *216*(15), 2798-2805. https://doi.org/10.1242/jeb.085738

Gagliardo, A., Ioalè, P., Odetti, F., & Bingman, V. P. (2001). The ontogeny of the homing pigeon navigational map: evidence for a sensitive learning period. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1463), 197-202. https://doi.org/10.1098/rspb.2000.1350

Gagliardo, A., Odetti, F., & Ioalè, P. (2005). Factors reducing the expected deflection in initial orientation in clock-shifted homing pigeons. *Journal of Experimental Biology*, *208*(3), 469-478. https://doi.org/10.1242/jeb.01383

Ganzhorn, J. U., Kiepenheuer, J., Ranvaud, R. D. P. K. C., & Schmidt-Koenig, K. (1989). How accurate is the sun compass of the homing pigeon? In *Orientation and Navigation — Birds, Humans, and other Animals.* (pp. No. 6). The Royal Institute of Navigation Animal Navigation Group Conference 1989, Cardiff. The Royal Institute of Navigation, London, United Kingdom.

Goforth, K. M., Lohmann, C. M. F., Gavin, A., Henning, R., Harvey, A., Hinton, T. L., Lim, D. S., & Lohmann, K. J. (2025). Learned magnetic map cues and two mechanisms of magnetoreception in turtles. *Nature*, *638*(8052), 1015-1022. https://doi.org/10.1038/s41586-024-08554-y

Gordon, D. A. (1948). Sensitivity of the Homing Pigeon to the Magnetic Field of the Earth. *Science*, *108*(2817), 710-711. https://doi.org/10.1126/science.108.2817.710

Gould, R. T. (1921). The History of the Chronometer. *The Geographical Journal*, *57*(4), 253-268. https://doi.org/10.2307/1780557

Graham, P., Fauria, K., & Collett, T. S. (2003). The influence of beacon-aiming on the routes of wood ants. *Journal of Experimental Biology*, *206*(3), 535-541. https://doi.org/10.1242/jeb.00115

Graham, T., Georges, A., & McElhinney, N. (1996). Terrestrial Orientation by the Eastern Long-Necked Turtle, *Chelodina longicollis*, from Australia. *Journal of Herpetology*, *30*(4), 467-477. https://doi.org/10.2307/1565689

Graue, L. C. (1963). The effect of phase shifts in the day-night cycle on pigeon homing at distances of less than one mile. *The Ohio Journal of Science*, *63*(5), 214–217.

Greene, C. M., & Cook, R. G. (1997). Landmark geometry and identity controls spatial navigation in rats. *Animal Learning & Behavior*, *25*(3), 312-323. https://doi.org/10.3758/BF03199089

Griffin, D. R. (1952). Bird navigation. *Biological Reviews*, *27*(4), 359-390. https://doi.org/10.1111/j.1469-185X.1952.tb01509.x

Grob, R., Fleischmann, P. N., Grübel, K., Wehner, R., & Rössler, W. (2017). The Role of Celestial Compass Information in *Cataglyphis* Ants during Learning Walks and for Neuroplasticity in the Central Complex and Mushroom Bodies. *Frontiers in Behavioral Neuroscience*, *11*. https://doi.org/10.3389/fnbeh.2017.00226

Grob, R., Wegmann, J. W., Rössler, W., & Fleischmann, P. N. (2024). *Cataglyphis* ants have a polarity-sensitive magnetic compass. *Current Biology*, *34*(24), 5833-5838.e5832. https://doi.org/10.1016/j.cub.2024.11.012

Guerra, P. A., Gegear, R. J., & Reppert, S. M. (2014). A magnetic compass aids monarch butterfly migration. *Nature Communications*, *5*(1), 4164. https://doi.org/10.1038/ncomms5164

Guilford, T., & Biro, D. (2014). Route following and the pigeon's familiar area map. *The Journal of Experimental Biology*, *217*(2), 169-179. https://doi.org/10.1242/jeb.092908

Guilford, T., & Burt de Perera, T. (2017). An associative account of avian navigation. *Journal of Avian Biology*, *48*(1). https://doi.org/10.1111/jav.01355

Guilford, T., Gagliardo, A., Chappell, J., Bonadonna, F., Burt de Perera, T., & Holland, R. (1998). Homing Pigeons Use Olfactory Cues for Navigation In England. *Journal of Experimental Biology*, *201*(6), 895-900. https://doi.org/10.1242/jeb.201.6.895

Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S., & Perrins, C. M. (2008). GPS tracking of the foraging movements of Manx Shearwaters Puffinus puffinus breeding on Skomer Island, Wales. *Ibis*, *150*(3), 462-473. https://doi.org/10.1111/j.1474-919X.2008.00805.x

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., Collett, M., Freeman, R., & Perrins, C. M. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society of London. Series B:*

*Biological Sciences*, *276*(1660), 1215-1223. https://doi.org/10.1098/rspb.2008.1577

Guilford, T., & Taylor, G. K. (2014). The sun compass revisited. *Animal Behaviour*, *97*, 135-143. https://doi.org/10.1016/j.anbehav.2014.09.005

Guilford, T., Wynn, R., McMinn, M., Rodríguez, A., Fayet, A., Maurice, L., Jones, A., & Meier, R. (2012). Geolocators reveal migration and pre-breeding behaviour of the critically endangered Balearic shearwater *Puffinus mauretanicus*. *PLoS One*, *7*(3), e33753. https://doi.org/10.1371/journal.pone.0033753

Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, *436*(7052), 801-806. https://doi.org/10.1038/nature03721

Hagstrum, J. T. (2000). Infrasound and the Avian Navigational Map. *Journal of Experimental Biology*, *203*(7), 1103-1111. https://doi.org/10.1242/jeb.203.7.1103

Haigh, G. R. (1979). Sun-Compasss Orientation in the Thirteen-Lined Ground Squirrel, *Spermophilus tridecemlineatus*. *Journal of Mammalogy*, *60*(3), 629-632. https://doi.org/10.2307/1380108

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., & Clarke, R. H. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods in Ecology and Evolution*, *12*(11), 2243-2255. https://doi.org/10.1111/2041-210X.13698

Harris, M. P. (1966). Breeding biology of the Manx shearwater *Puffinus puffinus*. *Ibis*, *108*(1), 17-33. https://doi.org/10.1111/j.1474-919X.1966.tb07249.x

Harten, L., Katz, A., Goldshtein, A., Handel, M., & Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science*, *369*(6500), 194-197. https://doi.org/10.1126/science.aay3354

Hawkes, W. L., Weston, S. T., Cook, H., Doyle, T., Massy, R., Guri, E. J., Wotton Jimenez, R. E., & Wotton, K. R. (2022). Migratory hoverflies orientate north during spring migration. *Biology Letters*, *18*(10), 20220318. https://doi.org/10.1098/rsbl.2022.0318

Heinze, S., Narendra, A., & Cheung, A. (2018). Principles of Insect Path Integration. *Current Biology*, *28*(17), R1043-R1058. https://doi.org/10.1016/j.cub.2018.04.058

Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology*, *28*(1), 9-12. https://doi.org/10.1007/BF00172133

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T., & Bloch, G. (2017). Two sides of a coin: ecological and chronobiological

perspectives of timing in the wild. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20160246. https://doi.org/10.1098/rstb.2016.0246

Henshaw, I., Fransson, T., Jakobsson, S., & Kullberg, C. (2010). Geomagnetic field affects spring migratory direction in a long distance migrant. *Behavioral Ecology and Sociobiology*, *64*(8), 1317-1323. https://doi.org/10.1007/s00265-010-0946-8

Hirschie Johnson, C., Elliott, J. A., & Foster, R. (2003). Entrainment of Circadian Programs. *Chronobiology international*, *20*(5), 741-774. https://doi.org/10.1081/CBI-120024211

Hoffmann, K. (1954). Versuche zu der im Richtungsfinden der Vögel enthaltenen Zeitschätzung. [Experiments on the time sense used in direction-finding by birds.]. *Zeitschrift für Tierpsychologie*, *11*, 453-475. https://doi.org/10.1111/j.1439-0310.1954.tb02169.x

Holland, R., Filannino, C., & Gagliardo, A. (2013). A magnetic pulse does not affect homing pigeon navigation: a GPS tracking experiment. *Journal of Experimental Biology*, *216*(12), 2192-2200. https://doi.org/10.1242/jeb.083543

Holland, R. A. (2014). True navigation in birds: from quantum physics to global migration. *Journal of Zoology*, *293*(1), 1-15. https://doi.org/10.1111/jzo.12107

Hore, P. J., & Mouritsen, H. (2016). The radical-pair mechanism of magnetoreception. *Annual review of biophysics*, *45*, 299-344. https://doi.org/10.1146/annurev-biophys-032116-094545

Hough, G. E., & Bingman, V. P. (2004). Spatial response properties of homing pigeon hippocampal neurons: correlations with goal locations, movement between goals, and environmental context in a radial-arm arena. *Journal of Comparative Physiology A*, *190*(12), 1047-1062. https://doi.org/10.1007/s00359-004-0562-z

Ioalè, P. (1980). Further investigations on the homing behaviour of pigeons subjected to reverse wind direction at the loft. *Monitore Zoologico Italiano - Italian Journal of Zoology*, *14*(1-2), 77-87. https://doi.org/10.1080/00269786.1980.10736349

Ioalè, P., Nozzolini, M., & Papi, F. (1990). Homing pigeons do extract directional information from olfactory stimuli. *Behavioral Ecology and Sociobiology*, *26*(5), 301-305. https://doi.org/10.1007/BF00171094

Ioalè, P., Papi, F., Fiaschi, V., & Baldaccini, N. E. (1978). Pigeon navigation: Effects upon homing behaviour by reversing wind direction at the loft. *Journal of comparative physiology*, *128*(4), 285-295. https://doi.org/10.1007/BF00657603

Ising, G. (1946). The physical possibility of a biological sense of orientation based on the rotation of the earth. *Arkiv för matematik, astronomi och fysik*, *32A*, 1.

Jandačka, P., Burda, H., & Ščučka, J. (2022). Investigating the impact of weak geomagnetic fluctuations on pigeon races. *Journal of Comparative Physiology A*, *208*(1), 177-184. https://doi.org/10.1007/s00359-021-01534-x

Johnson, C. C. (1970). Triangulation Theory and Techniques. *NAVIGATION*, *17*(3), 308-324. https://doi.org/10.1002/j.2161-4296.1970.tb00054.x

Jouventin, P., & Weimerskirch, H. (1990). Satellite tracking of Wandering albatrosses. *Nature*, *343*(6260), 746-748. https://doi.org/10.1038/343746a0

Keeton, W. T. (1974). The Orientational and Navigational Basis of Homing in Birds. In D. S. Lehrman, J. S. Rosenblatt, R. A. Hinde, & E. Shaw (Eds.), *Advances in the Study of Behavior* (Vol. 5, pp. 47-132). Academic Press. https://doi.org/10.1016/S0065-3454(08)60020-0, ISBN: 0065-3454

Keeton, W. T., Larkin, T. S., & Windsor, D. M. (1974). Normal fluctuations in the earth's magnetic field influence pigeon orientation. *Journal of comparative physiology*, *95*(2), 95-103. https://doi.org/10.1007/BF00610108

Keith, S. A., & Bull, J. W. (2017). Animal culture impacts species' capacity to realise climate-driven range shifts. *Ecography*, *40*(2), 296-304. https://doi.org/10.1111/ecog.02481

Keller, B. A., Putman, N. F., Grubbs, R. D., Portnoy, D. S., & Murphy, T. P. (2021). Map-like use of Earth's magnetic field in sharks. *Current Biology*, *31*(13), 2881-2886.e2883. https://doi.org/10.1016/j.cub.2021.03.103

Kelly, D. M., Cheng, K., Balda, R., & Kamil, A. C. (2019). Effects of sun compass error on spatial search by Clark's nutcrackers. *Integrative Zoology*, *14*(2), 172-181. https://doi.org/10.1111/1749-4877.12302

Kishkinev, D., Chernetsov, N., & Mouritsen, H. (2010). A Double-Clock or Jetlag Mechanism is Unlikely to be Involved in Detection of East—West Displacements in a Long-Distance Avian Migrant. *The Auk*, *127*(4), 773-780. https://doi.org/10.1525/auk.2010.10032

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., & Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Current Biology*, *25*(19), R822-R824. https://doi.org/10.1016/j.cub.2015.08.012

Kishkinev, D., Packmor, F., Zechmeister, T., Winkler, H.-C., Chernetsov, N., Mouritsen, H., & Holland, R. A. (2021). Navigation by extrapolation of geomagnetic cues in a migratory songbird. *Current Biology*, *31*(7), 1563-1569.e1564. https://doi.org/10.1016/j.cub.2021.01.051

Kluijver, H. N. (1935). Ergebnisse eines Versuches über das Heimfindevermögen von Staren. *Ardea*, *24*(3-4), 227-239.

Kramer, G. (1951). Eine neue Methode zur Erforschung der Zugorientierung und die bisher damit erzielten Ergebnisse. In *Proceedings of the International Ornithological Congress* (pp. 269-280). International Ornithological Congress 1950, Uppsala. Almqvist & Wiksell, Stockholm, Sweden.

Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *Journal für Ornithologie*, *94*(3-4), 201-219. https://doi.org/10.1007/BF01922508

Kullberg, C., Lind, J., Fransson, T., Jakobsson, S., & Vallin, A. (2003). Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). *Proceedings of the Royal Society of London. Series B:*

*Biological Sciences*, *270*(1513), 373-378. https://doi.org/10.1098/rspb.2002.2273

Lack, D., & Lockley, R. M. (1938). Skokholm bird observatory homing Experiments 1. 1936-37. Puffins, Storm-Petrels and Manx Shearwaters. *British Birds*, *32*, 242-248.

Landreth, H. F., & Ferguson, D. E. (1968). The Sun Compass of Fowler's Toad, *Bufo woodhousei fowleri*. *Behaviour*, *30*(1), 27-43. https://doi.org/10.1163/156853968X00162

Lau, K.-K., Roberts, S., Biro, D., Freeman, R., Meade, J., & Guilford, T. (2006). An edge-detection approach to investigating pigeon navigation. *Journal of Theoretical Biology*, *239*(1), 71-78. https://doi.org/10.1016/j.jtbi.2005.07.013

Lednor, A. J., & Walcott, C. (1983). Homing pigeon navigation: The effects of in-flight exposure to a varying magnetic field. *Comparative Biochemistry and Physiology Part A: Physiology*, *76*(4), 665-671. https://doi.org/10.1016/0300-9629(83)90127-5

Lewis, D., Gathercole, P. W., & Hodson, F. R. (1974). Voyaging stars: aspects of Polynesian and Micronesian astronomy. *Philosophical Transactions of the Royal Society of London. Series A: Mathematical and Physical Sciences*, *276*(1257), 133-148. https://doi.org/10.1098/rsta.1974.0015

Lihoreau, M., Chittka, L., & Raine, N. E. (2010). Travel optimization by foraging bumblebees through readjustments of traplines after discovery of new feeding locations. *American Naturalist*, *176*(6), 744-757. https://doi.org/10.1086/657042

Linssen, H., van Loon, E. E., Shamoun-Baranes, J. Z., Nuijten, R. J. M., & Nolet, B. A. (2023). Migratory swans individually adjust their autumn migration and winter range to a warming climate. *Global change biology*, *29*(24), 6888-6899. https://doi.org/10.1111/gcb.16953

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W., & Hahn, S. (2012). Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, *3*(3), 603-612. https://doi.org/10.1111/j.2041-210X.2012.00185.x

Lohmann, K., Lohmann, C., Ehrhart, L., Bagley, D., & Swing, T. (2004). Geomagnetic Map Used in Sea-Turtle Navigation. *Nature*, *428*, 909-910. https://doi.org/10.1038/428909a

Lohmann, K. J., Cain, S. D., Dodge, S. A., & Lohmann, C. M. (2001). Regional magnetic fields as navigational markers for sea turtles. *Science*, *294*(5541), 364-366. https://doi.org/10.1126/science.106455

Lohmann, K. J., & Catherine, M. F. L. (1993). A Light-Independent Magnetic Compass in the Leatherback Sea Turtle. *Biological Bulletin*, *185*(1), 149-151. https://doi.org/10.2307/1542138

Lohmann, K. J., Goforth, K. M., Mackiewicz, A. G., Lim, D. S., & Lohmann, C. M. F. (2022). Magnetic maps in animal navigation. *Journal of Comparative Physiology A*, *208*(1), 41-67. https://doi.org/10.1007/s00359-021-01529-8

Lohmann, K. J., Luschi, P., & Hays, G. C. (2008). Goal navigation and island-finding in sea turtles. *Journal of Experimental Marine Biology and Ecology*, *356*(1), 83-95. https://doi.org/10.1016/j.jembe.2007.12.017

MacGregor, E. G., & Thorpe, W. H. (1948). Odour as a Basis for Orientated Movement in Ants. *Behaviour*, *1*(3/4), 267-296. https://doi.org/10.1163/156853948X00137

Major, F. G. (2014). The Longitude Problem. In *Quo Vadis: Evolution of Modern Navigation: The Rise of Quantum Techniques* (pp. 113-129). Springer New York, New York, NY, United States. https://doi.org/10.1007/978-1-4614-8672-5_6, ISBN: 978-1-4614-8672-5

Mann, R., Freeman, R., Osborne, M., Garnett, R., Armstrong, C., Meade, J., Biro, D., Guilford, T., & Roberts, S. (2011). Objectively identifying landmark use and predicting flight trajectories of the homing pigeon using Gaussian processes. *Journal of The Royal Society Interface*, *8*(55), 210-219. https://doi.org/10.1098/rsif.2010.0301

Massa, B., Ioalè, S. B. P., Lo Valvo, M., & Papi, F. (1991). Homing of Cory's shearwaters (*Calonectris diomedea*) carrying magnets. *Bollettino di zoologia*, *58*(3), 245-247. https://doi.org/10.1080/11250009109355760

Matthews, G. V. T. (1951a). The Experimental Investigation of Navigation in Homing Pigeons. *Journal of Experimental Biology*, *28*(4), 508-536. https://doi.org/10.1242/jeb.28.4.508

Matthews, G. V. T. (1951b). The Sensory Basis of Bird Navigation. *Journal of Navigation*, *4*(3), 260-275. https://doi.org/10.1017/S0373463300046051

Matthews, G. V. T. (1953a). Navigation in the Manx Shearwater. *Journal of Experimental Biology*, *30*(3), 370-396. https://doi.org/10.1242/jeb.30.3.370

Matthews, G. V. T. (1953b). Sun Navigation in Homing Pigeons. *Journal of Experimental Biology*, *30*(2), 243-267. https://doi.org/10.1242/jeb.30.2.243

Matthews, G. V. T. (1964). Individual Experience as a Factor in the Navigation of Manx Shearwaters. *The Auk*, *81*(2), 132-146. https://doi.org/10.2307/4082764

May, W. E. (1973). *A History of Marine Navigation.* G. T. Foulis & Co. Ltd., Henley-on-Thames, Oxfordshire. ISBN: 0-85429-143-1

McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M.-B. (2006). Path integration and the neural basis of the 'cognitive map'. *Nature Reviews Neuroscience*, *7*(8), 663-678. https://doi.org/10.1038/nrn1932

Meade, J., Biro, D., & Guilford, T. (2005). Homing pigeons develop local route stereotypy. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *272*(1558), 17-23. https://doi.org/10.1098/rspb.2004.2873

Menzel, R., Geiger, K., Joerges, J., Müller, U. L. I., & Chittka, L. (1998). Bees travel novel homeward routes by integrating separately acquired vector memories. *Animal Behaviour*, *55*(1), 139-152. https://doi.org/10.1006/anbe.1997.0574

Merkel, F. W., & Wiltschko, W. (1965). Magnetismus und richtungsfinden zugunruhiger rotkehlchen (*Erithacus rubecula*). *Vogelwarte*, *23*(1), 71-77.

Mistlberger, R. E., & Rusak, B. (2021). Biological Rhythms and Behavior. In J. J. Bolhuis, L.-A. Giraldeau, & J. A. Hogan (Eds.), *The Behavior of Animals: Mechanisms, Function, and Evolution* (2nd ed., pp. 78-110). John Wiley & Sons, Hoboken, NJ, United States. https://doi.org/10.1002/9781119109556.ch4, ISBN: 9781119109518

Mittelstaedt, M. L., & Mittelstaedt, H. (1980). Homing by path integration in a mammal. *Naturwissenschaften*, *67*(11), 566-567. https://doi.org/10.1007/BF00450672

Mora, C. V., Davison, M., Wild, J. M., & Walker, M. M. (2004). Magnetoreception and its trigeminal mediation in the homing pigeon. *Nature*, *432*(7016), 508-511. https://doi.org/10.1038/nature03077

Mora, C. V., Ross, J. D., Gorsevski, P. V., Chowdhury, B., & Bingman, V. P. (2012). Evidence for discrete landmark use by pigeons during homing. *Journal of Experimental Biology*, *215*(19), 3379-3387. https://doi.org/10.1242/jeb.071225

Morford, J., Lewin, P., Jaggers, P., Wynn, J., Guilford, T., & Padget, O. (2025). Almost there: Learning to navigate approximately with a grid map. *Behavioural Processes*, *231*, 105245. https://doi.org/10.1016/j.beproc.2025.105245

Morford, J., Wynn, J., Lewin, P., Jaggers, P., Lancaster-Reeves, L., Sibeaux, A., Padget, O., & Guilford, T. (2025). Map and compass navigation: the mechanism and ontogeny of animal maps. *Animal Behaviour*, *227*, 123272. https://doi.org/10.1016/j.anbehav.2025.123272

Mouritsen, H., Atema, J., Kingsford, M. J., & Gerlach, G. (2013). Sun Compass Orientation Helps Coral Reef Fish Larvae Return to Their Natal Reef. *PLoS One*, *8*(6), e66039. https://doi.org/10.1371/journal.pone.0066039

Mouritsen, H., Huyvaert, K. P., Frost, B. J., & Anderson, D. J. (2003). Waved albatrosses can navigate with strong magnets attached to their head. *Journal of Experimental Biology*, *206*(22), 4155-4166. https://doi.org/10.1242/jeb.00650

Muheim, R. (2011). Behavioural and physiological mechanisms of polarized light sensitivity in birds. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *366*(1565), 763-771. https://doi.org/10.1098/rstb.2010.0196

Muheim, R., Moore, F. R., & Phillips, J. B. (2006). Calibration of magnetic and celestial compass cues in migratory birds - a review of cue-conflict experiments. *Journal of Experimental Biology*, *209*(1), 2-17. https://doi.org/10.1242/jeb.01960

Müller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences*, *85*(14), 5287-5290. https://doi.org/10.1073/pnas.85.14.5287

Müller, M., & Wehner, R. (2010). Path Integration Provides a Scaffold for Landmark Learning in Desert Ants. *Current Biology*, *20*(15), 1368-1371. https://doi.org/10.1016/j.cub.2010.06.035

Naisbett-Jones, L. C., Putman, N. F., Scanlan, M. M., Noakes, D. L. G., & Lohmann, K. J. (2020). Magnetoreception in fishes: the effect of magnetic pulses on orientation of juvenile Pacific salmon. *Journal of Experimental Biology*, *223*(10). https://doi.org/10.1242/jeb.222091

Naisbett-Jones, L. C., Putman, N. F., Stephenson, J. F., Ladak, S., & Young, K. A. (2017). A Magnetic Map Leads Juvenile European Eels to the Gulf Stream. *Current Biology*, *27*(8), 1236-1240. https://doi.org/10.1016/j.cub.2017.03.015

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059. https://doi.org/10.1073/pnas.0800375105

Newton, K. C., & Kajiura, S. M. (2020a). The yellow stingray (*Urobatis jamaicensis*) can discriminate the geomagnetic cues necessary for a bicoordinate magnetic map. *Marine Biology*, *167*(10), 151. https://doi.org/10.1007/s00227-020-03763-1

Newton, K. C., & Kajiura, S. M. (2020b). The yellow stingray (*Urobatis jamaicensis*) can use magnetic field polarity to orient in space and solve a maze. *Marine Biology*, *167*(3), 36. https://doi.org/10.1007/s00227-019-3643-9

Nimpf, S., Nordmann, G. C., Kagerbauer, D., Malkemper, E. P., Landler, L., Papadaki-Anastasopoulou, A., Ushakova, L., Wenninger-Weinzierl, A., Novatchkova, M., Vincent, P., Lendl, T., Colombini, M., Mason, M. J., & Keays, D. A. (2019). A Putative Mechanism for Magnetoreception by Electromagnetic Induction in the Pigeon Inner Ear. *Current Biology*, *29*(23), 4052-4059.e4054. https://doi.org/10.1016/j.cub.2019.09.048

Nordmann, G. C., Hochstoeger, T., & Keays, D. A. (2017). Magnetoreception—A sense without a receptor. *PLoS biology*, *15*(10), e2003234. https://doi.org/10.1371/journal.pbio.2003234

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Clarendon Press, Oxford, United Kingdom. ISBN: 0198572069

Padget, O., Bond, S. L., Kavelaars, M. M., van Loon, E., Bolton, M., Fayet, A. L., Syposz, M., Roberts, S., & Guilford, T. (2018). *In situ* clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology*, *28*(2), 275-279.e272. https://doi.org/10.1016/j.cub.2017.11.062

Padget, O., Dell'Ariccia, G., Gagliardo, A., González-Solís, J., & Guilford, T. (2017). Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. *Scientific Reports*, *7*(1), 9668. https://doi.org/10.1038/s41598-017-09738-5

Padget, O., Gillies, N., Syposz, M., Lockley, E., & Guilford, T. (2022). Shearwaters sometimes take long homing detours when denied natural outward journey

information. *Biology Letters*, *18*(2), 20210503. https://doi.org/10.1098/rsbl.2021.0503

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M., & Guilford, T. (2019). Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the National Academy of Sciences*, *116*(43), 21629-21633. https://doi.org/10.1073/pnas.1903829116

Pakhomov, A., & Chernetsov, N. (2020). A hierarchy of compass systems in migratory birds. *Biological Communications*, *65*(3), 262–276. https://doi.org/10.21638/spbu03.2020.306

Papi, F., & Casini, G. (1990). Pigeons with ablated pyriform cortex home from familiar but not from unfamiliar sites. *Proceedings of the National Academy of Sciences*, *87*(10), 3783-3787. https://doi.org/10.1073/pnas.87.10.3783

Papi, F., Fiore, L., Fiaschi, V., & Benvenuti, S. (1971). The influence of olfactory nerve section on the homing capacity of carrier pigeons. *Monitore Zoologico Italiano - Italian Journal of Zoology*, *5*(4), 265-267. https://doi.org/10.1080/00269786.1971.10736180

Papi, F., Fiore, L., Fiaschi, V., & Benvenuti, S. (1972). Olfaction and homing in pigeons. *Monitore Zoologico Italiano - Italian Journal of Zoology*, *6*(1), 85-95. https://doi.org/10.1080/00269786.1972.10736187

Papi, F., Ioalè, P., Fiaschi, V., Benvenuti, S., & Baldaccini, N. E. (1974). Olfactory navigation of pigeons: The effect of treatment with odorous air currents. *Journal of comparative physiology*, *94*(3), 187-193. https://doi.org/10.1007/BF00611866

Pardi, L., & Grassi, M. (1955). Experimental modification of direction-finding in *Talitrus saltator* (Montagu) and *Talorchestia deshayesei* (Aud.) (crustacea-amphipoda). *Experientia*, *11*(5), 202-205. https://doi.org/10.1007/BF02161321

Payne, H. L., Lynch, G. F., & Aronov, D. (2021). Neural representations of space in the hippocampus of a food-caching bird. *Science*, *373*(6552), 343-348. https://doi.org/10.1126/science.abg2009

Penney, R. L., & Emlen, J. (1967). Further experiments on distance navigation in the Adelie penguin *Pygoscelzs Adelzae*. *Ibis*, *109*(1), 99-109. https://doi.org/10.1111/j.1474-919X.1967.tb00006.x

Perdeck, A. C. (1958). Two Types of Orientation in Migrating Starlings, *Sturnus vulgaris* L., and Chaffinches, *Fringilla coelebs* L., as Revealed by Displacement Experiments. *Ardea*, *55*(1–2), 1-37. https://doi.org/10.5253/arde.v1i2.p1

Perez, S. M., Taylor, O. R., & Jander, R. (1997). A sun compass in monarch butterflies. *Nature*, *387*(6628), 29-29. https://doi.org/10.1038/387029a0

Philippides, A., Baddeley, B., Cheng, K., & Graham, P. (2011). How might ants use panoramic views for route navigation? *Journal of Experimental Biology*, *214*(3), 445-451. https://doi.org/10.1242/jeb.046755

Phillips, J. B. (1986). Two magnetoreception pathways in a migratory salamander. *Science*, *233*(4765), 765-767. https://doi.org/10.1126/science.3738508

Phillips, J. B., & Borland, S. C. (1992). Behavioural evidence for use of a light-dependent magnetoreception mechanism by a vertebrate. *Nature*, *359*(6391), 142-144. https://doi.org/10.1038/359142a0

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V., & Briggs, D. R. (2004). Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series*, *266*, 265-272. https://doi.org/10.3354/meps

Pogo, A. (1935). Gemma Frisius, His Method of Determining Differences of Longitude by Transporting Timepieces (1530), and His Treatise on Triangulation (1533). *Isis*, *22*(2), 469-506. https://doi.org/10.1086/346920

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., & Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific Reports*, *5*(1), 1-10. https://doi.org/10.1038/srep16486

Putman, N. F., Lohmann, K. J., Putman, E. M., Quinn, T. P., Klimley, A. P., & Noakes, D. L. (2013). Evidence for geomagnetic imprinting as a homing mechanism in Pacific salmon. *Curr Biol*, *23*(4), 312-316. https://doi.org/10.1016/j.cub.2012.12.041

Putman, N. F., Scanlan, M. M., Billman, E. J., O'Neil, J. P., Couture, R. B., Quinn, T. P., Lohmann, K. J., & Noakes, D. L. G. (2014). An Inherited Magnetic Map Guides Ocean Navigation in Juvenile Pacific Salmon. *Current Biology*, *24*(4), 446-450. https://doi.org/10.1016/j.cub.2014.01.017

Putman, N. F., Williams, C. R., Gallagher, E. P., & Dittman, A. H. (2020). A sense of place: pink salmon use a magnetic map for orientation. *The Journal of Experimental Biology*, *223*(4), jeb218735. https://doi.org/10.1242/jeb.218735

Ranvaud, R. D. P. K. C., Schmidt-Koenig, K., Kiepenheuer, J., Gasparotto, O. C., & Britto, L. R. G. d. (1989). Compass mechanisms of homing pigeons at the magnetic equator. In H. Ouellet (Ed.), *Acta XIX Congressus Internationalis Ornithologici* (pp. 297-304). 19th International Ornithological Congress 1988, National Museum of Natural Sciences. University of Ottawa Press, Ottawa, Canada.

Reppert, S. M., & de Roode, J. C. (2018). Demystifying Monarch Butterfly Migration. *Current Biology*, *28*(17), R1009-R1022. https://doi.org/10.1016/j.cub.2018.02.067

Ritz, T., Adem, S., & Schulten, K. (2000). A Model for Photoreceptor-Based Magnetoreception in Birds. *Biophysical Journal*, *78*(2), 707-718. https://doi.org/10.1016/S0006-3495(00)76629-X

Rossier, J., Haeberli, C., & Schenk, F. (2000). Auditory cues support place navigation in rats when associated with a visual cue. *Behavioural Brain Research*, *117*(1), 209-214. https://doi.org/10.1016/S0166-4328(00)00293-X

Savelli, F., & Knierim, J. J. (2019). Origin and role of path integration in the cognitive representations of the hippocampus: computational insights into open

questions. *Journal of Experimental Biology*, *222*(1). https://doi.org/10.1242/jeb.188912

Schiffner, I., & Wiltschko, R. (2011). Temporal fluctuations of the geomagnetic field affect pigeons' entire homing flight. *Journal of Comparative Physiology A*, *197*(7), 765-772. https://doi.org/10.1007/s00359-011-0640-y

Schmidt-Koenig, K. (1961). Die Sonne als Kompaß im Heim-Orientierungssystem der Brieftauben. *Zeitschrift für Tierpsychologie*, *18*(2), 221-241. https://doi.org/10.1111/j.1439-0310.1961.tb00229.x

Schmidt-Koenig, K. (1969). Weitere Versuche, durch Verstellung der inneren Uhr in den Heimkehrprozess der Brieftaube einzugreifen. *Zoologischer Anzeiger Supplement*, *33*, 200-205.

Schmidt-Koenig, K. (1972). New experiments on the effect of clock shifts on homing in pigeons. In *Animal Orientation and Navigation* (pp. 275-282). Animal Orientation and Navigation 1972, NASA, Washington, United States.

Schmidt-Koenig, K. (1990). The sun compass. *Experientia*, *46*, 336-342. https://doi.org/10.1007/BF01952166

Schmidt-Koenig, K., Ranvaud, R., Ganzhorn, J. U., & Gasparotto, O. C. (1991). Retardation of homing pigeons' ephemerides? *The Science of Nature*, *78*(7), 330-333. https://doi.org/10.1007/BF01221424

Schmidt-Koenig, K. (1958). Experimentelle Einflußnahme auf die 24-Stunden-Periodik bei Brieftauben und deren Auswirkungen unter besonderer Berücksichtigung des Heimfindevermögens. *Zeitschrift für Tierpsychologie*, *15*(3), 301-331. https://doi.org/10.1111/j.1439-0310.1958.tb00568.x

Seyfarth, E. A., & Barth, F. G. (1972). Compound slit sense organs on the spider leg: Mechanoreceptors involved in kinesthetic orientation. *Journal of comparative physiology*, *78*(2), 176-191. https://doi.org/10.1007/BF00693611

Shaffer, S. A., Tremblay, Y., Awkerman, J. A., Henry, R. W., Teo, S. L. H., Anderson, D. J., Croll, D. A., Block, B. A., & Costa, D. P. (2005). Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology*, *147*(4), 833-843. https://doi.org/10.1007/s00227-005-1631-8

Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*, *14*(11), 477-481. https://doi.org/10.1016/j.tics.2010.07.002

Shiomi, K., Yoda, K., Katsumata, N., & Sato, K. (2012). Temporal tuning of homeward flights in seabirds. *Animal Behaviour*, *83*(2), 355-359. https://doi.org/10.1016/j.anbehav.2011.11.010

Shu-hua, L. (1954). Origine de la Boussole II. Aimant et Boussole. *Isis*, *45*(2), 175-196. https://doi.org/10.1086/348315

Sibeaux, A., Newport, C., Green, J. P., Karlsson, C., Engelmann, J., & Burt de Perera, T. (2024). Taking a shortcut: what mechanisms do fish use? *Communications Biology*, *7*(1), 578. https://doi.org/10.1038/s42003-024-06179-5

Siddiqi-Davies, K., Wynn, J., Padget, O., Lewin, P., Gillies, N., Morford, J., Fisher-Reeves, L., Jaggers, P., Morgan, G., Danielsen, J., Kirk, H., Fayet, A., Shoji, A., Bond, S., Syposz, M., Maurice, L., Freeman, R., Dean, B., Boyle, D., & Guilford, T. (2024). Behavioural responses of a trans-hemispheric migrant to climate oscillation. *Proceedings of the Royal Society B: Biological Sciences*, *291*(2033), 20241944. https://doi.org/10.1098/rspb.2024.1944

Sjöberg, S., & Muheim, R. (2016). A New View on an Old Debate: Type of Cue-Conflict Manipulation and Availability of Stars Can Explain the Discrepancies between Cue-Calibration Experiments with Migratory Songbirds. *Frontiers in Behavioral Neuroscience*, *10*. https://doi.org/10.3389/fnbeh.2016.00029

Solstad, T., Boccara, C. N., Kropff, E., Moser, M.-B., & Moser, E. I. (2008). Representation of Geometric Borders in the Entorhinal Cortex. *Science*, *322*(5909), 1865-1868. https://doi.org/10.1126/science.1166466

Sølver, C. V. (1953). The Discovery of an Early Bearing-Dial. *Journal of Navigation*, *6*(3), 294-296. https://doi.org/10.1017/S0373463300027314

Steiner, I., Bürgi, C., Werffeli, S., Dell'Omo, G., Valenti, P., Tröster, G., Wolfer, D. P., & Lipp, H.-P. (2000). A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiology & Behavior*, *71*(5), 589-596. https://doi.org/10.1016/S0031-9384(00)00409-1

Sulzman, F. M., Ellman, D., Fuller, C. A., Moore-Ede, M. C., & Wassmer, G. (1984). *Neurospora* Circadian Rhythms in Space: a Reexamination of the Endogenous-Exogenous Question. *Science*, *225*(4658), 232-234. https://doi.org/10.1126/science.11540800

Svensson, G. P., Strandh, M., Löfstedt, C., Hansson, L.-A., & Akesson, S. (2014). Movements in the olfactory landscape. In *Animal movement across scales* (pp. 195). Oxford University Press, Oxford, United Kingdom. https://doi.org/10.1093/acprof:oso/9780199677184.003.0011, ISBN: 0199677182

Takahashi, S., Hombe, T., Matsumoto, S., Ide, K., & Yoda, K. (2022). Head direction cells in a migratory bird prefer north. *Science Advances*, *8*(5), eabl6848. https://doi.org/10.1126/sciadv.abl6848

Taube, J. S., Muller, R. U., & Ranck, J. B., Jr. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *J Neurosci*, *10*(2), 420-435. https://doi.org/10.1523/jneurosci.10-02-00420.1990

Tello-Ramos, M. C., Hurly, T. A., & Healy, S. D. (2015). Traplining in hummingbirds: flying short-distance sequences among several locations. *Behavioral Ecology*, *26*(3), 812-819. https://doi.org/10.1093/beheco/arv014

Thomson, J. D., Slatkin, M., & Thomson, B. A. (1997). Trapline foraging by bumble bees: II. Definition and detection from sequence data. *Behavioral Ecology*, *8*(2), 199-210. https://doi.org/10.1093/beheco/8.2.199

Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., & Nathan, R. (2020). Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. *Science*, *369*(6500), 188-193. https://doi.org/10.1126/science.aax6904

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*(4), 189-208. https://doi.org/10.1037/h0061626

Treiber, C. D., Salzer, M. C., Riegler, J., Edelman, N., Sugar, C., Breuss, M., Pichler, P., Cadiou, H., Saunders, M., Lythgoe, M., Shaw, J., & Keays, D. A. (2012). Clusters of iron-rich cells in the upper beak of pigeons are macrophages not magnetosensitive neurons. *Nature*, *484*(7394), 367-370. https://doi.org/10.1038/nature11046

Tsoar, A., Nathan, R., Bartan, Y., Vyssotski, A., Dell'Omo, G., & Ulanovsky, N. (2011). Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences*, *108*(37), E718-E724. https://doi.org/10.1073/pnas.1107365108

Ugolini, A., Melis, C., Innocenti, R., Tiribilli, B., & Castellini, C. (1999). Moon and sun compasses in sandhoppers rely on two separate chronometric mechanisms. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1420), 749-752. https://doi.org/10.1098/rspb.1999.0700

Verhoeven, M. A., Loonstra, A. H. J., Hooijmeijer, J. C. E. W., Masero, J. A., Piersma, T., & Senner, N. R. (2018). Generational shift in spring staging site use by a long-distance migratory bird. *Biology Letters*, *14*(2), 20170663. https://doi.org/10.1098/rsbl.2017.0663

von Hünerbein, K., Hamann, H. J., Rüter, E., & Wiltschko, W. (2000). A GPS-based system for recording the flight paths of birds. *Naturwissenschaften*, *87*(6), 278-279. https://doi.org/10.1007/s001140050721

von Saint Paul, U. (1982). Do Geese Use Path Integration for Walking Home? In F. Papi & H. G. Wallraff (Eds.), *Avian Navigation* (pp. 298-307). International Symposium on Avian Navigation 1981, Pisa, Italy. Springer Berlin Heidelberg, Berlin, Germany. https://doi.org/10.1007/978-3-642-68616-0_30

Walcott, C. (1972). The navigation of homing pigeons: Do they use sun navigation? In *Animal Orientation and Navigation* (pp. 283-292). Animal Orientation and Navigation 1972, NASA, Washington, United States.

Walcott, C., Gould, J. L., & Kirschvink, J. L. (1979). Pigeons Have Magnets. *Science*, *205*(4410), 1027-1029. https://doi.org/10.1126/science.472725

Walcott, C., & Michener, M. C. (1971). Sun navigation in homing pigeons—attempts to shift sun coordinates. *Journal of Experimental Biology*, *54*(2), 291-316. https://doi.org/10.1242/jeb.54.2.291

Walcott, C., & Schmidt-Koenig, K. (1973). The Effect on Pigeon Homing of Anesthesia during Displacement. *The Auk*, *90*(2), 281-286. https://doi.org/10.1093/auk/90.2.281

Wallraff, H. G. (1965). Über das Heimfindevermögen von Brieftauben mit durchtrennten Bogengängen. *Zeitschrift für vergleichende Physiologie*, *50*(3), 313-330. https://doi.org/10.1007/BF00339483

Wallraff, H. G. (2013). Ratios among atmospheric trace gases together with winds imply exploitable information for bird navigation: a model elucidating experimental results. *Biogeosciences*, *10*(11), 6929-6943. https://doi.org/10.5194/bg-10-6929-2013

Wallraff, H. G., & Foà, A. (1981). Pigeon navigation: Charcoal filter removes relevant information from environmental air. *Behavioral Ecology and Sociobiology*, *9*(1), 67-77. https://doi.org/10.1007/BF00299856

Wallraff, H. G., Papi, F., Ioalè, P., & Benvenuti, S. (1986). Magnetic fields affect pigeon navigation only while the birds can smell atmospheric odors. *Naturwissenschaften*, *73*(4), 215-217. https://doi.org/10.1007/BF00417729

Wang, R. F. (2016). Building a cognitive map by assembling multiple path integration systems. *Psychonomic Bulletin & Review*, *23*(3), 692-702. https://doi.org/10.3758/s13423-015-0952-y

Warrant, E., Frost, B., Green, K., Mouritsen, H., Dreyer, D., Adden, A., Brauburger, K., & Heinze, S. (2016). The Australian Bogong Moth *Agrotis infusa*: A Long-Distance Nocturnal Navigator. *Frontiers in Behavioral Neuroscience*, *10*. https://doi.org/10.3389/fnbeh.2016.00077

Wehner, R. (1984). Astronavigation in insects. *Annual review of entomology*, *29*(1), 277-298. https://doi.org/10.1146/annurev.en.29.010184.001425

Wehner, R., & Srinivasan, M. V. (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour*. Oxford University Press, Oxford, United Kingdom. https://doi.org/10.1093/acprof:oso/9780198515241.003.0001, ISBN: 0198515243

Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993). Foraging Strategy of Wandering Albatrosses Through The Breeding Season: A Study Using Satellite Telemetry. *The Auk*, *110*(2), 325-342. https://doi.org/10.1093/auk/110.2.325

Werkhoven, P., van Erp, J. B. F., & Philippi, T. G. (2014). Navigating virtual mazes: The benefits of audiovisual landmarks. *Displays*, *35*(3), 110-117. https://doi.org/10.1016/j.displa.2014.04.001

Whittington, J. C. R., McCaffary, D., Bakermans, J. J. W., & Behrens, T. E. J. (2022). How to build a cognitive map. *Nature Neuroscience*, *25*(10), 1257-1272. https://doi.org/10.1038/s41593-022-01153-y

Wiener, J., Shettleworth, S., Bingman, V., P., Cheng, K., Healy, S., Jacobs, L. F., Jeffery, K., J., Mallot, H., A., Menzel, R., Newcombe, N., S., Julia, F., & Randolf, M. (2011). Animal Navigation: A Synthesis. In *Animal Thinking* (pp. 51-76). The MIT Press, Cambridge, MA, United States. https://doi.org/10.7551/mitpress/9187.003.0008, ISBN: 9780262016636

Wikelski, M., Arriero, E., Gagliardo, A., Holland, R. A., Huttunen, M. J., Juvaste, R., Mueller, I., Tertitski, G., Thorup, K., Wild, M., Alanko, M., Bairlein, F., Cherenkov, A., Cameron, A., Flatz, R., Hannila, J., Hüppop, O., Kangasniemi, M., Kranstauber, B.,...Wistbacka, R. (2015). True navigation in migrating gulls requires intact olfactory nerves. *Scientific Reports*, *5*(1), 17061. https://doi.org/10.1038/srep17061

Wilkinson, D. H. (1949). Some physical principles of bird orientation. *Proceedings of the Linnean Society of London*, *160*(2), 94-99. https://doi.org/10.1111/j.1095-8312.1949.tb00518.x

Willemoes, M., Blas, J., Wikelski, M., & Thorup, K. (2015). Flexible navigation response in common cuckoos Cuculus canorus displaced experimentally during migration. *Scientific Reports*, *5*(1), 16402. https://doi.org/10.1038/srep16402

Wiltschko, R., Kumpfmüller, R., Muth, R., & Wiltschko, W. (1994). Pigeon homing: the effect of a clock-shift is often smaller than predicted. *Behavioral Ecology and Sociobiology*, *35*, 63-73. https://doi.org/10.1007/BF00167061

Wiltschko, R., Schiffner, I., & Wiltschko, W. (2009). A strong magnetic anomaly affects pigeon navigation. *Journal of Experimental Biology*, *212*(18), 2983-2990. https://doi.org/10.1242/jeb.032722

Wiltschko, R., Walker, M., & Wiltschko, W. (2000). Sun-Compass Orientation in Homing Pigeons: Compensation for Different Rates of Change in Azimuth? *Journal of Experimental Biology*, *203*(5), 889-894. https://doi.org/10.1242/jeb.203.5.889

Wiltschko, R., & Wiltschko, W. (1981). The development of sun compass orientation in young homing pigeons. *Behavioral Ecology and Sociobiology*, *9*(2), 135-141. https://doi.org/10.1007/BF00293584

Wiltschko, R., & Wiltschko, W. (2003). Mechanisms of orientation and navigation in migratory birds. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian migration* (pp. 433-456). Springer, Berlin, Germany and New York, United States. ISBN: 3540434089

Wiltschko, R., & Wiltschko, W. (2013). The magnetite-based receptors in the beak of birds and their role in avian navigation. *Journal of Comparative Physiology A*, *199*(2), 89-98. https://doi.org/10.1007/s00359-012-0769-3

Wiltschko, R., & Wiltschko, W. (2019). Magnetoreception in birds. *Journal of The Royal Society Interface*, *16*(158), 20190295. https://doi.org/10.1098/rsif.2019.0295

Wiltschko, W., & Balda, R. P. (1989). Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). *Journal of Comparative Physiology A*, *164*(6), 717-721. https://doi.org/10.1007/BF00616744

Wiltschko, W., & Wiltschko, R. (1972). Magnetic compass of European robins. *Science*, *176*(4030), 62-64. https://doi.org/10.1126/science.176.4030.62

Wiltschko, W., & Wiltschko, R. (1992). Migratory Orientation: Magnetic Compass Orientation of Garden Warblers (*Sylvia borin*) after a Simulated Crossing of the Magnetic Equator. *Ethology*, *91*(1), 70-74. https://doi.org/10.1111/j.1439-0310.1992.tb00851.x

Wiltschko, W., Wiltschko, R., & Keeton, W. T. (1976). Effects of a “permanent” clock-shift on the orientation of young homing pigeons. *Behavioral Ecology and Sociobiology*, *1*(3), 229-243. https://doi.org/10.1007/BF00300066

Wrensford, K. C., Angert, A. L., & Gaynor, K. M. (2025). Linking individual animal behavior to species range shifts under climate change. *Trends in Ecology & Evolution*, *40*(8), 805-817. https://doi.org/10.1016/j.tree.2025.06.002

Wynn, J., Padget, O., Mouritsen, H., Fayet, A. L., Kobylkov, D., Siddiqi-Davies, K., Syposz, M., Trapp, S., Gillies, N., & Guilford, T. (2021). *Twilight cue manipulation suggests a pelagic seabird uses a magnetic compass to calibrate its sun compass.* [Doctoral Thesis Chapter, University of Oxford]. Oxford, United Kingdom.

Wynn, J., Padget, O., Mouritsen, H., Morford, J., Jaggers, P., & Guilford, T. (2022). Magnetic stop signs signal a European songbird’s arrival at the breeding site following migration. *Science*, *375*(6579), 446-449. https://doi.org/10.1126/science.abj4210

Wynn, J., Padget, O., Mouritsen, H., Perrins, C., & Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology*, *30*(14), 2869-2873.e2862. https://doi.org/10.1016/j.cub.2020.05.039

Yeagley, H. L. (1951). A Preliminary Study of a Physical Basis of Bird Navigation. Part II. *Journal of Applied Physics*, *22*(6), 746-760. https://doi.org/10.1063/1.1700043

Yeagley, H. L., & Whitmore, F. C. (1947). A Preliminary Study of a Physical Basis of Bird Navigation. *Journal of Applied Physics*, *18*(12), 1035-1063. https://doi.org/10.1063/1.1697587

Yoda, K., Okumura, M., Suzuki, H., Matsumoto, S., Koyama, S., & Yamamoto, M. (2021). Annual variations in the migration routes and survival of pelagic seabirds over mountain ranges. *Ecology*, *102*(6), 1-4. https://doi.org/10.1002/ecy.3297

Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M., & Yamamoto, M. (2017). Compass orientation drives naïve pelagic seabirds to cross mountain ranges. *Current Biology*, *27*(21), R1152-R1153. https://doi.org/10.1016/j.cub.2017.09.009

Zannoni, N., Wikelski, M., Gagliardo, A., Raza, A., Kramer, S., Seghetti, C., Wang, N., Edtbauer, A., & Williams, J. (2020). Identifying volatile organic compounds used for olfactory navigation by homing pigeons. *Scientific Reports*, *10*(1), 15879. https://doi.org/10.1038/s41598-020-72525-2

Zeil, J. (1998). Homing in fiddler crabs (*Uca lactea annulipes* and *Uca vomeris*: Ocypodidae). *Journal of Comparative Physiology A*, *183*(3), 367-377. https://doi.org/10.1007/s003590050263

Zimmerman, P. H., Pope, S. J., Guilford, T., & Nicol, C. J. (2009). Involvement of the sun and the magnetic compass of domestic fowl in its spatial orientation. *Applied Animal Behaviour Science*, *116*(2-4), 204-210. https://doi.org/10.1016/j.applanim.2008.09.006

*"Vague theories of 'space sense' and telepathy need not concern us here."*

G. V. T. Matthews, *The Experimental Investigation of Navigation in Homing Pigeons* (1951)

# 2

# Jet-lagged birds: longitudinal flights cause clock-shift and sun compass error

With contributions from Wynn, J., Morford, J., Padget, O., Lancaster-Reeves, L., Siddiqi-Davies, K., Bond, S., Dean, B., Fayet, A. L., Freeman, R., Gillies, N., Harris, S. M., Jaggers, P., Kirk, H., Maurice, L., Shoji, A., Syposz, M. and Guilford, T.

## Contents

**2.1** Abstract ..... 60

**2.2** Introduction ..... 61

**2.3** Materials and Methods ..... 64

**2.4** Results ..... 72

**2.5** Discussion ..... 77

**2.6** Appendix ..... 80

*"Personally, I find it hard to believe that a bird has a sufficiently accurate way of telling the time."*

Mr R. F. Hansford in reply to G. V. T. Matthews at a meeting of the Royal Geographical Society held on 5th January 1951.

## 2.1 Abstract

Many animals use the sun compass to guide their movement, sometimes over thousands of kilometres. Consistent use of the sun compass relies on the endogenous clock to track the sun's arc, yet animals travelling east-west might experience mismatches between their internal clock and local time (clock-shift). Using GPS, we reveal that Manx shearwaters (*Puffinus puffinus*) experience such shifts during homing flights, generating predictable errors in sun compass orientation. Use of the sun compass persists even when shearwaters have access to compass-independent cues during coast-following. Our findings provide a new avenue for chronobiology research in the wild, suggest that rapid longitudinal movements may impact other processes governed by the endogenous clock, and that conserved chronobiological mechanisms impose remarkable constraints on navigation.

## 2.2 Introduction

Compass cues are central to navigation, allowing animals to determine the geographic direction of their heading during movements ranging from metres to thousands of kilometres. Their use is ubiquitous across animal taxa (Hasler et al., 1958; Lohmann & Lohmann, 1993; Lohmann et al., 1995; Marhold et al., 1997; Newcomer et al., 1974; Schmidt-Koenig, 1990; von Frisch, 1974; Willows, 1999) and a wide array of navigational contexts (Biro et al., 2007; Hasler et al., 1958; Helbig, 1996; Lindauer, 1960; Merlin et al., 2009; Müller & Wehner, 1988; Padget et al., 2018; Wiltschko & Balda, 1989), from relatively simple vector navigation to flexible map-and-compass navigation (Bingman & Cheng, 2005; Kramer, 1953). Animals use three main sources of compass information: the geomagnetic field, polar stars and the azimuth (horizontal) angle of the sun (Emlen, 1967, 1975; Schmidt-Koenig, 1960; Wiltschko & Wiltschko, 1972). To use the sun as a consistent compass cue, animals must adjust their heading relative to the sun as it moves across the sky over the course of day. This 'time-compensation' is controlled directly by an endogenous clock (Hoffmann, 1954; Mistlberger & Rusak, 2021) which is calibrated to local time using external cues, most notably dawn and dusk (Hirschie Johnson et al., 2003). Consequently, researchers can use artificial lights to shift the experienced light-dark cycle and induce discrepancies between an animal's endogenous clock and local solar time (Hoffmann, 1954; Schmidt-Koenig, 1960). After this 'clock-shifting', animals using a sun compass show predictable deflections away from their intended trajectory due to error in time-compensation (Schmidt-Koenig, 1960). Using this approach, sun compass orientation has been investigated thoroughly in homing pigeons (*Columba livia*), the main model of avian navigation (Schmidt-Koenig, 1990), but also demonstrated in a wide variety of avian and non-avian taxa (Duff et al., 1998; Fluharty et al., 1976; Kelly et al., 2019; Merlin et al., 2009; Müller & Wehner, 1988; Pardi, 1960; von Frisch, 1974; Wiltschko

& Balda, 1989; Zimmerman et al., 2009), including in wild Manx shearwaters homing after displacement (Padget et al., 2018).

Although use of the sun compass is widespread, our understanding of how the sun compass is integrated into wider navigational systems is rather limited outside Hymenoptera (Wehner, 1984). In homing pigeons, the sun compass is used as part of a map-and-compass strategy to facilitate homing from novel release sites (Schmidt-Koenig, 1990). However, reliance on the sun compass appears reduced at familiar sites (Gagliardo et al., 2005; Wiltschko et al., 1994). This has been attributed to learning of compass-independent pilotage routes (Biro et al., 2004, 2006; Meade et al., 2005). Nonetheless, small clock-shift effects persist even when pigeons are following highly familiar routes (Biro et al., 2007). This implies either that pigeons are using a landmark-based map-and-compass system from familiar sites or that they integrate some residual information from their large-scale map-and-compass system even when following pilotage routes. Whether other animals use the sun compass in a similar manner is unknown.

As well as mitigating against the accumulation of error, calibration of the endogenous circadian clock to light-dark cycles allows animals to adjust to changes in local solar time when they move across lines of longitude. Dawn provides a highly salient calibration cue (Hirschie Johnson et al., 2003; Kramer, 1959) so birds' clocks are expected to be in sync with local time at the start of each day (Wiltschko et al., 2000). However, they appear unable to use other time-varying cues, such as sun elevation, to calibrate their clocks between dawn and dusk (Schmidt-Koenig et al., 1991). As a result, clock-shift may be induced by longitudinal movement within a single day (Alerstam & Pettersson, 1991). Movement-induced clock-shifts might impact any behavioural or physiological processes influenced by the endogenous clock (Krittika & and Yadav, 2020; Pilorz et al., 2018), with the potential for adverse effects on migratory animals similar to those of jet lag in humans (Costa, 2003; Davidson et al., 2006; Rafnsson et al., 2001; Roenneberg & Merrow, 2016). Most

endogenous clock research has occurred in laboratory settings (Helm et al., 2017; Schwartz et al., 2017) but the ability to detect clock-shifts induced by longitudinal movement would create the potential to investigate the role of the clock in behaviour and physiology under natural conditions.

Due to its close link to the endogenous clock, such clock-shifts could be detected by their impacts on the sun compass and would facilitate investigations of sun compass use in the wild. Eastwards movements should cause the endogenous clock to lag behind local time, resulting in clockwise deflection from the intended direction, whilst westwards movements should cause the clock to run ahead of local time, with anticlockwise deflection. These predictions have been supported by rapid experimental displacements of Adélie penguins (*Pygoscelis adeliae*) across lines of longitude (Emlen & Penney, 1964; Penney & Emlen, 1967) and observations that the routes of wild migratory birds in the Arctic appear, as predicted, to follow changing compass bearings (Alerstam et al., 2008; Alerstam et al., 2001). However, these observations of migratory birds could not be linked directly to clock-shifts and sun compass error. To attribute orientation error to movement-induced clock-shifts via use of the sun compass without experimental manipulation, other sources of navigational error must first be excluded. Some birds use a geomagnetic compass with error caused by changes in geomagnetic declination (the angular difference between geographic and magnetic north), which varies across lines of longitude. Additionally, birds might correct their geomagnetic compass for changes in declination experienced each day, by calibrating against the sun compass at dawn or dusk (Muheim et al., 2006). As a result, error would increase roughly with longitudinal movement only within each day. Distinguishing these sources of error requires calculation of precise expected deflections under these alternate hypotheses which, for sun compass use, requires knowledge of an animal's longitudinal movement since dawn.

In this study, we use a long-term GPS tracking dataset from the foraging movements of breeding Manx shearwaters to demonstrate that rapid flights across lines of longitude induce clock-shift and sun compass error. We show that shearwaters use the sun compass during homing both when out of sight of land and, like pigeons, when following linear features (in this case, the coastline). This reveals the remarkably conserved constraints of the endogenous circadian clock, use of the sun compass by a wild, free-ranging animal and potential for this natural jet lag to provide a powerful natural experiment in chronobiology.

## 2.3 Materials and Methods

### 2.3.1 Data collection

Breeding adult Manx shearwaters were tracked between 2004 and 2023 on colonies around the UK: Skomer Island (n = 792 tracks; 51°44′15.7″N, 5°16′58.8″W), Ramsey Island (n = 27 tracks; 51° 51' 58.3"N, 5° 20' 20.9”W) and Skokholm Island (n = 42 tracks; 51°41′38.6″N, 5°17′7.5″W), Pembrokeshire, Wales; Lighthouse Island (n = 577 tracks; 51° 41′ 38.5″N, 5°31′32.9″W), Copeland Islands, Northern Ireland; Rum (n = 26 tracks; 56°58′59.4″N, 6°17′41.3″W), Hebrides, Scotland; Lundy (n = 55 tracks; 51°10′7.6″N, 4°40′7.8″ W), Bristol Channel, England. Shearwaters were tracked with Mobile Action i-gotU GT-120 (17 g), TechnoSmart AxyTrek Marine (13 g), TechnoSmart AxyTrek Gypsy 6 (11 g), SnapperGPS (11 g, see Beuchert et al., 2023) or custom-built (17 g, see Guilford et al., 2008) archival loggers that were attached dorsally using Tesa tape and superglue following the protocol laid out in Guilford et al. (2008). Devices weighed no more than 5% of each bird’s total body mass and smaller devices used later in the study weighed < 3% body mass. All tracking was conducted under Special Methods licence from the British Trust for Ornithology and approved by the University of Oxford Animal Welfare Ethical Review Body.

### 2.3.2 Data processing

Data processing and statistical analysis were conducted in R version 4.4.2 (R Core Team, 2024), using the packages *dplyr*, *data.table*, *stringr* and *lubridate* (Barrett et al., 2025; Grolemund & Wickham, 2011; Wickham, 2023; Wickham et al., 2023). Figures were created using *ggplot2*, *effects*, *ggspatial*, *sf*, *rnaturalearth*, *rnaturalearthdata* and *rnaturalearthhires* (Dunnington, 2025; Fox & Weisberg, 2018, 2019; Massicotte & South, 2025; Pebesma, 2018; South et al., 2025a; South et al., 2025b; Wickham, 2016).

### 2.3.3 Filtering and interpolation

Tracks were first filtered to remove any unrealistic positions (< 45° or > 75°N, < 35°W or > 6°E) or duplicate fixes. The median fix interval was calculated for each track and gaps between fixes longer than 10 median intervals were identified. These represent periods where the GPS receiver was likely occluded and did not receive sufficient satellite signal to estimate position. Positional data from SnapperGPS loggers are generated through a post-processing algorithm (Beuchert & Rogers, 2021) which assigns each fix a value of 'confidence' (in arbitrary units), with missing values representing failure to estimate a location; fixes with missing values of confidence were removed. For remaining fixes, we calculated the great circle distance between each fix and the preceding fix using the *distHaversine* function from the package *geosphere* (Hijmans, 2019) and calculated the speed between fixes. We iteratively removed fixes associated with unrealistic speeds (> 80 $kmh^{-1}$). We then again identified gaps of greater than 10 fixes. To ensure consistent measures of orientation error, we interpolated to 5-minute resolution within each continuous section of track (i.e. not across gaps), using a cubic polynomial approach via the *pchip* function from the package *pracma* (Borchers, 2023). After interpolation, speeds were recalculated and filtered again. Finally, we calculated distance from the colony at each fix and considered the bird to have returned to the colony when it was within 3 km. Using this rule, we split

tracks into separate trips, ignoring periods when the bird was more than 3 km from the colony for less than 2 hours. After this processing, we retained 3,025 trips from 1,370 tracks for analysis.

### 2.3.4 Homing identification

Homing is sometimes identified as the final period of rapid, directed movement during a trip, where this ends at or near the breeding colony (Padget et al., 2018; Padget et al., 2019). However, we used a broader approach due to the distance of many shearwater trips which necessitates homing over multiple bouts or even days, and the fact that they detour around landmasses, both of which we wished to capture. We aimed to identify periods of continuous travel which were, overall, directed towards the colony and resulted in substantial movement towards it, even if they involved detours around obstacles and did not actually end at the colony. To identify periods of continuous travel, we calculated mean speed over a rolling 15-minute window. Rolling mean speed was bimodally distributed and we used a Gaussian mixture model (via the *normalmixEM* function from *mixtools*; Benaglia et al., 2009) on the natural logarithm of rolling mean speed to identify bouts of commuting (> 15.6 $kmh^{-1}$), ignoring bouts which were less than 15 minutes long and ignoring gaps between bouts which were up to 60 minutes long. To quantify whether each bout involved substantial, directed movement towards the colony, we measured the initial distance from the colony, the final distance from the colony and the great circle bearing from the start to the end. We identified homing bouts as those with bearings within 75° of the homeward direction (threshold derived from a Gaussian mixture model on the natural logarithms of the absolute deflections), that started at least 50 km from the colony, and ended at least 25% closer to the colony. Within each of the bouts, only those fixes when the bird was in flight over the 5-minute fix interval (raw speed > 15.5 $kmh^{-1}$, as identified by a Gaussian mixture model) were considered as representing active homing.

### 2.3.5 Orientation data and expected deflection predictors

To measure orientation error, we calculated the bearing to the next fix, as well as the bearing to the colony using the *bearing* and function from *geosphere* (Hijmans, 2019). During homing, the breeding island can be defined as the intended target of the shearwater *a priori* and the angular deflection away from the most direct route can be calculated. The difference between the instantaneous bearing and the bearing to the colony was the measured instantaneous deflection (orientation error). However, when following a geographic bearing, animals could either follow the shortest route – the great circle – which requires constantly changing compass directions, or a simpler rhumb line which is less direct but follows a fixed compass bearing. In our study area, rhumb lines would follow a compass bearing clockwise of an eastward great circle route and anticlockwise of a westward great circle route. We used great circle bearings in our analysis. Therefore, if shearwaters actually followed rhumb lines, we might observe systematic deflections during longitudinal movements, even without clock-shifts. To account for this, we also calculated the rhumb line bearing from each fix to the colony. The difference between the great circle bearing to the colony and the rhumb bearing to the colony was the expected angular deflection if shearwaters follow rhumb lines.

In addition, the Coriolis effect, which is generated by the difference in the speed of movement of the earth's surface between the equator and the poles, causes objects in the northern hemisphere to deflect clockwise when in motion in the air. The magnitude of the deflection can be predicted by the distance travelled both longitudinally and latitudinally, and the latitude at which the movement occurs. Consequently, we calculated a predictor to account for this expected clockwise deflection. For periods of continuous flight, we calculated the distance travelled from the start of the period in both longitudinal and latitudinal components. The sum of these components multiplied by the sine of the bird's latitude constituted the magnitude of expected clockwise deflection as a result of the Coriolis effect.

To generate predictions for orientation error under sun compass use, we identified when the bird could see the sun directly by extracting local sunrise and sunset times for each fix. The expected clockwise error increases at an average rate of 1° for every 1° of eastward longitudinal displacement but with variation depending on the time of day, due to changes in the rate of solar azimuth change. This allowed us to calculate precise values of expected deflection. To do so, we extracted the azimuth angle of the sun visible from each fix and the azimuth angle that would have been visible at the same time if the shearwater had remained at the place it experienced sunrise, using the *suncalc* package (Thieurmel & Elmarhraoui, 2025). We calculated the difference between these azimuth values, which gives the expected deflection if shearwaters use a time-compensated sun compass without accounting for longitudinal movement within days (Fig. 2.1).

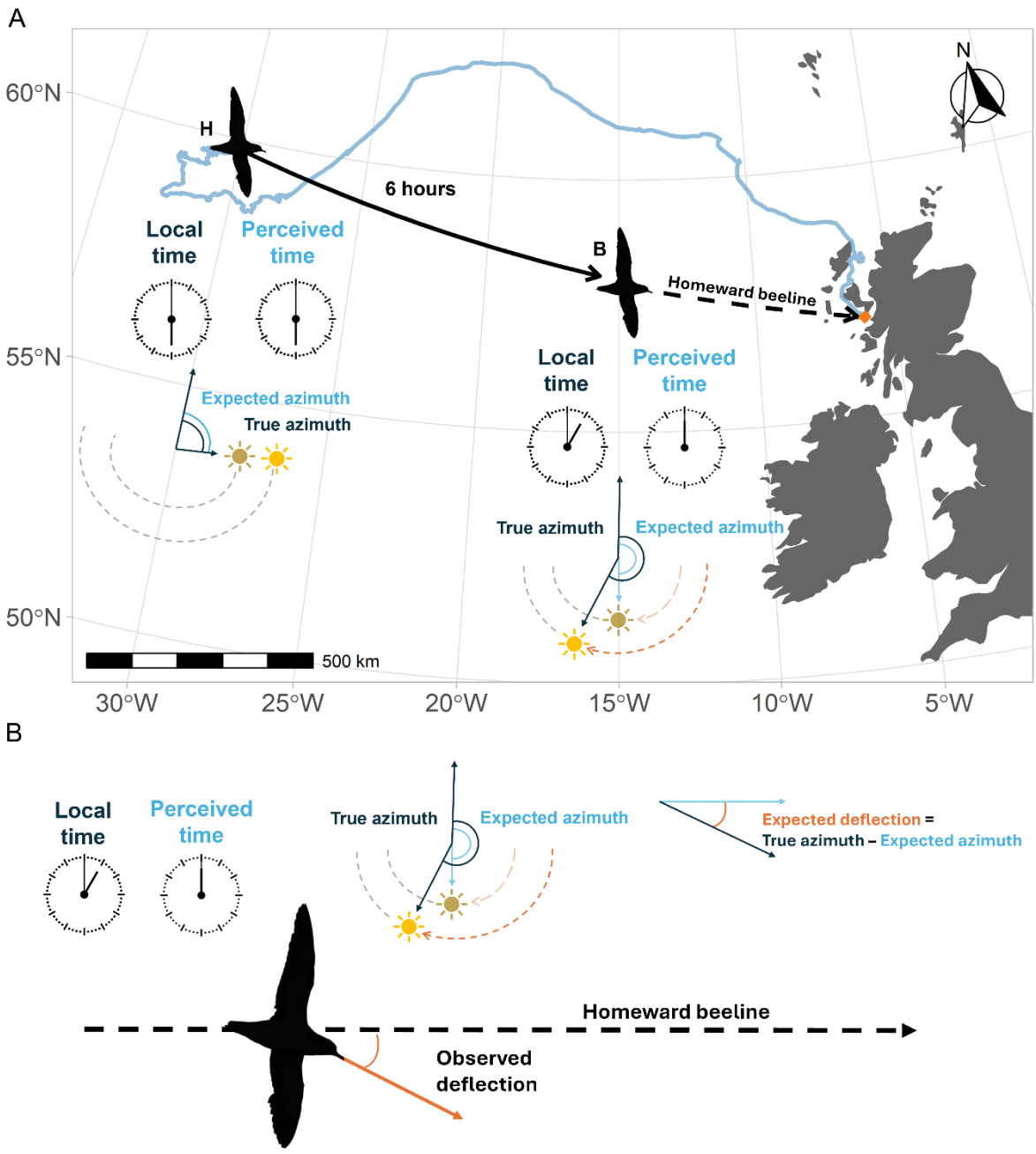



Fig. 2.1. Schematic of expected clock-shift during longitudinal homing flights of shearwaters. (A) An example foraging trip with outbound flight and foraging in blue. The bird begins to home at point H. On the first day of homing, its endogenous clock is calibrated to local time at 30°W. However, the shearwater travels eastwards to 15°W over 6 hours to point B. Here, sunrise happened an hour earlier, so the shearwater's perceived time lags local time by an hour and the sun is roughly 20° further clockwise than the shearwater expects. (B) At point B, this discrepancy causes the shearwater to orient roughly 20° clockwise of the correct direction. Clock images were reproduced without modification under CC BY-SA 4.0 from https://commons.wikimedia.org/wiki/File:Clock_12-00.svg and https://commons.wikimedia.org/wiki/File:Clock_01-00.svg.

To generate predictions for orientation error under geomagnetic compass use, we also extracted the geomagnetic declination angle at each fix and the declination at each colony on 1st July in each year of the study from the International Geomagnetic Reference Field 13 via the GEOMAG70 program (Alken et al., 2021). We then calculated the difference between the local declination and the colony's declination, which represents the expected orientation error if shearwaters rely on a geomagnetic compass without calibration. To generate expected error if shearwaters use a geomagnetic compass that is corrected for changes in declination during dawn or dusk, we calculated difference in geomagnetic declination from the current location to where the bird experienced sunrise.

### 2.3.6 Coast-following and distance from land

We identified whether any landmass in the British Isles was visible from each fix using a grid of steradians of visible land around the British Isles (*raster* package; Hijmans, 2025), whether the home colony was visible and whether the fix was within 30 km of any major landmass (area greater than 20 $km^2$, using the package *sf*; Pebesma, 2018; Pebesma & Bivand, 2023). We determined whether, from each fix, there was a clear beeline to the colony, without intervening landmasses. For fixes within 30 km of land, we calculated the clockwise and anticlockwise bearings perpendicular to the instantaneous bearing. We then identified whether any land was present within 30 km along these bearings and calculated the distance from the fix to this landmass.

### 2.3.7 Identification of continuous diurnal periods out of sight of land and land-following

Although shearwaters avoid flying over land, they do not anticipate landmasses until after they come within sight, and instead orient on the direct homeward beeline, using map-and-compass navigation (Gagliardo et al., 2013; Padget et al., 2017; Padget et al., 2019; Pollonara et al., 2015). For this reason, and to exclude a variety of other spatial or directional cues available along coastlines which might

mask sun compass error, we initially focused on homing behaviour out of sight of land. We identified periods of continuous homing that occurred between sunrise and sunset, out of sight of land (including the colony), ignoring periods shorter than 15 minutes and ignoring gaps between periods of less than 30 minutes. For each of these bouts, including only fix intervals where the bird was in flight, we calculated the mean orientation error expected under sun compass use, and both geomagnetic compass predictions, as well as the mean observed orientation error, using the *mean.circular* function from the package *circular* (Agostinelli & Lund, 2024). We also calculated the mean angular deflection expected if shearwaters followed a rhumb, rather than great circle bearing, and the mean Coriolis predictor. For each bout, we calculated a number of covariates that might predict changes in orientation: mean time since dawn, mean cumulative distance travelled so far that day and mean distance from the colony.

Using the same procedure, we also identified bouts of homing between sunrise and sunset where birds were flying with a coastline perpendicular clockwise or anticlockwise to their direction of travel within 30 km, where either the bird was beyond the maximum distance at which their colony was visible or where the beeline to their colony was blocked by an intervening landmass. For each bout, we recorded the expected orientation error under the sun compass predictions, as well as the same covariates listed above. In addition, we calculated the mean perpendicular distance from the coastline and recorded whether that coastline was clockwise or anticlockwise of the direction of travel.

### 2.3.8 Statistical analysis

We constructed linear mixed effects models to test whether (a) orientation error and (b) distance from land were predicted by predicted sun compass error. The first model included mean orientation error as the response, and expected sun compass error, both magnetic compass errors, colony, the Coriolis effect, mean time since dawn, mean cumulative distance travelled and mean distance from the colony as

fixed effects. The second model included mean distance from the coastline as the response, and the same fixed effects, excluding the Coriolis effect and magnetic compass errors but with an additional effect of the interaction between predicted sun compass error and direction of land (clockwise or anticlockwise of direction of travel). Both models included individual as a random intercept. For each term in each model we calculated VIF using the *check_collinearity* function from the *performance* package (Lüdecke et al., 2021). Terms with VIF > 5 were excluded from the model. This applied to distance from the colony and the uncalibrated magnetic compass prediction in the first model. Coefficients for each variable were extracted from the model and are presented ± 95% confidence intervals (CI). The significance of each predictor was assessed using a likelihood ratio test on nested full and restricted models. In the second model, the significance of the additive effects of relative distance from land and expected deflection were not assessed because, in the absence of the interaction, these terms are not expected to predict distance from land. As a result of high collinearity with the uncalibrated magnetic compass prediction, we removed both magnetic compass predictions and instead conducted non-nested comparisons between models. Each model was identical apart from the predicted orientation error from (a) sun compass use, (b) geomagnetic compass use calibrated at the colony and (c) geomagnetic compass use calibrated each day. For model comparisons we used the corrected Akaike Information Criterion (AICc) from the *AICcmodavg* package (Mazerolle, 2023).

## 2.4 Results

After filtering and processing, our dataset comprised 3025 foraging trips from 886 individuals. Shearwaters from major UK colonies generally forage in the Irish Sea and Northeast Atlantic, up to around 1,500 km west of their breeding islands. After foraging, they home back to these colonies, orienting with remarkable efficiency (Fig.2.1A; Padget et al., 2019) and we isolated 2101 of such homing bouts which were used for further analysis (see Fig. 2.2B and Materials and Methods for details).

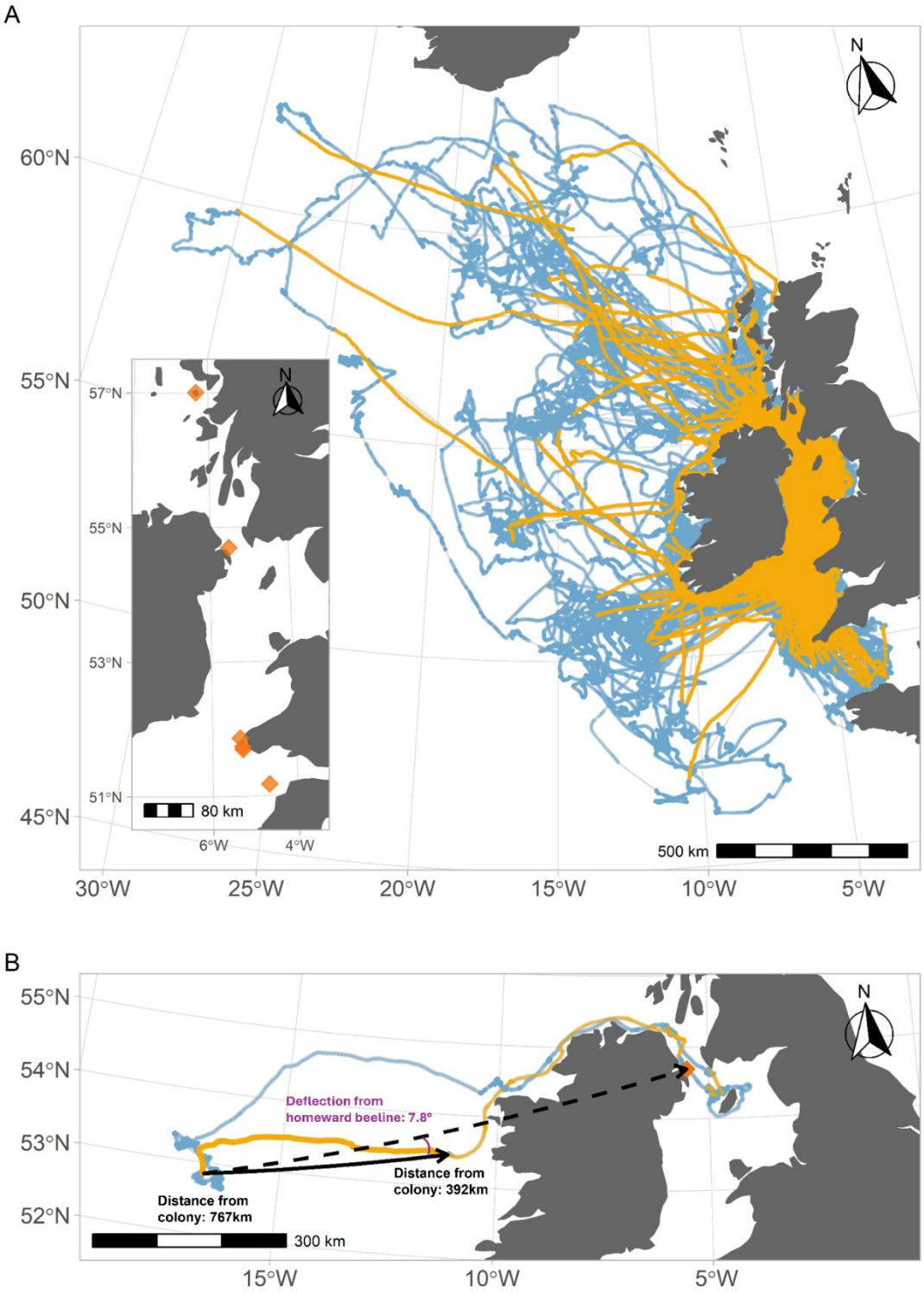



Fig. 2.2. 20 years of tracking data from adult Manx shearwaters breeding on islands across the western coasts the UK. (A) Full tracking dataset with outbound flight and foraging in blue, and homing flights highlighted in orange. The positions of breeding colonies (orange diamonds) are shown in the inset. (B) Schematic detailing identification of homing. Outbound travel and foraging are shown in blue and homing in orange. A single continuous homing bout is highlighted in brighter orange. Homing was identified as bouts with bearings within 75° of the homeward direction and which end at least 25% closer to

the colony than they started. For this bout, deflection from the homeward beeline is 7.8° and the bout ends around 50% closer to the colony.

### 2.4.1 Movement-induced clock-shift and sun compass use

We tested whether observed deflection from the homeward beeline was predicted by sun compass error based on the assumption that birds clock-shift themselves during longitudinal movements (see Materials and Methods and Fig. 2.1 for details). Clockwise deflection increased with increasing expected deflection (4.62 ± 4.27° observed deflection per 1° expected deflection [mean ± 95% CI], $\chi^2_1 = 4.45$, $P = 0.035$), consistent with use of the sun compass to navigate when out of sight of land and clock-shift resulting from longitudinal movement (Fig. 2.3). In addition, expected rhumb line deflection did not predict observed deflection ($\chi^2_1 = 0.24$, $P = 0.627$), suggesting that, in the absence of sun compass error, shearwaters orient along the most direct great circle beelines. No other covariates predicted observed orientation error (test statistics are reported in Table 2.1). The slope between observed and expected deflection is steeper than the expected 1:1 relationship but not significantly so. Although estimating the precise magnitude of orientation error from tracking data is difficult (see Chapter 7.1), this suggests heavy reliance on the sun compass as part of a map-and-compass system, without complete correction from compass-independent mechanisms or other compass cues. This mirrors findings in homing pigeons released outside their familiar area (Gagliardo et al., 2005; Wiltschko et al., 1994), where they are thought to use the sun compass in combination with a map of large-scale gradients in atmospheric olfactants (Wallraff, 2005), perhaps similarly to wild shearwaters (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015). This result also necessarily suggests that animals clock-shift themselves during their natural longitudinal movements, with a range of potential behavioural and physiological consequences.




**Fig. 2.3. The relationship between expected and observed deflection, based on use of the sun compass and clock-shift during longitudinal movement.** The fitted slope is a marginal effect derived from the linear mixed effects model.

To ensure that this result was not driven by magnetic compass error, we included predicted geomagnetic compass error in our models. Inclusion of error from an uncalibrated geomagnetic compass resulted in high multicollinearity (VIF = 29.29) so we instead constructed two models identical to the main model but with magnetic rather than sun compass predictions, to conduct non-nested model comparison. We found that the sun compass model fitted substantially better than both magnetic models ($\Delta$AICc = -3.56 and -2.99, respectively). As the expected deflections under sun and magnetic compasses are so similar in most of the dataset, we constructed linear models using only the data where the absolute difference between the sun and both magnetic compass predictions was >2°. In this case, when the disparity between predictions was greatest (and despite the very small size of this subset: n = 14), support for the sun compass model was even stronger ($\Delta$AICc = -7.82 and -8.62, respectively). These comparisons indicate that the observed deflections result from use of the sun compass, not a magnetic compass. This is consistent with existing research on shearwaters; although there is evidence

that they are magnetosensitive (Wynn et al., 2020), attachment of strong neodymium magnets does not appear to affect their orientation (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015; see also Chapter 5), unlike in species that have been robustly shown to use a geomagnetic compass (Packmor et al., 2021). In contrast, experimentally induced clock-shift has demonstrated that shearwaters use a time-compensated sun compass (Padget et al., 2018) and are not able to orient accurately when it is manipulated, suggesting that the sun is their primary source of compass information.

### 2.4.2 Use of the sun compass in combination with compass-independent cues

We found a significant interaction between shearwaters' predicted deflection and the relative direction of land during coast-following ($\chi^2_1 = 9.68$, $P = 0.002$); shearwaters fly closer to land when their expected deflection is in the same direction as the coast they are flying along (-0.64 km per 1° expected clockwise deflection when land is clockwise of direction of travel and 0.56 km per 1° when land is anticlockwise, difference: 1.20 ± 0.76 km; **Fig. 2.4**). Distance from land was not predicted by any other term with the exception of colony ($\chi^2_5 = 42.22$, $P < 0.001$) and time since dawn; shearwaters moved closer to land later in the day (-0.09 ± 0.09 km per hour, $\chi^2_1 = 4.29$, $P = 0.038$). To ensure that values with extreme expected deflections were not driving the relationship given their potentially high leverage, we conducted the same analysis on data with expected deflections between -2° and 2°, yielding the same significant relationship with very similar coefficients (Appendix; **Fig. 2.5**). This suggests that shearwaters use the sun compass in combination with compass-independent mechanisms (e.g. pilotage) along coastlines even when these mechanisms conflict.

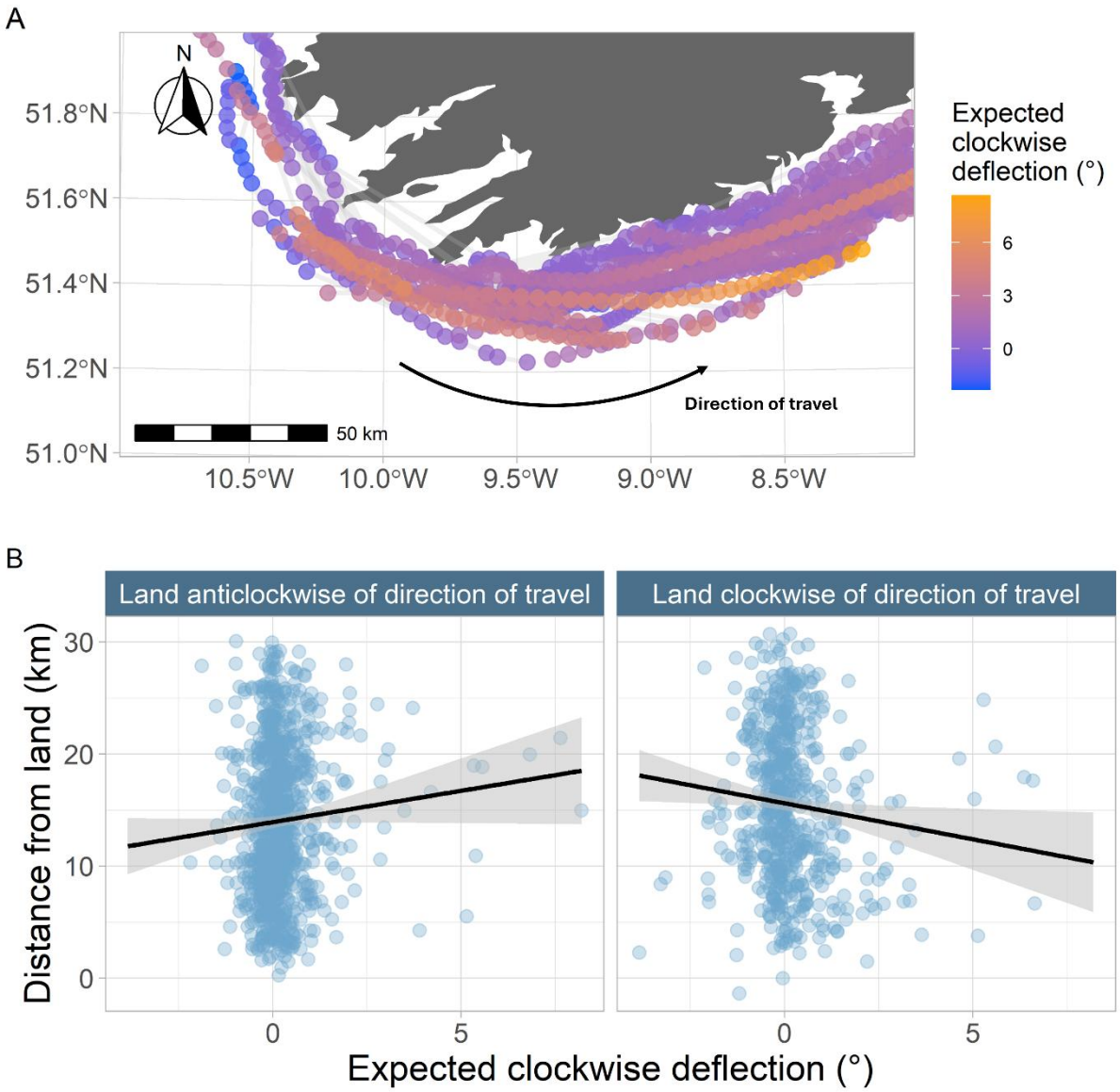



**Fig. 2.4. The relationship between expected deflection and distance from land.** (**A**) An example set of homing bouts following the southern coast of Ireland. Land is anticlockwise of the direction of travel and those birds with the most clockwise predicted deflection are furthest from the coast. (**B**) Marginal effect plot showing the relationship between expected clockwise deflection and perpendicular distance from land whilst coast-following. Shearwaters fly closer to land when the expected deflection aligns more strongly with the relative direction of land. See **Fig. 2.5** for a detailed view of the relationship within the cluster of points around expected deflection = 0°.

## 2.5 Discussion

Previous studies have used longitudinal displacement to generate clock-shift effects (Emlen & Penney, 1964; Penney & Emlen, 1967) and theoretical work has suggested that this might occur naturally during long-distance migration (Alerstam et al., 2008; Alerstam et al., 2001; Alerstam & Pettersson, 1991; McLaren et al., 2022). Here,

we demonstrate that rapid longitudinal movements can indeed lead to jet-lag-like clock-shifts in wild animals and that these result in sun compass error. We show that shearwaters use the sun compass throughout homing. Our results provide further support for the notion that shearwaters use map-and-compass navigation when homing from distant locations beyond sight of land (Padget et al., 2019) with solar azimuth as the main compass cue (Padget et al., 2018). We also provide evidence that when shearwaters follow coastlines (Padget et al., 2017; Pollonara et al., 2015), presumably using compass-independent pilotage, they balance this with information from the sun compass. These findings provide insight into how animals use the sun compass under natural conditions but match well to those generated from experimental displacement of homing pigeons (Biro et al., 2007; Gagliardo et al., 2005; Wiltschko et al., 1994), despite their relatively distant phylogenetic relationship and markedly different environment.

The angular deflections induced by this error are relatively small (up to a maximum of around 15° in shearwaters) but such errors could accumulate over long-distance migrations, especially in birds relying on clock-and-compass navigation without the ability to reorient toward a goal. For instance, Northern wheatears (*Oenathe oenathe*) making non-stop flights over the Atlantic from Baffin Island, Canada, to the British Isles traverse around 3,400 km and 60° of longitude in four days (Bairlein et al., 2012). If wheatears, like shearwaters, use a time-compensated sun compass and cannot correct for clock-shifts within each day, they would be predicted to end up hundreds of kilometres from the endpoint of their initial bearing. Alternatively, if such deflections are not observed, animals relying on a sun compass must use mechanisms to account for these time-compensation errors either through calibrating their endogenous clocks against as yet unknown cues available throughout the day, monitoring their own longitudinal movement to adjust their time-compensation or combining sun compass information with other cues. By shifting the orientations of migratory animals and perhaps driving

the evolution of strategies to mitigate for these shifts, this phenomenon has the potential to shape global animal movement and navigational strategies.

In this study, it was possible to detect clock-shifts through shearwaters' use of a time-compensated sun compass. Predominantly through laboratory studies, endogenous clocks are known to influence a wide array of animal physiological and behavioural processes (Krittika & and Yadav, 2020; Pilorz et al., 2018) with downstream impacts on ecological interactions (Bloch et al., 2017; Kronfeld-Schor et al., 2017; Rijnsdorp et al., 1981) and adverse effects of disruption to the clock, including in humans (Costa, 2003; Davidson et al., 2006; Rafnsson et al., 2001; Roenneberg & Merrow, 2016). Due to its inherent reliance on the endogenous clock, with little potential for masking by other cues (Mrosovsky, 1999), sun compass orientation might be a particularly powerful way to detect clock-shifts in wild animals. We hope that this study will help bridge the gap between chronobiology and ecology (Helm et al., 2017; Schwartz et al., 2017), opening the door to investigations into the influence of the endogenous clock on behaviour and physiology under natural conditions, the impacts of clock-shift on long-distance migratory animals, sun compass use in the wild, and perhaps how some animals might be able to cope with frequent clock-shifts. Although these clock-shifts will be most detectable and ecologically relevant for animals travelling long distances, our findings imply that any animals moving east-west between dawn and dusk might be subject to clock-shifts, with broad implications for the ecology and chronobiology of wild animals.

## 2.6 Appendix

### 2.6.1 Full model results

**Table 2.1. Full statistical results for linear mixed effects models.** Degrees of freedom, $\chi^2$ and *P*-values relate to likelihood ratio tests between full and restricted models for each term. The significance of the additive terms *Mean expected deflection* and *Relative direction of land* was not assessed due to their strong interaction. Significant predictors are highlighted in bold and the level of significance is indicated by asterisks: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

| Response [Sample size] | Predictor | Coefficient [95% CI] | DF | $\chi^2$ | *P*-value |
|---|---|---|---|---|---|
| **Mean deflection from the beeline (°)** [n = 445] | Intercept (Copeland) | -8.73 [-31.30, 13.99] | - | - | - |
| | **Mean expected deflection** (°) | 4.62 [ 0.33, 8.90] | 1 | 4.46 | **0.035*** |
| | Mean expected rhumb deflection (°) | -1.34 [ -6.73, 4.07] | 1 | 0.24 | 0.627 |
| | Colony | Lundy: 15.89 [-10.18, 42.19]<br>Ramsey: 30.91 [ -5.02, 67.04]<br>Rum: -7.79 [-59.23, 43.56]<br>Skomer: 15.73 [ - 5.01, 36.64]<br>Skokholm: 7.59 [-16.24, 31.51] | 5 | 5.87 | 0.319 |
| | Mean Coriolis deflection (°) | -0.05 [ -0.18, 0.07] | 1 | 0.75 | 0.387 |
| | Mean time since dawn (hours) | -0.15 [ -1.21, 0.91] | 1 | 0.08 | 0.783 |
| | Mean cumulative distance travelled (km) | 0.01 [ -0.04, 0.05] | 1 | 0.08 | 0.782 |
| **Mean distance from land (km)** [n = 1,427] | Intercept (Copeland, land clockwise) | 15.95 [ 14.44, 17.45] | 1 | - | - |
| | **Mean expected deflection** (°) **: Relative direction of land** | 1.20 [ 0.45, 1.96] | 1 | 9.68 | **0.002**** |
| | Mean expected deflection (°) | -0.64 [ -1.19, -0.10] | 1 | NA | NA |
| | Relative direction of land (anticlockwise) | -1.68 [ -2.46, -0.90] | 1 | NA | NA |
| | **Colony** | Lundy: 3.99 [ 1.33, 6.66]<br>Ramsey: 3.33 [ 0.80, 5.85]<br>Rum: -1.97 [ -5.63, 1.70]<br>Skomer: 2.46 [ 1.49, 3.42]<br>Skokholm: -1.32 [ -3.48, 8.29] | 5 | 42.22 | **<0.001***** |
| | **Time since dawn** (hours) | -0.09 [ -0.18, -0.01] | 1 | 4.29 | **0.038*** |
| | Mean cumulative distance travelled (km) | -0.00 [ -0.01, 0.00] | 1 | 3.69 | 0.054 |
| | Mean distance from the colony (km) | 0.00 [ -0.01, 0.01] | 1 | 0.01 | 0.913 |

### 2.6.2 Accounting for high leverage of extreme values in land-following model

In the analysis of distance from land in relation to the relative direction of expected clock-shift, 95.7% of expected deflections were between -2° and 2°. However, the largest values were up to around 8°, so the roughly 4% of data beyond the -2° to 2° range potentially had extreme leverage in this model. We therefore conducted the same analysis but using only data from the -2° to 2° range (n = 1366). The coefficients of the model were very similar to those of the full model (-0.93 km per

1° when land was clockwise of direction of travel and 0.52 km per 1° when land was anticlockwise, difference: 1.46 ± 1.24 km) and the interaction between the relative direction of land and the expected clockwise deflection remained significant ($\chi^{2} = 5.34$, $P = 0.021$). The results of this model are shown in Fig. 2.5, with the slopes from the full model overlaid for comparison.

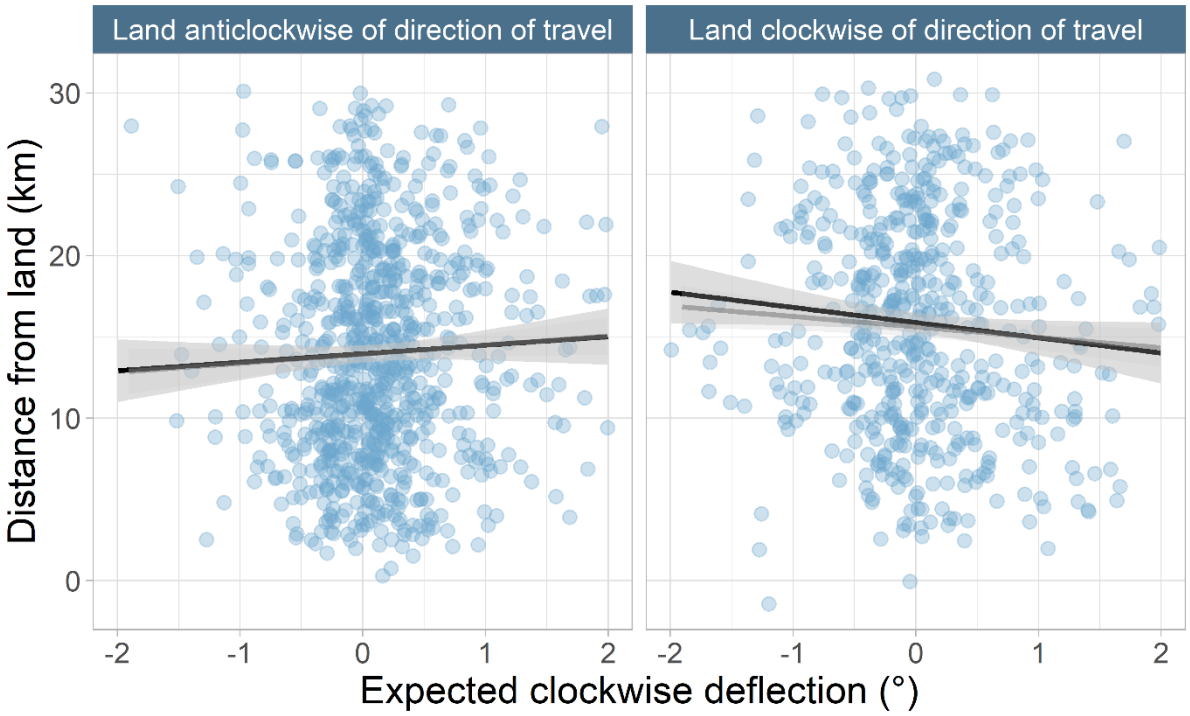



**Fig. 2.5. The relationship between expected clockwise deflection and distance from land for values of expected deflection between -2° and 2°.** The marginal effect of expected deflection on distance from land in this model are shown with black lines and the marginal effect from the full model is overlaid for comparison using grey lines.

## References

Agostinelli, C., & Lund, U. (2024). *R package 'circular': Circular Statistics*. R package version 0.5-1. https://CRAN.R-project.org/package=circular

Alerstam, T., Bäckman, J., Strandberg, R., Gudmundsson, G. A., Hedenström, A., Henningsson, S. S., Karlsson, H., & Rosén, M. (2008). Great-circle migration of Arctic passerines. *The Auk*, *125*(4), 831-838. https://doi.org/10.1525/auk.2008.07142

Alerstam, T., Gudmundsson, G. A., Green, M., & Hedenstrom, A. (2001). Migration along orthodromic sun compass routes by arctic birds. *Science*, *291*(5502), 300-303. https://doi.org/10.1126/science.291.5502.300.

Alerstam, T., & Pettersson, S.-G. (1991). Orientation along great circles by migrating birds using a sun compass. *Journal of Theoretical Biology*, *152*(2), 191-202. https://doi.org/10.1016/S0022-5193(05)80452-7

Alken, P., Thébault, E., Beggan, C. D., Amit, H., Aubert, J., Baerenzung, J., Bondar, T. N., Brown, W. J., Califf, S., Chambodut, A., Chulliat, A., Cox, G. A., Finlay, C. C., Fournier, A., Gillet, N., Grayver, A., Hammer, M. D., Holschneider, M., Huder, L.,...Zhou, B. (2021). International Geomagnetic Reference Field: the thirteenth generation. *Earth, Planets and Space*, *73*(1), 49. https://doi.org/10.1186/s40623-020-01288-x

Bairlein, F., Norris, D. R., Nagel, R., Bulte, M., Voigt, C. C., Fox, J. W., Hussell, D. J. T., & Schmaljohann, H. (2012). Cross-hemisphere migration of a 25 g songbird. *Biology Letters*, *8*(4), 505-507. https://doi.org/10.1098/rsbl.2011.1223

Barrett, T., Dowle, M., Srinivasan, A., Gorecki, J., Chirico, M., Hocking, T., Schwendinger, B., & Krylov, I. (2025). *data.table: Extension of 'data.frame'*. R package version 1.17.99. https://r-datatable.com

Benaglia, T., Chauveau, D., Hunter, D. R., & Young, D. S. (2009). mixtools: An R Package for Analyzing Mixture Models. *Journal of Statistical Software*, *32*(6), 1 - 29. https://doi.org/10.18637/jss.v032.i06

Beuchert, J., Matthes, A., & Rogers, A. (2023). SNAPPERGPS: open hardware for energy-efficient, low-cost wildlife location tracking with snapshot GNSS. *Journal of Open Hardware*, *7*(1). https://doi.org/10.5334/joh.48

Beuchert, J., & Rogers, A. (2021). SnapperGPS: Algorithms for energy-efficient low-cost location estimation using GNSS signal snapshots. In *Proceedings of the 19th ACM Conference on Embedded Networked Sensor Systems* (pp. 165-177). The 19th ACM Conference on Embedded Networked Sensor Systems 2021, Coimbra, Portugal. Association for Computing Machinery, New York, NY, United States. https://doi.org/10.1145/3485730.3485931

Bingman, V. P., & Cheng, K. (2005). Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethology Ecology & Evolution*, *17*(4), 295-318. https://doi.org/10.1080/08927014.2005.9522584

Biro, D., Freeman, R., Meade, J., Roberts, S., & Guilford, T. (2007). Pigeons combine compass and landmark guidance in familiar route navigation. *Proceedings*

*of the National Academy of Sciences*, *104*(18), 7471-7476. https://doi.org/10.1073/pnas.0701575104

Biro, D., Meade, J., & Guilford, T. (2004). Familiar route loyalty implies visual pilotage in the homing pigeon. *Proceedings of the National Academy of Sciences*, *101*(50), 17440-17443. https://doi.org/10.1073/pnas.0406984101

Biro, D., Meade, J., & Guilford, T. (2006). Route recapitulation and route loyalty in homing pigeons: pilotage from 25 km? *The Journal of Navigation*, *59*(1), 43-53. https://doi.org/10.1017/S0373463305003541

Bloch, G., Bar-Shai, N., Cytter, Y., & Green, R. (2017). Time is honey: circadian clocks of bees and flowers and how their interactions may influence ecological communities. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20160256. https://doi.org/10.1098/rstb.2016.0256

Borchers, H. (2023). *pracma: Practical Numerical Math Functions. R package version 2.4.4*. https://CRAN.R-project.org/package=pracma

Costa, G. (2003). Shift work and occupational medicine: an overview. *Occupational medicine*, *53*(2), 83-88. https://doi.org/10.1093/occmed/kqg045

Davidson, A. J., Sellix, M. T., Daniel, J., Yamazaki, S., Menaker, M., & Block, G. D. (2006). Chronic jet-lag increases mortality in aged mice. *Current Biology*, *16*(21), R914-R916. https://doi.org/10.1016/j.cub.2006.09.058

Duff, S. J., Brownlie, L. A., Sherry, D. F., & Sangster, M. (1998). Sun compass and landmark orientation by black-capped chickadees (*Parus atricapillus*). *Journal of Experimental Psychology: Animal Behavior Processes*, *24*(3), 243-253. https://doi.org/10.1037/0097-7403.24.3.243

Dunnington, D. (2025). *ggspatial: Spatial Data Framework for ggplot2*. R package version 1.1.9.9000. https://github.com/paleolimbot/ggspatial

Emlen, J. T., & Penney, R. L. (1964). Distance navigation in the Adelie Penguin. *Ibis*, *106*(4), 417-431. https://doi.org/10.1111/j.1474-919X.1964.tb03724.x

Emlen, S. T. (1967). Migratory orientation in the Indigo Bunting, *Passerina cyanea*. Part II: Mechanism of celestial orientation. *The Auk*, *84*(4), 463-489. https://doi.org/10.2307/4083330

Emlen, S. T. (1975). The stellar-orientation system of a migratory bird. *Scientific American*, *233*(2), 102-111. https://doi.org/10.1038/scientificamerican0875-102

Fluharty, S. L., Taylor, D. H., & Barrett, G. W. (1976). Sun-Compass Orientation in the Meadow Vole, *Microtus pennsylvanicus*. *Journal of Mammalogy*, *57*(1), 1-9. https://doi.org/10.2307/1379508

Fox, J., & Weisberg, S. (2018). Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. *Journal of Statistical Software*, *87*(9), 1-27. https://doi.org/10.18637/jss.v087.i09

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd ed.). Sage, Thousand Oaks, CA, United States.

https://socialsciences.mcmaster.ca/jfox/Books/Companion/index.html, ISBN: 9781544336473

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *Journal of Experimental Biology*, *216*(15), 2798-2805. https://doi.org/10.1242/jeb.085738

Gagliardo, A., Odetti, F., & Ioalè, P. (2005). Factors reducing the expected deflection in initial orientation in clock-shifted homing pigeons. *Journal of Experimental Biology*, *208*(3), 469-478. https://doi.org/10.1242/jeb.01383

Grolemund, G., & Wickham, H. (2011). Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, *40*(3), 1-25. https://doi.org/10.18637/jss.v040.i03

Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S., & Perrins, C. M. (2008). GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis*, *150*(3), 462-473. https://doi.org/10.1111/j.1474-919X.2008.00805.x

Hasler, A. D., Horrall, R. M., Wisby, W. J., & Braemer, W. (1958). Sun-Orientation and Homing in Fishes. *Limnology and Oceanography*, *3*(4), 353-361. https://doi.org/10.4319/lo.1958.3.4.0353

Helbig, A. J. (1996). Genetic Basis, Mode of Inheritance and Evolutionary Changes of Migratory Directions in Palearctic Warblers (Aves: Sylviidae). *Journal of Experimental Biology*, *199*(1), 49-55. https://doi.org/10.1242/jeb.199.1.49

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T., & Bloch, G. (2017). Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20160246. https://doi.org/10.1098/rstb.2016.0246

Hijmans, R. (2025). *raster: Geographic Data Analysis and Modeling*. R package version 3.6-32. https://rspatial.org/raster

Hijmans, R. J. (2019). *geosphere: Spherical Trigonometry*. R package version 1.5-10. https://CRAN.R-project.org/package=geosphere

Hirschie Johnson, C., Elliott, J. A., & Foster, R. (2003). Entrainment of Circadian Programs. *Chronobiology international*, *20*(5), 741-774. https://doi.org/10.1081/CBI-120024211

Hoffmann, K. (1954). Versuche zu der im Richtungsfinden der Vögel enthaltenen Zeitschätzung. *Zeitschrift für Tierpsychologie*. https://doi.org/10.1111/j.1439-0310.1954.tb02169.x

Kelly, D. M., Cheng, K., Balda, R., & Kamil, A. C. (2019). Effects of sun compass error on spatial search by Clark's nutcrackers. *Integrative Zoology*, *14*(2), 172-181. https://doi.org/10.1111/1749-4877.12302

Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *Journal für Ornithologie*, *94*(3-4), 201-219. https://doi.org/10.1007/BF01922508

Kramer, G. (1959). Recent experiments on bird orientation. *Ibis*, *101*(3-4), 399-416. https://doi.org/10.1111/j.1474-919X.1959.tb02396.x

Krittika, S., & and Yadav, P. (2020). Circadian clocks: an overview on its adaptive significance. *Biological Rhythm Research*, *51*(7), 1109-1132. https://doi.org/10.1080/09291016.2019.1581480

Kronfeld-Schor, N., Visser, M. E., Salis, L., & van Gils, J. A. (2017). Chronobiology of interspecific interactions in a changing world. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20160248. https://doi.org/10.1098/rstb.2016.0248

Lindauer, M. (1960). Time-compensated sun orientation in bees. In *Cold Spring Harbor Symposia on Quantitative Biology* (25th ed., pp. 371-377). Biological Clocks 1960, Cold Spring Harbor, NY, United States. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, United States. https://doi.org/10.1101/sqb.1960.025.01.039

Lohmann, K. J., & Lohmann, C. (1993). A Light-Independent Magnetic Compass in the Leatherback Sea Turtle. *The Biological Bulletin*, *185*(1), 149-151. https://doi.org/10.2307/1542138

Lohmann, K. J., Pentcheff, N. D., Nevitt, G. A., Stetten, G. D., Zimmer-Faust, R. K., Jarrard, H. E., & Boles, L. C. (1995). Magnetic Orientation of Spiny Lobsters in the Ocean: Experiments with Undersea Coil Systems. *Journal of Experimental Biology*, *198*(10), 2041-2048. https://doi.org/10.1242/jeb.198.10.2041

Lüdecke, D., Ben-Schachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, *6*(60). https://doi.org/10.21105/joss.03139

Marhold, S., Wiltschko, W., & Burda, H. (1997). A Magnetic Polarity Compass for Direction Finding in a Subterranean Mammal. *Naturwissenschaften*, *84*(9), 421-423. https://doi.org/10.1007/s001140050422

Massicotte, P., & South, A. (2025). *rnaturalearth: World Map Data from Natural Earth*. R package version 1.1.0. https://docs.ropensci.org/rnaturalearth/

Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3.3. https://cran.r-project.org/package=AICcmodavg

McLaren, J. D., Schmaljohann, H., & Blasius, B. (2022). Predicting performance of naïve migratory animals, from many wrongs to self-correction. *Communications Biology*, *5*(1), 1058. https://doi.org/10.1038/s42003-022-03995-5

Meade, J., Biro, D., & Guilford, T. (2005). Homing pigeons develop local route stereotypy. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *272*(1558), 17-23. https://doi.org/10.1098/rspb.2004.2873

Merlin, C., Gegear, R. J., & Reppert, S. M. (2009). Antennal Circadian Clocks Coordinate Sun Compass Orientation in Migratory Monarch Butterflies. *Science*, *325*(5948), 1700-1704. https://doi.org/10.1126/science.1176221

Mistlberger, R. E., & Rusak, B. (2021). Biological Rhythms and Behavior. In J. J. Bolhuis, L.-A. Giraldeau, & J. A. Hogan (Eds.), *The Behavior of Animals: Mechanisms, Function, and Evolution* (2nd ed., pp. 78-110). John Wiley & Sons, Hoboken, NJ, United States. https://doi.org/10.1002/9781119109556.ch4, ISBN: 9781119109518

Mrosovsky, N. (1999). Masking: history, definitions, and measurement. *Chronobiology international*, *16*(4), 415-429. https://doi.org/10.3109/07420529908998717

Muheim, R., Moore, F. R., & Phillips, J. B. (2006). Calibration of magnetic and celestial compass cues in migratory birds - a review of cue-conflict experiments. *Journal of Experimental Biology*, *209*(1), 2-17. https://doi.org/10.1242/jeb.01960

Müller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences*, *85*(14), 5287-5290. https://doi.org/10.1073/pnas.85.14.5287

Newcomer, R. T., Taylor, D. H., & Guttman, S. I. (1974). Celestial Orientation in Two Species of Water Snakes (Natrix sipedon and Regina septemvittata). *Herpetologica*, *30*(2), 194-200. https://doi.org/10.2307/3892040

Packmor, F., Kishkinev, D., Bittermann, F., Kofler, B., Machowetz, C., Zechmeister, T., Zawadzki, L. C., Guilford, T., & Holland, R. A. (2021). A magnet attached to the forehead disrupts magnetic compass orientation in a migratory songbird. *Journal of Experimental Biology*, *224*(22), jeb243337. https://doi.org/10.1242/jeb.243337

Padget, O., Bond, S. L., Kavelaars, M. M., van Loon, E., Bolton, M., Fayet, A. L., Syposz, M., Roberts, S., & Guilford, T. (2018). *In situ* clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology*, *28*(2), 275-279.e272. https://doi.org/10.1016/j.cub.2017.11.062

Padget, O., Dell'Ariccia, G., Gagliardo, A., González-Solís, J., & Guilford, T. (2017). Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. *Scientific Reports*, *7*(1), 9668. https://doi.org/10.1038/s41598-017-09738-5

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M., & Guilford, T. (2019). Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the National Academy of Sciences*, *116*(43), 21629-21633. https://doi.org/10.1073/pnas.1903829116

Pardi, L. (1960). Innate components in the solar orientation of littoral amphipods. In *Cold Spring Harbour Symposia on Quantitative Biology* (25th ed., pp. 395-

401). Biological Clocks 1960, Cold Spring Harbor, NY, United States. Cold Spring Harbor Laboratory Press, Cold Spring Harbour, NY, United States. https://doi.org/10.1101/sqb.1960.025.01.042

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, *10*(1), 439-446. https://doi.org/10.32614/RJ-2018-009

Pebesma, E., & Bivand, R. (2023). *Spatial Data Science: With applications in R*. Chapman and Hall/CRC, Boca Raton, FL, United States. https://doi.org/10.1201/9780429459016, ISBN: 0-429-45901-7

Penney, R. L., & Emlen, J. (1967). Further experiments on distance navigation in the Adelie penguin *Pygoscelzs Adelzae*. *Ibis*, *109*(1), 99-109. https://doi.org/10.1111/j.1474-919X.1967.tb00006.x

Pilorz, V., Helfrich-Förster, C., & Oster, H. (2018). The role of the circadian clock system in physiology. *Pflügers Archiv - European Journal of Physiology*, *470*(2), 227-239. https://doi.org/10.1007/s00424-017-2103-y

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., & Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific Reports*, *5*(1), 1-10. https://doi.org/10.1038/srep16486

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rafnsson, V., Tulinius, H., Jónasson, J. G., & Hrafnkelsson, J. (2001). Risk of breast cancer in female flight attendants: a population-based study (Iceland). *Cancer Causes & Control*, *12*, 95-101. https://doi.org/10.1023/a:1008983416836

Rijnsdorp, A., Daan, S., & Dijkstra, C. (1981). Hunting in the kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. *Oecologia*, *50*(3), 391-406. https://doi.org/10.1007/BF00344982

Roenneberg, T., & Merrow, M. (2016). The Circadian Clock and Human Health. *Current Biology*, *26*(10), R432-R443. https://doi.org/10.1016/j.cub.2016.04.011

Schmidt-Koenig, K. (1960). Internal clocks and homing. In *Cold Spring Harbor Symposia on Quantitative Biology* (25th ed., pp. 389-393). Biological Clocks 1960, Cold Spring Harbor, NY, United States. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, United States. https://doi.org/10.1101/sqb.1960.025.01.041

Schmidt-Koenig, K. (1990). The sun compass. *Experientia*, *46*, 336-342. https://doi.org/10.1007/BF01952166

Schmidt-Koenig, K., Ganzhorn, J. U., & Ranvaud, R. (1991). The Sun Compass. In P. Berthold (Ed.), *Orientation in birds* (pp. 1-15). Birkhäuser Basel, Basel. https://doi.org/10.1007/978-3-0348-7208-9_1, ISBN: 978-3-0348-7208-9

Schwartz, W. J., Helm, B., & Gerkema, M. P. (2017). Wild clocks: preface and glossary. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20170211. https://doi.org/10.1098/rstb.2017.0211

South, A., Michael, S., & Massicotte, P. (2025a). *rnaturalearthdata: World Vector Map Data from Natural Earth Used in 'rnaturalearth'*. R package version 1.0.0.9000. https://docs.ropensci.org/rnaturalearthdata/

South, A., Michael, S., & Massicotte, P. (2025b). *rnaturalearthhires: High Resolution World Vector Map Data from Natural Earth used in rnaturalearth*. R package version 1.0.0.9000. https://docs.ropensci.org/rnaturalearthhires

Thieurmel, B., & Elmarhraoui, A. (2025). *suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.5.2*. https://github.com/datastorm-open/suncalc

von Frisch, K. (1974). Decoding the Language of the Bee. *Science*, *185*(4152), 663-668. https://doi.org/10.1126/science.185.4152.663

Wallraff, H. G. (2005). *Avian navigation: pigeon homing as a paradigm*. Springer Science & Business Media, Berlin, Germany and New York, United States. https://doi.org/10.1007/b137573, ISBN: 3540223851

Wehner, R. (1984). Astronavigation in insects. *Annual review of entomology*, *29*(1), 277-298. https://doi.org/10.1146/annurev.en.29.010184.001425

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, United States. https://ggplot2.tidyverse.org, ISBN: 978-3-319-24277-4

Wickham, H. (2023). *stringr: Simple, Consistent Wrappers for Common String Operations*. R package version 1.5.1. https://github.com/tidyverse/stringr

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A Grammar of Data Manipulation*. R package version 1.1.4. https://github.com/tidyverse/dplyr

Willows, A. O. D. (1999). Shoreward orientation involving geomagnetic cues in the nudibranch mollusc Tritonia diomedea. *Marine and Freshwater Behaviour and Physiology*, *32*(2-3), 181-192. https://doi.org/10.1080/10236249909379046

Wiltschko, R., Kumpfmüller, R., Muth, R., & Wiltschko, W. (1994). Pigeon homing: the effect of a clock-shift is often smaller than predicted. *Behavioral Ecology and Sociobiology*, *35*, 63-73. https://doi.org/10.1007/BF00167061

Wiltschko, R., Walker, M., & Wiltschko, W. (2000). Sun-Compass Orientation in Homing Pigeons: Compensation for Different Rates of Change in Azimuth? *Journal of Experimental Biology*, *203*(5), 889-894. https://doi.org/10.1242/jeb.203.5.889

Wiltschko, W., & Balda, R. P. (1989). Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). *Journal of Comparative Physiology A*, *164*(6), 717-721. https://doi.org/10.1007/BF00616744

Wiltschko, W., & Wiltschko, R. (1972). Magnetic compass of European robins. *Science*, *176*(4030), 62-64. https://doi.org/10.1126/science.176.4030.62

Wynn, J., Padget, O., Mouritsen, H., Perrins, C., & Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology*, *30*(14), 2869-2873.e2862. https://doi.org/10.1016/j.cub.2020.05.039

Zimmerman, P. H., Pope, S. J., Guilford, T., & Nicol, C. J. (2009). Involvement of the sun and the magnetic compass of domestic fowl in its spatial orientation. *Applied Animal Behaviour Science*, *116*(2-4), 204-210. https://doi.org/10.1016/j.applanim.2008.09.006

# 3

# Sun compass orientation during foraging commutes in shearwaters

With contributions from Wynn, J., Morford, J., Padget, O., Lancaster-Reeves, L., Siddiqi-Davies, K., Bond, S., Dean, B., Fayet, A. L., Freeman, R., Gillies, N., Harris, S. M., Jaggers, P., Kirk, H., Maurice, L., Shoji, A., Syposz, M. and Guilford, T.

## Contents

**3.1** Abstract ..... 92

**3.2** Introduction ..... 93

**3.3** Materials and Methods ..... 96

**3.4** Results ..... 100

**3.5** Discussion ..... 102

*"Do you know the way of the pigeon? It flies in one direction, only to where is home."*

Marlon James, *Black Leopard, Red Wolf* (2019)

## 3.1 Abstract

Despite their importance to many animals' lives, surprisingly little is known about the mechanisms by which animals navigate to memorised foraging patches. Previous work has shown that some animals use trap-lining to move efficiently and flexibly between a number of familiar patches but the cues and navigational strategies which facilitate this are largely unknown. In contrast, research into animal navigation has generally focused on homing and migratory orientation. Many animals also use memory of their outward journeys to foraging patches to orient homewards after finding food. Here, we use endogenous clock error induced by rapid east-west flights in free-ranging Manx shearwaters to investigate whether a time-compensated sun compass guides their movements during long-distance multi-patch foraging trips. Subtle shifts in their coast-following routes reveal that they integrate sun compass information when in sight of land but we find no evidence that they use the sun compass when commuting out of sight of land nor that memory of outward compass bearings contributes to homing orientation. Our findings shed light on how animals find their way back to familiar foraging areas efficiently, even over large distances in relatively featureless environments.

## 3.2 Introduction

Movement is central to almost all aspects of animal behaviour, from foraging over metres to migrations over thousands of kilometres (Nathan et al., 2008). Animal navigation research aims to elucidate the mechanisms by which animals find their way between important locations yet has remained focused almost exclusively on homing and migration (Wiltschko & Wiltschko, 2009). Through these studies, many animals are known to rely on vector or map-and-compass navigation to navigate between locations without relying on cues directly associated with the goal. In vector navigation, animals follow a certain compass bearing for a certain duration or distance. This strategy allows animals to reach broad areas without relying on specific local cues which can only be learned through experience, and sequential vectors can be combined to produce more complex routes (reviewed in Bingman & Cheng, 2005). Vector navigation is most prominent in the inherited clock-and-compass strategy of first-time passerine migrants (Berthold, 1984, 1990; Helbig, 1991). In contrast, map-and-compass navigation (Kramer, 1953) allows animals to orient to precise goals (because they are able to compensate for drift by re-estimating their location) and to navigate flexibly between multiple known locations, including by taking novel shortcuts (Bingman & Cheng, 2005). Both strategies rely on a compass to guide orientation and sensory manipulation experiments have revealed that animals rely on three main sources of compass information: the geomagnetic field, the polar stars and solar azimuth (Emlen, 1967, 1975; Schmidt-Koenig, 1960; Wiltschko & Wiltschko, 1972).

However, as well as migration and homing back to central locations, animals in the wild must move efficiently away from central locations, towards and between important locations such as foraging patches. The cues and navigational strategies facilitating such movements, and whether memory of these cues contributes to orientation during homing, are poorly understood outside eusocial Hymenoptera (Collett, 2010; Collett et al., 1992; Wehner et al., 2006; Wehner & Srinivasan, 2003).

This is, at least in part, because of practical constraints; in captive model systems, navigational responses tend to be generated through migratory restlessness or artificial displacement from the home location. Nonetheless, honeybees have been shown to use the sun compass to follow memorised vectors (sometimes communicated by a nestmate) towards food sources (Lindauer, 1960; von Frisch, 1974) and a small number of studies suggest food-caching birds may use similar mechanisms (Duff et al., 1998; Kelly et al., 2019; Wiltschko & Balda, 1989). Both ants and bees rely on integration of their outward path to facilitate homing (Kirchner & Braun, 1994; Müller & Wehner, 1988). Although this could be achieved by measuring turning angles alongside travel distances, evidence suggests that Hymenopterans memorise their travel direction using the sun compass (i.e. utilise an allocentric, not egocentric system; Cheung & Vickerstaff, 2010; Heinze et al., 2018). In environments with multiple known food sources, some animals employ an efficient trap-lining strategy to visit all locations whilst minimising travel distance (Lihoreau et al., 2010; Tello-Ramos et al., 2015; Thomson et al., 1997). This strategy appears flexible to changes in resource locations (Lihoreau et al., 2010), perhaps relying on a cognitive map to encode the distances and directions between patches, similar to that which allows wild bats to take novel shortcuts between fruiting trees (Harten et al., 2020; Toledo et al., 2020). However, the navigational strategies and cues which facilitate this flexible multi-patch foraging are relatively unknown, especially at larger spatial scales.

Here, we investigate navigation in the long-distance foraging movements of Manx shearwaters (*Puffinus puffinus*) breeding on islands around the western coasts of the United Kingdom, using a long-term GPS tracking dataset. These birds can travel hundreds of kilometres to forage in the Irish Sea and Northeast Atlantic, exploiting patchily distributed prey resources through multi-patch foraging trips (Freeman et al., 2013; Guilford et al., 2008). Whilst the ability of shearwaters to orient towards known foraging patches (Harris et al., 2025; Jaggers, 2023) and the navigational

mechanisms employed during their homing flights have received attention in recent years (Gagliardo et al., 2013; Padget et al., 2018; Padget et al., 2017; Padget et al., 2019; Pollonara et al., 2015), the mechanisms by which they navigate towards and between foraging patches remain elusive.

Following Chapter 2 we exploit the fact that rapid east-west flights of shearwaters induce small orientation errors when shearwaters rely on a sun-compass. As solar azimuth changes from east to west over the course of each day, animals must use an endogenous clock to adjust their directional response relative to the sun. However, longitudinal movement creates discrepancies between an animal's endogenous clock and local solar time if the clock is not corrected by external cues. This is expected to generate errors in use of a time-compensated sun compass (Alerstam et al., 2001; Alerstam & Pettersson, 1991; Emlen & Penney, 1964; Penney & Emlen, 1967). Shearwaters, like many animals, appear to rely solely on sunrise and sunset to provide these cues, so clock discrepancies and associated sun compass error increase with east-west movement within a single day (Hirschie Johnson et al., 2003; Kramer, 1959). If the movement is rapid enough, these clock-shifts can become substantial – up to around 1 hour in our dataset – with associated sun compass error of 15° per hour of clock-shift, on average. This approach has previously been used to show that Manx shearwaters rely on the sun-compass whilst homing, both when out of sight of land and when following the coast (see Chapter 2.4.2). Here, we combine this phenomenon with a behavioural output of sun compass use – shifts towards or away from land during coast following – which requires no assumptions about the shearwater's intended goal and is thus suitable for investigations of foraging movements.

We also use this sun compass error to investigate whether shearwaters rely on memory of their outbound movement directions to inform homing orientation. By predicting shearwaters' sun compass error, we are able to project their 'perceived' outward route should they use a path-integration-like-system with the sun

compass providing the directional component. We can then test whether these errors in perceived path and, therefore, perceived position during homing correlates with orientation error.

We show that shearwaters use the sun compass on their outward journeys, at least while following coastlines. However, whether they use the sun compass while moving toward foraging sites out of sight of land and whether their use of the sun compass represents map-and-compass or vector navigation is unresolved. Finally, we investigate whether memory of compass orientations during the outward journey contributes to homing navigation and find that this does not appear to be the case.

## 3.3 Materials and Methods

The dataset is the same as that used in Chapter 2.3. Basic processing, filtering and interpolation followed the same methods exactly.

### 3.3.1 Behavioural state identification

To investigate navigation towards foraging grounds, both commuting and foraging behaviour first had to be identified. Via the *movehmm* package (Michelot et al., 2016), we implemented a 3-state Hidden Markov Model based on step length and turning angle to identify rest, commuting and foraging, similarly to previous studies of Manx shearwaters (Freeman et al., 2013). We used starting parameters informed by visual assessment of variable distributions and those chosen in Harris et al. (2025). Consecutive bouts were grouped together until they contained at least one bout of commuting followed by a bout of foraging or until they reached the end of the track, whichever was sooner. We recorded the great circle bearing from the start to the end of each cycle and the great circle bearing from the start of the cycle to the colony. The difference between these values was the overall angular deflection from home. We also recorded the great circle distance from the colony at the start and end of each cycle. Cycles for which overall deflection from the colony was greater than 75° and the cycle ended less than 50% closer to the colony

than it started were considered to be outward commutes. Only cycles which contained foraging were retained as outward commutes. Conversely, homing bouts were identified as those with overall bearings within 75° of the homeward direction, which started at least 50 km from the colony and ended at least 25% closer to the colony than they started.

### 3.3.2 Coast-following and distance from land

Identification of coast-following and measures of distance from land were identical to Chapter 2.3.6.

### 3.3.3 Orientation data, expected deflection predictors and outward journey information

Within each outward commuting bout, we calculated the great circle bearing from each fix to the median location of the next foraging bout, which was assumed to be the goal. The difference between this bearing and the travel direction, therefore, represented observed orientation error during outward commute. For homing bouts, we calculated the great circle bearing to the colony; the difference between instantaneous bearing and this bearing represented orientation error. Calculation of sun compass error followed the method outlined in Chapter 2.3.5. In addition, we used these expected sun compass errors to investigate whether shearwaters use memory of their compass bearings during their outward journeys to inform their homing orientation. To do this, we calculated the bearing the shearwater would have perceived itself as having flown along, had it been relying on the sun compass but unaware of its sun compass error. This was equal to the observed bearing between fixes minus the expected sun compass deflection. Starting from the beginning of each trip, we used the perceived bearing and true distance travelled from the first to the second fix to project to a ‘perceived location’ at the second timepoint. We repeated this process through the track, using the last perceived location as the starting point for the next projection. For each perceived location, we calculated the initial great circle bearing towards the colony. The difference between this perceived homeward bearing and the homeward bearing

from the true location at each timepoint was the expected angular deflection if shearwaters use memory of their outward compass bearings to navigate homewards (Fig. 3.1).

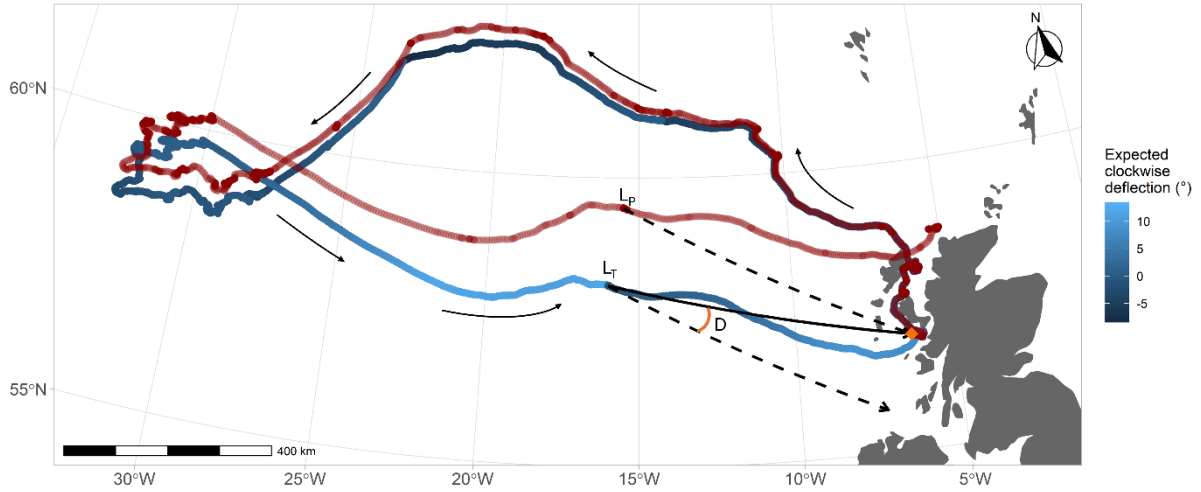



**Fig. 3.1. The accumulation of positional error through memory of incorrect sun compass bearings.** The shearwater's foraging trip starts at the colony on Rum (orange diamond) and proceeds northwest, as indicated by the arrows. As the bird travels westward, clock-shift induces anticlockwise sun-compass error so the bird ends up in locations (in blue) anticlockwise of where it expected to be (in red). This positional error, based on memory of wrongly perceived sun compass bearings, accumulates through the trip. At the start of the second day of homing, the bird's true location is $L_T$. However, its perceived location is at $L_P$. D, the difference between the bearing to home from $L_P$ and the bearing to home from $L_T$, is the deflection from the homeward beeline expected if the shearwater relies on memory of its perceived outward compass bearings to estimate its position.

### 3.3.4 Identification of continuous diurnal periods out of sight of land and land-following

Analysis of coast-following followed Chapter 2 but was applied to the outward commuting bouts, rather than homing.

Similarly, we identified bouts of outward commute out of sight of land, following Chapter 2. We calculated the observed angular deflection from the first foraging location after each bout, using the *mean.circular* function from the package *circular* (Agostinelli & Lund, 2024). We also calculated two variations of expected orientation error, corresponding to different navigational strategies. The mean expected sun compass error represents the expected deflection from the next foraging location if shearwaters are using map-and-compass navigation to orient

towards that location (just as the colony acts as the goal during homing; Fig. 3.2). In addition, we calculated the mean change in expected sun compass error over the course of the bout. This is expected to predict deflection from the foraging patch negatively if shearwaters orient towards foraging grounds by vector navigation, without reorienting via use of a map (Fig. 3.2).

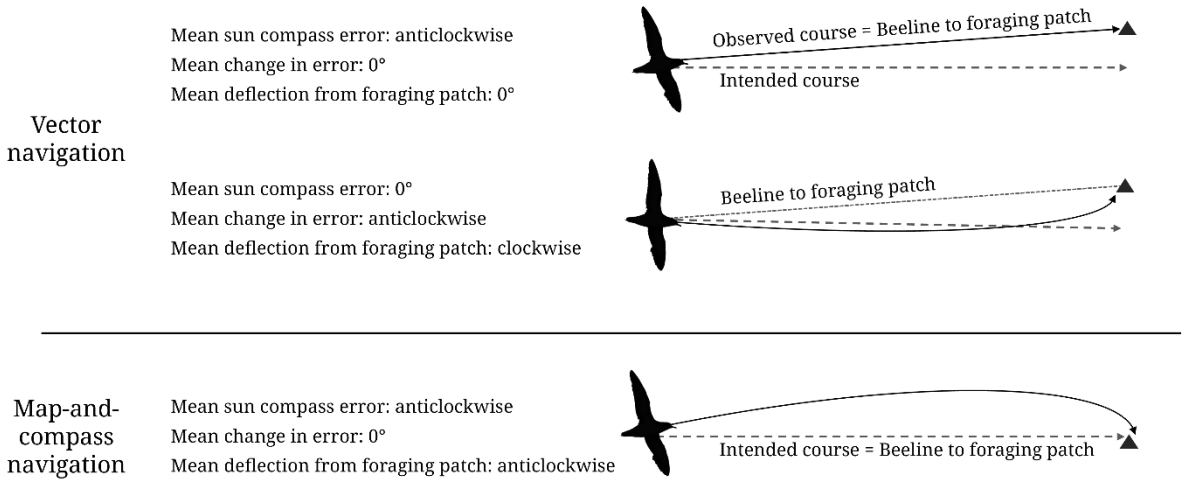



**Fig. 3.2. Predicted deflection from the next foraging location depending on whether shearwaters rely on the sun compass for vector or map-and-compass navigation.** Under vector navigation, the bird cannot correct for error, so the foraging location is not at the end of the intended course. Instead, it is a product of the intended course plus average sun compass error during the commuting bout. As a result, deflection from the foraging location is not predicted by sun compass error. However, if the shearwater uses a sun compass as part of vector navigation, changes in sun compass error should produce curved trajectories, where deflection from the eventual location is inversely predicted by change in sun compass error. Under map-and-compass navigation, the bird can correct for positional error by re-estimating its location and doing so until it reaches the target. Under this scenario, deflection from the foraging location is predicted simply by average sun compass error plus average change in sun compass error over the course of the commuting bout.

We applied the same approach to bouts of homing flight. For this analysis, we calculated the mean observed angular deflection from the homeward beeline and the mean expected deflection based on error in 'perceived location' resulting from memory of perceived sun compass bearings during the outward journey (Fig. 3.1).

For all analyses, we recorded covariates of colony, mean distance from the colony and mean time since sunrise.

### 3.3.5 Statistical analysis

We constructed three linear mixed effects models with (a) distance from the coast, (b) deflection from the next foraging location, and (c) deflection from the homeward beeline as the responses. All models included colony, mean distance from the colony and mean time since sunrise as fixed effects and individual as a random intercept. The first model additionally included an interaction between expected sun compass error and the relative direction of land. To better meet the assumption of normally distributed error, we square-root transformed distance from land. The second model included change in expected sun compass error as well as mean expected sun compass error. The third model included expected deflection resulting from error in perceived location in addition to mean expected sun compass error. For each term we calculated VIF using the *check_collinearity* function from the *performance* package (Lüdecke et al., 2021). All terms had VIF < 5 so were retained. Although the second model fit poorly, modelling circular data with multiple continuous predictors is difficult and results in models with complex interpretation. Therefore, we retained the linear modelling approach but suggest that results should be interpreted with caution. Coefficients for each variable were extracted from the model and are presented ± 95% confidence intervals (CI). The significance of each predictor was assessed using a likelihood ratio test on nested full and restricted models. In the first model, the significance of the additive effects of relative distance from land and expected deflection were not assessed because, in the absence of the interaction, these terms are not expected to predict distance from land.

## 3.4 Results

After processing, 3025 foraging trips from 886 birds remained with sufficient data for use in further analysis. These trips yielded 6,355 outward commuting bouts with 2,136 continuous sections of at least 30 minutes of coast-following and 420 continuous sections of at least 30 minutes out of sight of land. In addition, we

identified 1,031 homing bouts with 142 continuous sections of at least 30 minutes out of sight of land.

We found that shearwaters use the sun compass whilst following coastlines; when the coast was clockwise of the shearwater's direction of travel, they flew closer to land with increasing clockwise expected sun compass error (-0.105 $km^{1/2}$), whereas when land was anticlockwise of their direction of travel, this relationship was reversed (0.127 $km^{1/2}$, difference: 0.232 ± 0.118 $km^{1/2}$ [mean ± 95% CI], $\chi^2_1 = 14.81$, $P < 0.001$; **Fig. 3.3**). Distance from land was also predicted by colony ($\chi^2_5 = 77.94$, $P < 0.001$) and time since dawn ($\chi^2_1 = 4.68$, $P = 0.030$) but not by distance from the colony ($\chi^2_1 = 0.14$, $P = 0.713$).

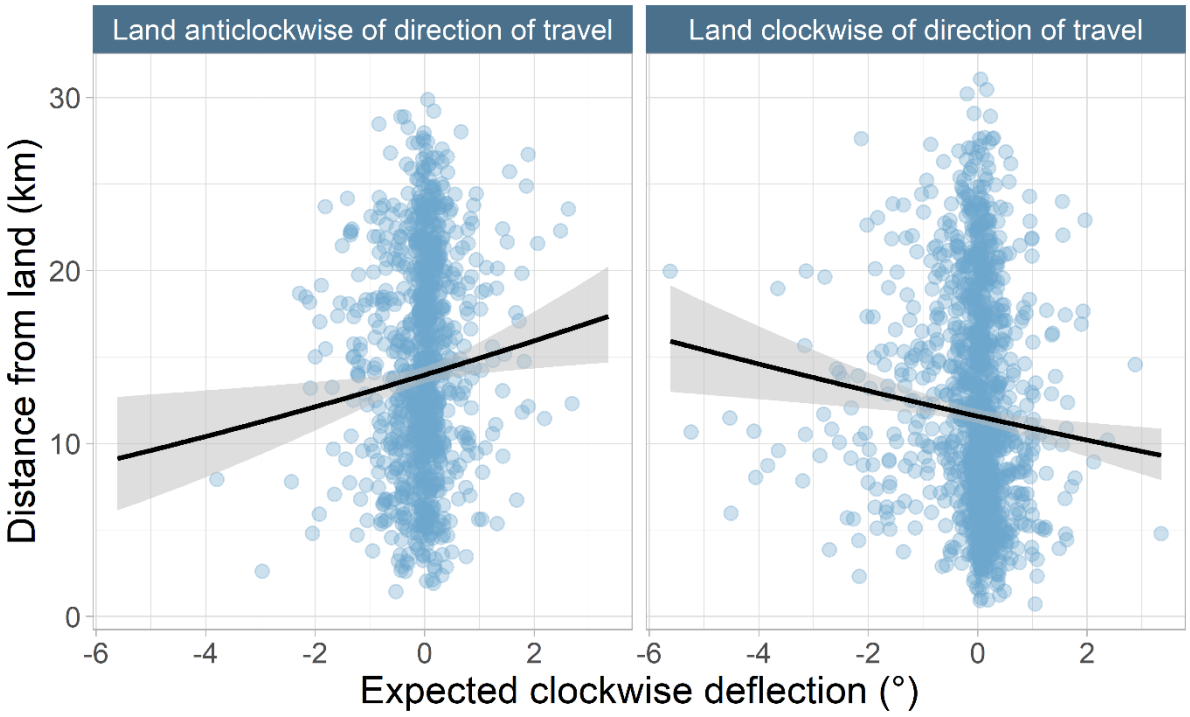



**Fig. 3.3. The relationship between expected deflection from sun compass error and distance from land during outward commute.** The fitted slope is the marginal effect of expected deflection on square-root distance from land, accounting for the interaction with the direction of land.

However, neither the mean expected sun compass error nor the change in expected sun compass error predicted observed deflection from the next foraging patch when shearwaters were commuting out of sight of land ($\chi^2_1 < 0.01$ $P = 0.970$ and $\chi^2_1 = 0.15$, $P = 0.701$, respectively). No other covariates predicted observed

deflection from the foraging patch (colony: $\chi^2_5 = 5.34$, $P = 0.376$, time since dawn: $\chi^2_1 = 0.02$, $P = 0.895$, distance from home: $\chi^2_1 = 1.71$, $P = 0.191$). Although the high spread of orientation in these data mean that linear modelling approaches should be interpreted with caution, analysis of the 93% of data with observed deflections between -90° and 90° supports these conclusions. None of the fixed effects significantly predicted deflection from the next foraging patch in this range (expected sun compass error: $\chi^2_1 = 0.27$, $P = 0.600$; change in expected sun compass error: $\chi^2_1 = 0.45$, $P = 0.502$; colony: $\chi^2_5 = 3.93$, $P = 0.560$; time since sunrise: $\chi^2_1 = 0.28$, $P = 0.597$), although the significance of distance from the colony was marginal ($\chi^2_1 = 3.52$, $P = 0.061$).

Finally, when examining homing orientation, we find no effect of error in compass perception during the outward journey ($\chi^2_1 = 0.08$, $P = 0.776$). Similarly, colony did not predict observed deflection ($\chi^2_5 = 7.20$, $P = 0.206$). Deflection from the homeward beeline was predicted by expected sun compass error ($\chi^2_1 = 4.03$, $P = 0.045$), time since dawn ($\chi^2_1 = 5.33$, $P = 0.022$) and distance from the colony ($\chi^2_1 = 4.64$, $P = 0.031$).

## 3.5 Discussion

Many animals face the challenge of moving efficiently between numerous locations, most obviously foraging locations. Navigation in this context must be similarly important to homing or long-distance migration, yet these have traditionally received far greater study. Investigating the mechanisms of navigation in multi-patch foraging movements presents a number of additional challenges; motivation is more complex to predict and the goal cannot necessarily be identified *a priori*. Despite these issues, a small number of studies have revealed the flexible trap-lining strategy used by some animals to navigate efficiently between multiple known foraging patches (Janson, 1998; Lemke, 1984; Lihoreau et al., 2010; Tello-Ramos et al., 2015; Thomson et al., 1997) and the map-based navigational strategies which might facilitate this (Harten et al., 2020; Toledo et al.,

2020). Nonetheless, the cues used to facilitate these movements are almost entirely unknown. Here, we use an approach blind to the intended goal to demonstrate that free-ranging birds use the sun-compass to orient during long-distance foraging commutes.

We find evidence that shearwaters use the sun-compass whilst following coastlines towards foraging patches, just as they appear to during homing (Chapter 2.4.2). This finding represents an interesting navigational strategy; shearwaters are using the sun compass in combination with a map of (presumably visual) landmarks along coastlines or they are piloting, using the coastline as a linear feature to follow, but with some residual input from their sun compass. The latter possibility is perhaps supported by the fact that shearwaters do not anticipate landmasses during homing, despite accurate homeward orientation, but are able to choose the shortest route around them with remarkable accuracy (Lancaster-Reeves et al., unpublished; Padget et al., 2022; Padget et al., 2019). This implies that landmasses are not integrated into the large-scale spatial representation that facilitates homing orientation but are part of a separate familiar-area navigational system. These two systems might be used in parallel by shearwaters, with the large-scale map-and-compass being given only minor weighting during following of familiar coastlines. This mirrors interpretations of similar findings in homing pigeons (*Columba livia*). Like shearwaters, pigeons appear to rely primarily on an olfactory map and the sun compass to home from distant, unfamiliar sites (Gagliardo, 2013; Schmidt-Koenig, 1990). However, when released repeatedly from the same site, they learn idiosyncratic routes back to their loft, often following linear features such as roads (Biro et al., 2004; Meade et al., 2005). These routes appear to be based on visual pilotage (Biro et al., 2004, 2006) and reliance on the sun compass decreases as pigeons become increasingly familiar with a route (Biro et al., 2007; Gagliardo et al., 2005; Wiltschko et al., 1994). Nonetheless, clock-shifted pigeons still show small lateral shifts to one side of their familiar routes, even when in sight of their home

loft (Armstrong et al., 2013; Biro et al., 2007; Graue, 1963), and this has been interpreted as representing partial retention of the large-scale map-and-compass system, even when homing in the familiar area. These similarities, both between different taxa and different navigational contexts, might imply that parallel use of large-scale map-and-compass navigation and pilotage in the familiar area is a conserved navigational strategy. Much greater research is required on the navigational mechanisms of birds outside of migration and homing, to determine whether efficient and flexible navigation between resource locations is underpinned by similar sensory and cognitive mechanisms.

However, when we analysed bouts of outward commute which occurred beyond sight of land, we found no effect on deflection from the next foraging patch of predicted sun compass error or change in this error during a commuting bout. This could suggest that shearwaters do not rely primarily on the sun compass during this phase of foraging search (as part of either map-and-compass or vector navigation, respectively). Shearwaters are known to be magnetosensitive (Wynn et al., 2020) and perhaps possess a geomagnetic compass (Takahashi et al., 2022). They might, therefore, rely on this compass for orientating towards foraging patches out of sight of land, though this would be in contrast to homing and the coast-following stage of foraging commutes, where the sun compass appears to dominate (Chapter 2.4; Padget et al., 2018). However, this result could equally be explained if shearwaters use a map-and-compass strategy to find known foraging areas but the assumption that the next foraging patch is the goal is not appropriate. Furthermore, the extent to which shearwaters target known foraging patches varies with the energy landscape – when winds are higher and flight costs vary more strongly with direction of travel relative to the wind, shearwaters' outward commutes are governed more strongly by wind direction and might therefore not involve compass orientation (Harris et al., 2025).

Additionally, we find no evidence that compass error during the outward journey predicts deflection during homing. This implies that shearwaters do not use an allocentric path-integration-like system reliant on the sun compass to perceive movement direction. Whilst this aligns with some existing evidence (Padget et al., 2019) and the assumption that path integration is unlikely to be useful for animals travelling over such large distances through a fluid medium, it does not rule out the use of other forms of outward journey information. For instance, shearwaters might use memory of their path around landmasses to choose the shortest route home when encountering the same obstacles again on the return journey (Padget et al., 2022; Padget et al., 2019), or might estimate distance from home based on optic flow. Given the richness of navigational information available from outward journeys and the ubiquity of outward journey information in the navigation of other taxa (Collett & Collett, 2000; Etienne & Jeffery, 2004; Sibeaux et al., 2024; von Saint Paul, 1981), it seems likely that such cues may play some part in long-distance homing.

The importance of efficient foraging search to individual fitness and effective conservation have long been recognised but the navigational mechanisms evolved to enable such movements have rarely been investigated. Arguably, these tasks present a greater challenge than migration or homing, requiring orientation between multiple targets and flexibility in response to changes in resource availability or environmental conditions. Here, we find that shearwaters use the sun compass to guide foraging commutes across large scales. Our results extend a substantial body of work demonstrating the importance of the sun compass to navigation across a wide range of taxa and contexts to include long-distance foraging movements. Similarly to the homing navigation of both shearwaters and homing pigeons, outbound shearwaters appear to combine information from the sun compass and visual linear features. Further research will be required to generate deeper insight into the mechanisms by which animals navigate efficiently

within complex resource landscapes, and whether these similarities represent highly conserved navigational strategies.

## References

Agostinelli, C., & Lund, U. (2024). *R package 'circular': Circular Statistics*. R package version 0.5-1. https://CRAN.R-project.org/package=circular

Alerstam, T., Gudmundsson, G. A., Green, M., & Hedenstrom, A. (2001). Migration along orthodromic sun compass routes by arctic birds. *Science*, *291*(5502), 300-303. https://doi.org/10.1126/science.291.5502.300.

Alerstam, T., & Pettersson, S.-G. (1991). Orientation along great circles by migrating birds using a sun compass. *Journal of Theoretical Biology*, *152*(2), 191-202. https://doi.org/10.1016/S0022-5193(05)80452-7

Armstrong, C., Wilkinson, H., Meade, J., Biro, D., Freeman, R., & Guilford, T. (2013). Homing pigeons respond to time-compensated solar cues even in sight of the loft. *PLoS One*, *8*(5), e63130. https://doi.org/10.1371/journal.pone.0063130

Berthold, P. (1984). The endogenous control of bird migration: a survey of experimental evidence. *Bird Study*, *31*(1), 19-27. https://doi.org/10.1080/00063658409476810

Berthold, P. (1990). Spatiotemporal programs and genetics of orientation. *Experientia*, *46*(4), 363-371. https://doi.org/10.1007/BF01952169

Bingman, V. P., & Cheng, K. (2005). Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethology Ecology & Evolution*, *17*(4), 295-318. https://doi.org/10.1080/08927014.2005.9522584

Biro, D., Freeman, R., Meade, J., Roberts, S., & Guilford, T. (2007). Pigeons combine compass and landmark guidance in familiar route navigation. *Proceedings of the National Academy of Sciences*, *104*(18), 7471-7476. https://doi.org/10.1073/pnas.0701575104

Biro, D., Meade, J., & Guilford, T. (2004). Familiar route loyalty implies visual pilotage in the homing pigeon. *Proceedings of the National Academy of Sciences*, *101*(50), 17440-17443. https://doi.org/10.1073/pnas.0406984101

Biro, D., Meade, J., & Guilford, T. (2006). Route recapitulation and route loyalty in homing pigeons: pilotage from 25 km? *The Journal of Navigation*, *59*(1), 43-53. https://doi.org/10.1017/S0373463305003541

Cheung, A., & Vickerstaff, R. (2010). Finding the Way with a Noisy Brain. *PLoS computational biology*, *6*(11), e1000992. https://doi.org/10.1371/journal.pcbi.1000992

Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proceedings of the National Academy of Sciences*, *107*(25), 11638-11643. https://doi.org/10.1073/pnas.1001401107

Collett, T. S., & Collett, M. (2000). Path integration in insects. *Current Opinion in Neurobiology*, *10*(6), 757-762. https://doi.org/10.1016/S0959-4388(00)00150-1

Collett, T. S., Dillmann, E., Giger, A., & Wehner, R. (1992). Visual landmarks and route following in desert ants. *Journal of Comparative Physiology A*, *170*(4), 435-442. https://doi.org/10.1007/BF00191460

Duff, S. J., Brownlie, L. A., Sherry, D. F., & Sangster, M. (1998). Sun compass and landmark orientation by black-capped chickadees (*Parus atricapillus*). *Journal of Experimental Psychology: Animal Behavior Processes*, *24*(3), 243-253. https://doi.org/10.1037/0097-7403.24.3.243

Emlen, J. T., & Penney, R. L. (1964). Distance navigation in the Adelie Penguin. *Ibis*, *106*(4), 417-431. https://doi.org/10.1111/j.1474-919X.1964.tb03724.x

Emlen, S. T. (1967). Migratory orientation in the Indigo Bunting, *Passerina cyanea*. Part II: Mechanism of celestial orientation. *The Auk*, *84*(4), 463-489. https://doi.org/10.2307/4083330

Emlen, S. T. (1975). The stellar-orientation system of a migratory bird. *Scientific American*, *233*(2), 102-111. https://doi.org/10.1038/scientificamerican0875-102

Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus*, *14*(2), 180-192. https://doi.org/10.1002/hipo.10173

Freeman, R., Dean, B., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C. M., & Guilford, T. (2013). Predictive ethoinformatics reveals the complex migratory behaviour of a pelagic seabird, the Manx Shearwater. *Journal of The Royal Society Interface*, *10*(84), 20130279. https://doi.org/10.1098/rsif.2013.0279

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *The Journal of Experimental Biology*, *216*(12), 2165-2171. https://doi.org/10.1242/jeb.070250

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *Journal of Experimental Biology*, *216*(15), 2798-2805. https://doi.org/10.1242/jeb.085738

Gagliardo, A., Odetti, F., & Ioalè, P. (2005). Factors reducing the expected deflection in initial orientation in clock-shifted homing pigeons. *Journal of Experimental Biology*, *208*(3), 469-478. https://doi.org/10.1242/jeb.01383

Graue, L. C. (1963). The effect of phase shifts in the day-night cycle on pigeon homing at distances of less than one mile. *The Ohio Journal of Science*, *63*(5), 214–217.

Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S., & Perrins, C. M. (2008). GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis*, *150*(3), 462-473. https://doi.org/10.1111/j.1474-919X.2008.00805.x

Harris, S. M., Bishop, C. M., Bond, S., Fernandes, P. G., Guilford, T., Lewin, P. J., Padget, O., Robins, P., Schneider, W. T., Waggitt, J. J., Wilmes, S. B., & Cordes, L. S. (2025). Adjustable wind selectivity in shearwaters implies knowledge of the foraging landscape. *Current Biology*, *35*(4), 889-897.e883. https://doi.org/10.1016/j.cub.2024.12.017

Harten, L., Katz, A., Goldshtein, A., Handel, M., & Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science*, *369*(6500), 194-197. https://doi.org/10.1126/science.aay3354

Heinze, S., Narendra, A., & Cheung, A. (2018). Principles of Insect Path Integration. *Current Biology*, *28*(17), R1043-R1058. https://doi.org/10.1016/j.cub.2018.04.058

Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology*, *28*(1), 9-12. https://doi.org/10.1007/BF00172133

Hirschie Johnson, C., Elliott, J. A., & Foster, R. (2003). Entrainment of Circadian Programs. *Chronobiology international*, *20*(5), 741-774. https://doi.org/10.1081/CBI-120024211

Jaggers, P. E. (2023). *Causes and consequences of individual behavioural variability in a pelagic seabird.* [MPhil Thesis, University of Oxford]. Oxford, United Kingdom.

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *55*(5), 1229-1243. https://doi.org/10.1006/anbe.1997.0688

Kelly, D. M., Cheng, K., Balda, R., & Kamil, A. C. (2019). Effects of sun compass error on spatial search by Clark's nutcrackers. *Integrative Zoology*, *14*(2), 172-181. https://doi.org/10.1111/1749-4877.12302

Kirchner, W. H., & Braun, U. (1994). Dancing honey bees indicate the location of food sources using path integration rather than cognitive maps. *Animal Behaviour*, *48*(6), 1437-1441. https://doi.org/10.1006/anbe.1994.1379

Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *Journal für Ornithologie*, *94*(3-4), 201-219. https://doi.org/10.1007/BF01922508

Kramer, G. (1959). Recent experiments on bird orientation. *Ibis*, *101*(3-4), 399-416. https://doi.org/10.1111/j.1474-919X.1959.tb02396.x

Lancaster-Reeves, L., Wynn, J., Lewin, P., Morford, J., Guilford, T., & Padget, O. (unpublished). *Evidence for learning in the circumnavigation decisions of at-sea obstacles in free-ranging shearwaters.*

Lemke, T. O. (1984). Foraging Ecology of the Long-Nosed Bat, *Glossophaga Soricina*, With Respect to Resource Availability. *Ecology*, *65*(2), 538-548. https://doi.org/10.2307/1941416

Lihoreau, M., Chittka, L., & Raine, N. E. (2010). Travel optimization by foraging bumblebees through readjustments of traplines after discovery of new feeding locations. *American Naturalist*, *176*(6), 744-757. https://doi.org/10.1086/657042

Lindauer, M. (1960). Time-compensated sun orientation in bees. In *Cold Spring Harbor Symposia on Quantitative Biology* (25th ed., pp. 371-377). Biological Clocks 1960, Cold Spring Harbor, NY, United States. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, United States. https://doi.org/10.1101/sqb.1960.025.01.039

Lüdecke, D., Ben-Schachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, *6*(60). https://doi.org/10.21105/joss.03139

Meade, J., Biro, D., & Guilford, T. (2005). Homing pigeons develop local route stereotypy. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *272*(1558), 17-23. https://doi.org/10.1098/rspb.2004.2873

Michelot, T., Langrock, R., & Patterson, T. A. (2016). moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, *7*(11), 1308-1315. https://doi.org/10.1111/2041-210X.12578

Müller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences*, *85*(14), 5287-5290. https://doi.org/10.1073/pnas.85.14.5287

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059. https://doi.org/10.1073/pnas.0800375105

Padget, O., Bond, S. L., Kavelaars, M. M., van Loon, E., Bolton, M., Fayet, A. L., Syposz, M., Roberts, S., & Guilford, T. (2018). *In situ* clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology*, *28*(2), 275-279.e272. https://doi.org/10.1016/j.cub.2017.11.062

Padget, O., Dell'Ariccia, G., Gagliardo, A., González-Solís, J., & Guilford, T. (2017). Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. *Scientific Reports*, *7*(1), 9668. https://doi.org/10.1038/s41598-017-09738-5

Padget, O., Gillies, N., Syposz, M., Lockley, E., & Guilford, T. (2022). Shearwaters sometimes take long homing detours when denied natural outward journey information. *Biology Letters*, *18*(2), 20210503. https://doi.org/10.1098/rsbl.2021.0503

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M., & Guilford, T. (2019). Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the National Academy of Sciences*, *116*(43), 21629-21633. https://doi.org/10.1073/pnas.1903829116

Penney, R. L., & Emlen, J. (1967). Further experiments on distance navigation in the Adelie penguin *Pygoscelzs Adelzae*. *Ibis*, *109*(1), 99-109. https://doi.org/10.1111/j.1474-919X.1967.tb00006.x

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., & Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation

in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific Reports, 5*(1), 1-10. https://doi.org/10.1038/srep16486

Schmidt-Koenig, K. (1960). Internal clocks and homing. In *Cold Spring Harbor Symposia on Quantitative Biology* (25th ed., pp. 389-393). Biological Clocks 1960, Cold Spring Harbor, NY, United States. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, United States. https://doi.org/10.1101/sqb.1960.025.01.041

Schmidt-Koenig, K. (1990). The sun compass. *Experientia, 46*, 336-342. https://doi.org/10.1007/BF01952166

Sibeaux, A., Newport, C., Green, J. P., Karlsson, C., Engelmann, J., & Burt de Perera, T. (2024). Taking a shortcut: what mechanisms do fish use? *Communications Biology*, *7*(1), 578. https://doi.org/10.1038/s42003-024-06179-5

Takahashi, S., Hombe, T., Matsumoto, S., Ide, K., & Yoda, K. (2022). Head direction cells in a migratory bird prefer north. *Science Advances*, *8*(5), eabl6848. https://doi.org/10.1126/sciadv.abl6848

Tello-Ramos, M. C., Hurly, T. A., & Healy, S. D. (2015). Traplining in hummingbirds: flying short-distance sequences among several locations. *Behavioral Ecology*, *26*(3), 812-819. https://doi.org/10.1093/beheco/arv014

Thomson, J. D., Slatkin, M., & Thomson, B. A. (1997). Trapline foraging by bumble bees: II. Definition and detection from sequence data. *Behavioral Ecology*, *8*(2), 199-210. https://doi.org/10.1093/beheco/8.2.199

Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., & Nathan, R. (2020). Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. *Science*, *369*(6500), 188-193. https://doi.org/10.1126/science.aax6904

von Frisch, K. (1974). Decoding the Language of the Bee. *Science, 185*(4152), 663-668. https://doi.org/10.1126/science.185.4152.663

von Saint Paul, U. (1982). Do geese use path integration for walking home? In F. Papi & H. G. Wallraff (Eds.), *Avian Navigation* (pp. 298-307). International Symposium on Avian Navigation 1981, Pisa, Italy. Springer Berlin Heidelberg, Berlin, Germany. https://doi.org/10.1007/978-3-642-68616-0_30

Wehner, R., Boyer, M., Loertscher, F., Sommer, S., & Menzi, U. (2006). Ant navigation: one-way routes rather than maps. *Current Biology*, *16*(1), 75-79. https://doi.org/10.1016/j.cub.2005.11.035

Wehner, R., & Srinivasan, M. V. (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour*. Oxford University Press, Oxford, United Kingdom. https://doi.org/10.1093/acprof:oso/9780198515241.003.0001, ISBN: 0198515243

Wiltschko, R., Kumpfmüller, R., Muth, R., & Wiltschko, W. (1994). Pigeon homing: the effect of a clock-shift is often smaller than predicted. *Behavioral Ecology and Sociobiology*, *35*, 63-73. https://doi.org/10.1007/BF00167061

Wiltschko, R., & Wiltschko, W. (2009). Avian Navigation. *The Auk*, *126*(4), 717-743. https://doi.org/10.1525/auk.2009.11009

Wiltschko, W., & Balda, R. P. (1989). Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). *Journal of Comparative Physiology A*, *164*(6), 717-721. https://doi.org/10.1007/BF00616744

Wiltschko, W., & Wiltschko, R. (1972). Magnetic compass of European robins. *Science*, *176*(4030), 62-64. https://doi.org/10.1126/science.176.4030

Wynn, J., Padget, O., Mouritsen, H., Perrins, C., & Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology*, *30*(14), 2869-2873.e2862. https://doi.org/10.1016/j.cub.2020.05.039

# 4

# Endogenous timing of foraging movements in free-living shearwaters

With contributions from Lancaster-Reeves, L., Padget, O. and Guilford, T.

## Contents

**4.1** Abstract....116

**4.2** Introduction....117

**4.3** Materials and Methods....119

**4.4** Results....125

**4.5** Discussion....129

**4.6** Appendix....134

*"They can still take up the training direction even when they are released earlier or later than their normal time [... ] This argues an accurate time sense [... ] based on some physiological process."*

G. V. T. Matthews, *The Sensory Basis of Bird Navigation* (1951)

## 4.1 Abstract

Appropriate timing of foraging in relation to abiotic and biotic environmental cycles is an important determinant of animals' fitness and the endogenous circadian clock is thought to underpin this temporal coordination. In addition, animals might use a time-compensated sun compass to find memorised foraging locations, relying on the endogenous circadian clock as a time-reference. However, chronobiological research has historically focused on laboratory model organisms because manipulation of wild animals' endogenous clocks *in situ* has proved near impossible. As a result, the relative importance of the endogenous clock versus direct environmental cues in governing the foraging decisions of wild animals, and the role of the sun compass in navigating to foraging grounds are unresolved. Here, we build on the use of *in situ* clock-shift procedures in a wild seabird, the Manx shearwater (*Puffinus puffinus*) to investigate how the endogenous clock influences foraging movements through contributions to both the timing of foraging movements, and their directions via use of the sun compass. We show that clock-shifting affects shearwaters' rate of movement away from the colony at the start of a foraging trip, indicating that the decision to commute to foraging grounds is under circadian clock control. However, whether clock-shifting affects the orientation of these commuting flights remains unclear. We suggest that our refined protocol for clock-shifting shearwaters could facilitate further investigation of chronobiology in the wild.

## 4.2 Introduction

All animals possess endogenous clocks: mechanisms by which they track the passing of time to control time-sensitive behaviours and physiological processes (Mistlberger & Rusak, 2021). These clocks vary in period from less than a day to entire years, but the best-understood is the circadian clock, which follows daily cycles. The existence of internal circadian clocks was proved by the containment of plants and animals inside laboratories (or even in space) under constant conditions and sealed off from any external time-cues (Aschoff, 1951; de Mairan, 1729; Sulzman et al., 1984). These organisms continued to exhibit roughly daily cycles in behaviour. However, animals' free-running endogenous clocks do not keep perfect 24-hour periods spontaneously and must be periodically corrected by external environmental cues (termed *zeitgebers* – from German, meaning 'time-givers'; Aschoff, 1951, 1954). Most prominent among these cues are dawn and dusk; animals effectively regulate the period and phase of their internal clocks by matching them to the light-dark cycle (Hirschie Johnson et al., 2003).

Circadian clocks are known from laboratory studies to control a wide range of behavioural and physiological processes (Krittika & and Yadav, 2020; Pilorz et al., 2018; Yerushalmi & Green, 2009), with adverse effects resulting from disruption to the clock or mismatch with local time (Costa, 2003; Davidson et al., 2006; Rafnsson et al., 2001; Roenneberg & Merrow, 2016). However, to disentangle the influence of the endogenous clock from direct response to time-varying environmental cues, such cues are generally eliminated or held constant in the laboratory (Helm et al., 2017). On the other hand, the timing of behaviours such as foraging is a major determinant of fitness in the wild (Bloch et al., 2017; Gerkema & van der Leest, 1991; Levy et al., 2012; Rijnsdorp et al., 1981), but whether this coordination relies on the endogenous clock is unclear because manipulating the clock *in situ* is challenging. The endogenous clock can be shifted, relative to external time, by exposing animals to an artificial light-dark cycle which is offset in time from the

natural cycle. However, this clock-shifting generally progresses at a rate of only around 1-2 hours per day (Schmidt-Koenig, 1990). Few animals can be held under artificial light cycles long enough to create detectable effects in subsequent natural behaviour without taking them into a laboratory and these effects only last until the clock is next reset by an external zeitgeber (i.e. usually only to the end of the current light or dark period). Due to these practical difficulties in bridging chronobiological and ecological studies, the degree to which external cues directly influence behaviour and physiology (i.e. 'mask' the role of the internal clock) under natural conditions and the residual importance of the endogenous clock are unclear (Helm et al., 2017; Schwartz et al., 2017).

Whilst some behaviours may be masked by environmental cues, others are inextricably linked to the endogenous clock; use of a time-compensated sun compass is one such example (Schmidt-Koenig, 1990). As the earth rotates, the horizontal (azimuth) angle of the sun changes throughout the day from east to west, progressing clockwise through south in the northern hemisphere. Animals must accurately anticipate these changes if they are to use sun as a reliable compass cue, and without access to constant time-cues, animals must rely on their internal clock as the reference for these predictions. This means that discrepancies between internal clock phase and local solar time map directly onto error in sun compass orientation (Schmidt-Koenig, 1990). If an animal's clock is fast (i.e. perceived time is later in the day than external time), the sun will not have progressed as far clockwise as the animal predicts, causing anticlockwise orientation error. For those whose clocks are slow, the sun is further through its clockwise arc than expected, so they orient with clockwise error. This clock-shifting approach and the predictable errors that ensue have been used to show that phylogenetically diverse animals use the sun compass in a range of contexts under captive conditions (Fluharty et al., 1976; Merlin et al., 2009; Müller & Wehner, 1988; Pardi, 1960; Schmidt-Koenig, 1990), including whilst finding memorised food

sources over short distances (Chappell & Guilford, 1995; Duff et al., 1998; Kelly et al., 2019; von Frisch, 1974; Wiltschko & Balda, 1989; Zimmerman et al., 2009).

In 2018, Padget et al. reported the results of the first clock-shift of a wild bird, having exploited the long underground incubation stints of breeding Manx shearwaters to complete the procedure. They showed that shearwaters rely on the sun compass to orient back to their breeding colony after artificial displacement. Yet shearwaters naturally travel over hundreds of kilometres to reach foraging areas, returning to memorised patches (Jaggers, 2023) and making strategic, flexible decisions about which areas to target based on variation flight costs associated with wind fields (Harris et al., 2025). Shearwaters also appear to time their foraging movements in relation to the distance of their goal (Guilford et al., 2008), similarly to their allocation of time to homing based on their distance from the colony (Padget et al., 2019). However, compass orientation in foraging movements beyond the scale of metres is poorly understood and the role of the endogenous clock in timing wild animals' foraging movements is unknown. Building on the *in situ* clock-shift protocol in Manx shearwaters to overcome the practical difficulties of chronobiology research in the wild, we investigated shearwaters' chronobiology and orientation during the outbound portion of free-ranging foraging trips. We show that a shearwater's decision to travel towards distant foraging grounds is influenced by its endogenous clock, although whether these movements are guided by the sun compass is less clear. Our findings have implications for the adaptive significance of the endogenous clock and individual variation in clock traits through impacts on foraging efficiency.

## 4.3 Materials and Methods

### 4.3.1 Site, subjects & experimental protocol

The experiment was conducted using adult Manx shearwaters breeding on Lighthouse Island, Copeland Islands, Northern Ireland (51° 41′ 38.5″N, 5°31′32.9″W). Birds were breeding in monitored study burrows with a nest

chamber accessible by hand either from the entrance or from a purpose-built access hatch. Handling and device deployment were conducted under British Trust for Ornithology ringing and Special Methods permits. All work was licenced by the Northern Ireland Environment Agency and approved by the University of Oxford Animal Welfare Ethical Review Body, after consultation with the Home Office.

Starting at the beginning of June 2024, burrows containing an egg within the first two thirds of the incubation period were monitored daily to check the presence and identity of the incubating parent. When a pair changed over (i.e. the previously incubating partner departed on a foraging trip, while the other returned from foraging to take over incubation), they were brought into the experiment and were randomly allocated to a treatment group (control, fast and slow, see description below). This process occurred in two rounds and the control group was only included in the first round, to provide a baseline measure for the direction taken by non-manipulated birds towards the foraging grounds. All statistical comparisons were conducted only between fast and slow groups. For the clock-shift procedure, a transparent plastic box containing a full-spectrum LED, timer circuit and rechargeable lithium-ion battery was placed at the side of the burrow entrance. The timer was programmed so that the LED switched on and off either 4 hours before (fast group), 4 hours after (slow group) or at the same time (control group) as local sunrise and sunset, respectively. Burrows were then covered with a 3 mm rubber sheet measuring 1 m x 1 m, painted on the outside with thermally reflective paint (to avoid heating under sunlight) and pierced by a 50 mm diameter, 0.5 m length black PVC pipe. The pipe was fitted with 3 alternating and overlapping baffles at each end to allow airflow whilst blocking light.

Once the clock-shift equipment was in place, burrows remained undisturbed for 4 days, apart from battery changes after 2-3 days. Once four days had elapsed, the rubber mat was moved at night so that the entrance of the burrow was uncovered. The LED apparatus remained in place so that the clock-shift procedure was not

interrupted. Small knock-down sticks were placed in the burrow entrance so that entry or exit of birds could be monitored without having to disturb the incubating parent. When the sticks were knocked down, the burrow was checked by hand. If both partners were present, the burrow was blocked loosely with a towel to allow the birds to perform changeover behaviours (e.g. allopreening, duetting calls) whilst temporarily impeding their departure for 30-45 minutes. After this time, the towel was removed and the departing, clock-shifted partner was removed. If a changeover did not occur on a given night, the mat was replaced before dawn and the clock-shift procedure continued. On every subsequent night the mat was removed and the procedure repeated until either changeover took place or seven days had elapsed since the beginning of the clock-shift procedure. At this point, all remaining birds were removed from their burrows for attachment of GPS loggers and subsequent release.

Birds were dorsally fitted with waterproofed Mobile Action GT120 i-gotU archival GPS loggers (17 g) using TESA tape and superglue, following the procedure from (Guilford et al., 2008). Loggers were programmed to attempt a GPS fix every 5 minutes. After device deployment, birds were released onto the sea at the edge of the colony in random order between 09:00 and 10:30 am, during all birds' subjective daytimes. On each subsequent night, the burrows of released birds were checked and when the bird returned from its foraging trip, the device was removed and downloaded.

### 4.3.2 Data processing

Processing and analysis were conducted in R version 4.2.2, using the packages *zoo*, *data.table*, *dplyr*, *stringr* and *lubridate* (Barrett et al., 2025; Grolemund & Wickham, 2011; R Core Team, 2024; Wickham, 2023; Wickham et al., 2023; Zeileis & Grothendieck, 2005). Figures were made using the packages *ggplot2* and *ggpspatial* (Dunnington, 2025; Wickham, 2016).

To generate measures of internal clock state from the GPS data, we subset the data to after the bird first left 1 km of the colony and 30 minutes had elapsed since release, to exclude initial escape response. We then calculated travel speed between successive fixes and the mean speed over a rolling 2-hour window, as a measure of general locomotor activity level. Through visual interrogation of these activity patterns, it was clear that shearwaters showed distinct activity peaks over the course of the first day, following release. We used a peak detection algorithm to identify peaks when rolling mean speed exceeded the second order mean speed by more than half the variance for at least 1 hour. Each bird displayed between one and three peaks before dusk on the release day and these peaks varied in their intensity. During natural foraging trips, shearwaters usually show two peaks in activity, associated with greater foraging and commuting intensity following dawn and preceding dusk. A third peak around midday is sometimes discernible (Shoji et al., 2016). We considered the peaks we observed as probably analogous so believe they offer insight into the timing of shearwaters' behaviour, in relation to their endogenous clock or external cues. We therefore recorded the timing of the centre of each peak and the maximum rolling mean speed within each peak.

To investigate use of the sun compass during departure from the colony, we identified bouts of outward commuting flight. To do this, we calculated a second rolling mean speed, this time over a 15-minute window. We used a Gaussian mixture model (*normalmixEM* from the package *mixtools*; Benaglia et al., 2009) on the log-transformed rolling mean speeds to identify a threshold of 13.6 $kmh^{-1}$, above which fixes were considered to be period of travel. We then identified bouts of continuous rapid travel lasting at least 15 minutes, ignoring gaps of up to 60 minutes. For each of these bouts, we calculated the distance from the colony at the start of the bout, the distance from the colony at the end of the bout, the difference between these values divided by the distance at the start, and the initial great circle bearing relative to the colony from the start to the end of the bout (using

the function *bearing* from the package *geosphere*; Hijmans, 2019). Bouts which ended no more than 25% closer to the colony than they started and which were directed more than 70° away from the colony direction (threshold identified using Gaussian mixture model on log-transformed absolute deflections from the colony) were considered outward commute. Conversely, bouts which started at least 5 km from the colony, ended at least 40% closer to the colony than they started and were oriented within 70° of the colony were considered homing. We performed a Gaussian mixture model on the log-transformed raw speed values, identifying 15.2 $kmh^{-1}$ as the threshold above which the shearwater was in flight during the fix interval. Within each bout, only fixes where travel speed from the preceding fix was greater than this were identified as actively commuting or homing.

For each bird we recorded a number of variables to be used in analysis. These were:

- Whether changeover occurred before the bird was removed from its burrow
- Release time
- Timing of first activity peak on release day
- Maximum rolling speed during first activity peak on release day
- Timing of last activity peak on release day
- Maximum rolling speed during last activity peak on release day
- Mean bearing between fixes during outward commute up to 10 km from the colony on release day (using the function *mean.circular* from the package *circular*; Agostinelli & Lund, 2024)
- Mean resultant vector length during outward commute to 10 km from the colony on release day (using the function *rho.circular* from the package *circular*; Agostinelli & Lund, 2024)
- Bearing from the colony by the end of release day
- Distance from the colony by the end of release day (using the function *distHaversine* from the package *geosphere*; Hijmans, 2019)
- How many days after release the bird first homed
- The mean deflection from the homeward beeline during homing

We calculated the mean time of day across all birds for (a) the first activity peak on release day and (b) the last activity peak on release day. We then subtracted the mean from each of these variables to calculate a relative timing. This allowed us to combine first with last activity peaks into a single variable.

### 4.3.3 Statistical analysis

To test whether manipulation of the endogenous clock affected the timing and intensity of locomotor activity in shearwaters at sea, we constructed two linear mixed effects models using the function *lmer* from *lme4* (Bates et al., 2015). In the first, the response was maximum rolling mean speed during each peak, with treatment and type of peak (first or last) as additive fixed effects. In the second model, the response was the relative timing of each peak, predicted by additive fixed effects of treatment and release time. Individual was included as a random intercept in both models. *P*-values for each term were calculated using likelihood ratios on full and restricted models. We used a t-test on the distance travelled by the end of the release day in each group to investigate whether differences in activity resulting from clock-shift affected the decision to embark on a long-distance outward commute. Distance was log-transformed to meet the assumption of normality.

We next aimed to test whether treatment affected the probability of a bird choosing to return to the colony on the day of release. We also wished to account for and investigate the effect of changeover behaviour on the probability of homing immediately. We therefore constructed a generalised linear model with a logit link to a binomial error distribution. The response was whether the bird homed on the first day and the additive predictors were treatment and presence/absence of changeover. *P*-values were calculated using likelihood ratio tests.

To test for differences in orientation within 10 km of home and by the end of the first day, we conducted Watson $U^2$ tests between the fast and slow treatment groups using the function *watson.two.test* from *circular* (Agostinelli & Lund, 2024). To

account for differences in motivation, we also included measures of directedness. These were the mean resultant vector length for mean orientation within 10 km of the colony and distance travelled from the colony with bearing from the colony by the end of the release day. To incorporate these measures into statistical tests, we used Hotelling's $T^2$ test (via *HotellingsT2Test* from the package *DescTools*; Signorell, 2025) on the x and y positions of these vectors within the unit circle.

## 4.4 Results

The clock-shift protocol was applied to 50 burrows, with 8 in the control group and 21 in each of the fast and slow groups. Of these, 8 birds left their burrows by pushing from under the mat before the procedure was completed and the remaining 42 were captured after clock-shifting but before departure. These birds were fitted with GPS loggers and 36 produced sufficient data for use in analysis, with 15 in each of the fast and slow groups.

Shearwaters in each treatment group showed pronounced differences in their activity after release. Birds in the fast group showed less intense activity during activity peaks, travelling $8.33 \pm 8.06\ kmh^{-1}$ slower than the slow group ([mean ± 95% CI], $\chi^2_1 = 4.09$, $P = 0.043$; **Fig. 4.1A**) and these peaks occurred $1.53 \pm 1.45$ hours earlier in the day than birds in the slow group ($\chi^2_1 = 4.30$, $P = 0.038$; **Fig. 4.1C**). Speed during peaks was not predicted by whether it was the first or last peak ($\chi^2_1 = 2.19$, $P = 0.139$), nor was the timing of peaks predicted by release time ($\chi^2_1 = 0.01$, $P = 0.919$). These differences in activity appear to have impacted the distance travelled from the colony on the day of release. Birds in the slow group ended the day 19.45 km from the colony, on average, whereas birds in the fast group averaged only 2.19 km from the colony ($t_{28} = 2.35$, $P = 0.026$; **Fig. 4.1D**). Despite these differences, treatment did not affect the probability of a shearwater homing on the day of release ($\chi^2_1 = 1.03$, $P = 0.310$). Instead, this was strongly predicted by changeover behaviours; the log odds of homing were 3.94

lower if the bird completed changeover than if it was removed from its burrow before its partner returned ($\chi^2_1 = 11.85$, $P < 0.001$; Fig. 4.1B).

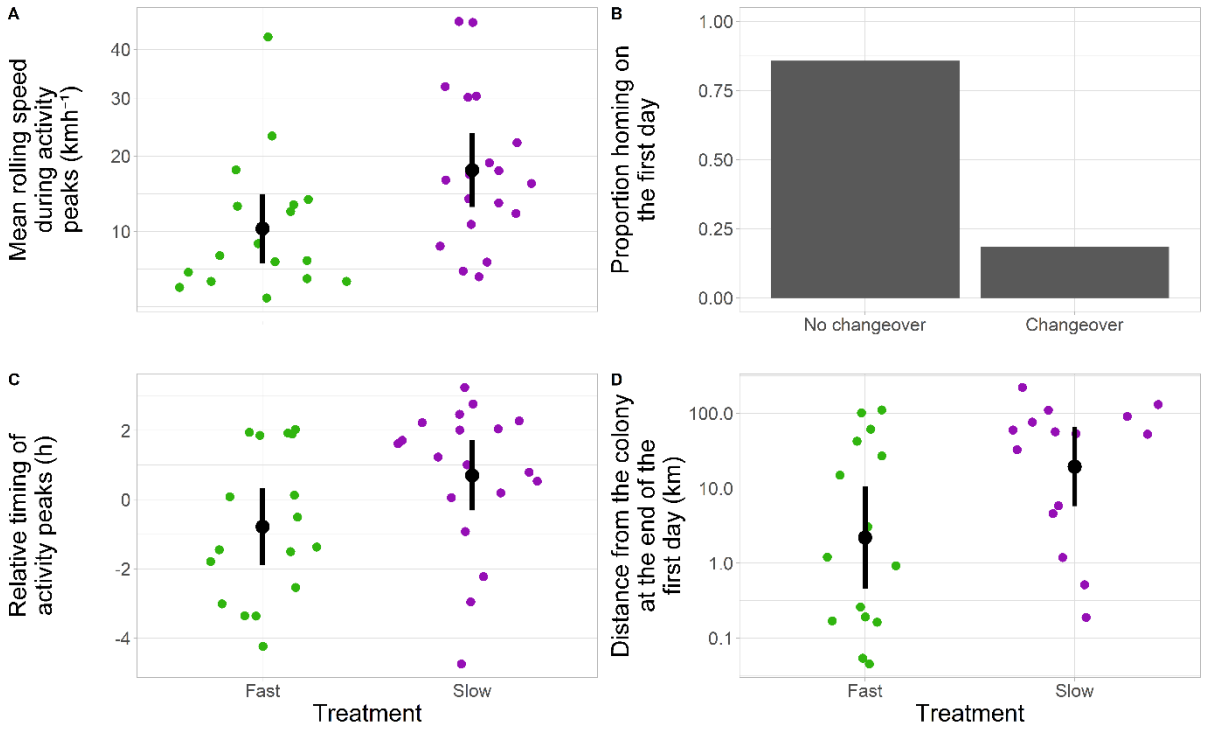



**Fig. 4.1. Differences in activity levels and resulting trip parameters across treatment groups.** Panels A, C and D show the mean with 95% confidence interval. (A) Differences in mean movement speed of travel during activity peaks, showing lower locomotor activity in the fast-shifted group. Y-axis is square-root transformed. (B) Proportion of birds homing on the day of release, depending on whether they had completed changeover behaviour before removal from the burrow. (C) Timing of activity in each treatment group, showing locomotor activity occurring earlier in fast-shifted birds. (D) Displacement from the colony by the end of the release day, showing that slow birds travelled further, on average. The y-axis is log-transformed.

Differences in orientation were less clear. Between release and sunset on release day, the second order mean expected deflection in the fast group was roughly 62° anticlockwise, while in the slow group it was 67° clockwise. The second order mean direction travelled from the colony to each bird's position at the end of the release day was 2.80° anticlockwise of north, as the majority of birds moved out towards the Atlantic or Belfast Lough. There was a significant difference between treatments: birds in the fast group flew 174.82° anticlockwise and birds in the slow group flew 20.49° clockwise of the mean direction ($U^2 = 0.198$, $0.010 < P < 0.050$). However, we wished to account for variation in directedness, so we incorporated

distance from the colony at the end of the first day to produce a vector for each bird. Hotelling's $T^2$ test conducted on the 2-D vector positions was non-significant ($T^2_{2,27} = 1.29$, $P = 0.291$; Fig. 4.2).

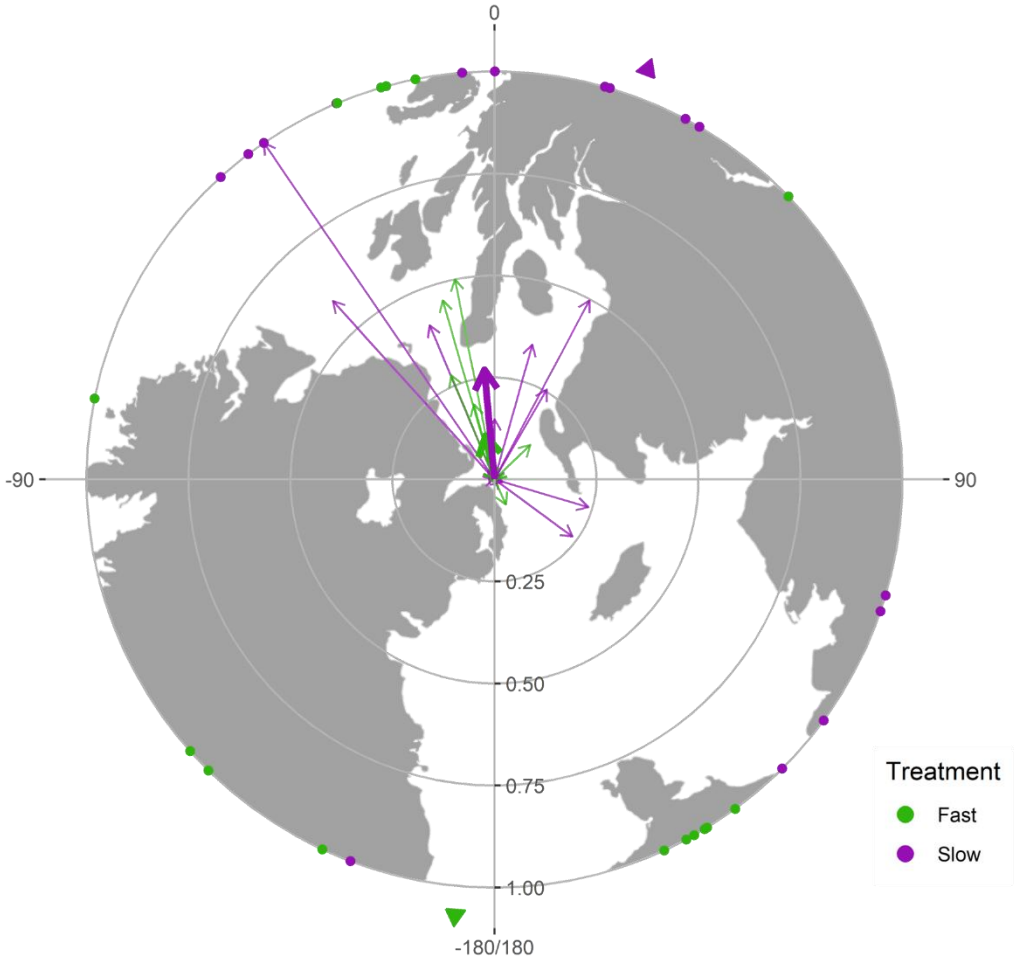



**Fig. 4.2. Bearing from the colony to position at the end of the first day.** Bearings are shown as points on the outside perimeter. Triangles outside the diagram represent circular mean bearings in each group. Arrows inside the circle show the vector of each individual's bearing and distance travelled, whilst the bold arrows show the mean resultant vector for each treatment group. Differences between treatment groups are much less pronounced after accounting for distance travelled.

To account for the fact that an interaction between distance travelled and the position of surrounding landmasses may have affected shearwaters' bearings by the end of the first day, we also investigated orientation during outward commute

between 1 and 10 km from the colony on the day of release. During flight within this range, the second order mean expected deflection was approximately 82° anticlockwise in the fast group and 64° clockwise in the slow group. Second order mean direction of flight among all birds was 15.53° clockwise of north, corresponding to movement away from the Northern Irish coast and into the North Channel. Birds in the fast group flew 6.29° clockwise of the mean direction, on average, and birds in the slow group flew 21.38° clockwise of this direction; a difference of 15.09° further clockwise in the slow group. This difference was not significant when tested using a Watson $U^2$ test ($U^2 = 0.1703$, $0.050 < P < 0.100$). Similarly, when accounting for directedness using the mean resultant vector for each bird, Hotelling's $T^2$ test on the 2-D position of these vectors was marginally non-significant ($T^2_{2,23} = 3.15$, $P = 0.062$; **Fig. 4.3**).

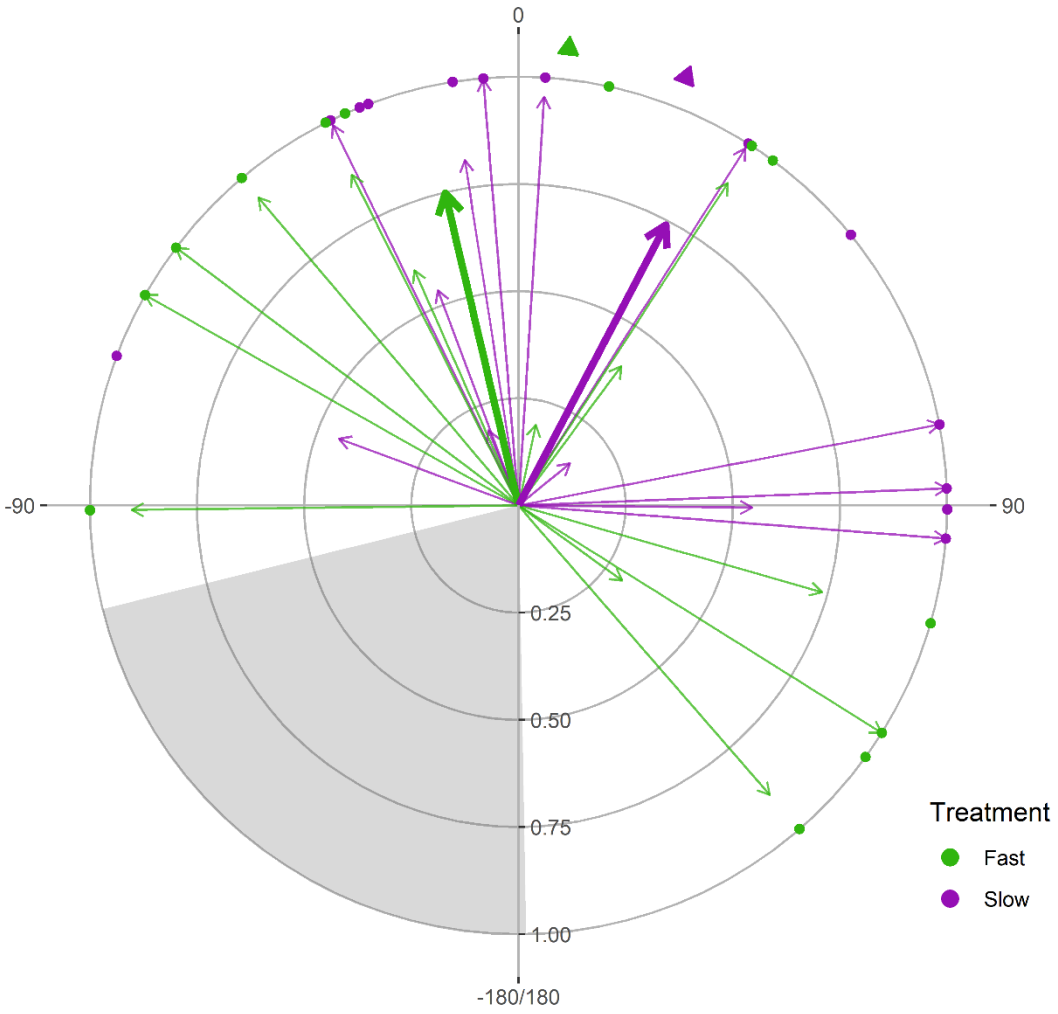



**Fig. 4.3. Mean bearing of outward flight between 1 and 10 km from the colony.** Bearings are shown as points on the outside of the circle. Triangles outside the diagram represent circular mean bearings in each group. Arrows inside the circle show the vector of each individual's bearing resultant vector length across successive bearings, whilst the bold arrows show the second order mean resultant vector for each treatment group. The grey shaded area illustrates the directions along which there is land within 10 km of the colony.

## 4.5 Discussion

The endogenous clock and the time-compensated sun compass are inextricably linked but the difficulty of clock-shift procedures has generally precluded experimental investigation of these phenomena in wild, free-ranging animals (Helm et al., 2017; Schwartz et al., 2017). We refined an existing clock-shift procedure exploiting the long incubation stints and underground nests of wild

Manx shearwaters (Padget et al., 2018) to investigate the influence of the endogenous clock on foraging movements. Our findings provide evidence that the endogenous clock governs the timing of foraging decisions in a free-living animal, although whether its role in use of a time-compensated sun compass shapes foraging directions remains unclear.

Previous work has shown that shearwaters use the sun compass to guide homing orientation after experimental displacement and during natural foraging trips (Chapter 2.4; Padget et al., 2018), and that this extends to at least some portions of outward commuting flight (see Chapter 3.4). Using our experimentally induced clock-shift, we aimed to test whether shearwaters use a time-compensated sun compass to orient on chosen departure directions from the colony. Whilst shearwaters' movement directions to the end of the first day were affected by treatment, this difference was not significant after accounting for differences in directedness, due to a lack of strongly directed flight across both treatments. Indeed, the difference in bearing to the end of the first day could be explained by the fact that birds in the slow group, travelling further than those in the fast group, encountered different areas of land around which they had to orient. We therefore also examined the orientations of shearwaters during outward commute between 1 and 10 km of the colony, where they faced identical obstacles. Within this range, shearwaters in the fast and slow groups showed marginally non-significant differences in orientation, even when accounting for differences in directedness. These results are equivocal as the to the role of the sun compass in determining the departure directions of foraging trips. We suggest that this likely results from shearwaters' avoidance of land; most birds in the fast group appeared to orient towards the south-west but the island of Ireland lies in this direction, close to the colony, so birds were effectively forced to orient either west or east of this direction. Similarly, birds in the slow group mostly appeared to orient north or slightly east of north. This will have brought them towards Scotland and forced birds to travel

either further eastwards or further westwards. This bimodality in each group's orientations may have obscured differences in their intended orientations. Investigations in Hymenoptera and birds foraging over short distances have shown that the sun compass may often be used to find known food sources (Chappell & Guilford, 1995; von Frisch, 1974; Wiltschko & Balda, 1989; Zimmerman et al., 2009), sometimes in combination with visual landmarks (Duff et al., 1998; Kelly et al., 2019). However, the role of the sun compass in guiding foraging search over larger scales, and the navigational mechanisms underlying foraging movements more generally are poorly understood. Given the importance of these mechanisms to animals' survival and successful reproduction, they are deserving of further study.

Decades of evidence from laboratory studies has demonstrated that the endogenous clock influences the timing of a wide array of behavioural and physiological processes, including foraging (Challet, 2019; Fonken et al., 2010; Strubbe et al., 1986; Turek et al., 2005; Xu et al., 2008), at least when environmental cues are excluded or held constant. Nonetheless, the possibility that masking by environmental cues plays a far more important role under natural conditions remains open (Helm et al., 2017). Reliance on an endogenous mechanism for timing behaviour has a number of intuitive advantages, especially if the relevant environmental conditions to which behavioural timing is related are difficult to predict from external cues. This might include, for example, timing migration to match seasonal conditions at the distant destination, preparation for breeding in advance of optimal conditions, or perhaps commuting to foraging patches where food availability is temporally variable. On the other hand, endogenous mechanisms might lead to sub-optimal timing of behaviour if they are error-prone or if the relevant environmental conditions themselves vary in their timing between clock cycles, such as if food availability is related strongly to precipitation or wind speed.

In the wild, animals, including seabirds, often show pronounced daily rhythms in foraging (Montevecchi et al., 2010; Siddiqi-Davies et al., 2025), with evidence for substantial impacts on individual fitness and wider ecology through interactions with time-varying abiotic and biotic elements of the environment (Bloch et al., 2017; Halle, 2000; Levy et al., 2012; Rijnsdorp et al., 1981). However, evidence that these differences in free-living animals are underpinned by the endogenous clock has remained elusive (Helm et al., 2017). Here, we show that direct environmental time cues can at most only partially compensate for endogenous clock error in the wild, suggesting that the clock plays an important role in decision-making and the timing of foraging movements, even when animals have access to potentially informative external cues. Birds in the fast group, whose subjective dawn was 8 hours before those in the slow group, were active around 1.5 hours earlier and show less intense movement even when active. This effect was significantly smaller than the expected 8-hour change in timing, suggesting either that the clock-shifting procedure was only partially effective (e.g. if secondary zeitgebers such as temperature or cues from conspecifics contributed to entrainment; Chen et al., 2015; Fuchikawa et al., 2016) or that some level of masking by environmental cues occurs (Mrosovsky, 1999). Nonetheless, this clock-shift appears to have affected shearwaters' decisions to commute towards foraging areas; despite being released at the same time, slow-shifted birds travelled almost 9 times further on average than fast-shifted birds on the first day. Differences in the probability of homing on the first day, however, suggest that changeover behaviour, rather than an interaction between distance from home and the endogenous clock mediates the homing response of shearwaters. Therefore, we suggest that shearwaters in the fast group still decided to embark on a foraging trip but delayed substantial travel due to a perceived lack of time before dusk.

For breeding shearwaters, finding food is a difficult task – prey is patchily distributed and the most productive patches may be up to around 1,500 km from

the colony. The efficiency of long-distance foraging trips is underpinned by both the accuracy with which shearwaters navigate to foraging grounds and appropriate allocation of time to commuting, resting and foraging, in relation to daily cycles in environmental conditions. Here, we show that the endogenous clock plays an important role in at least one and perhaps both parts of this foraging strategy. Our findings add to a small but growing body of evidence which directly demonstrates the importance of the endogenous clock to the behaviour of free-ranging animals (Dominoni et al., 2013; Tomotani et al., 2024; Tomotani et al., 2023). We are able to demonstrate explicitly that the endogenous clock influences the timing of foraging movements in this species. Although most animals do not embark on foraging trips as long as those of shearwaters, they often face similar challenges over smaller scales and the timing of foraging has been shown to impact fitness proxies, as well as interactions with both conspecifics and heterospecifics. Consequently, the role of the endogenous clock in governing foraging decisions demonstrated here likely has important consequences for individuals' fitness and ecological interactions across a wide variety of animals.

## 4.6 Appendix

A subset of birds were fitted with TechnoSmArt AxyTrek Marine accelerometer devices (12-15 g) to monitor their activity during the clock-shifting procedure. Devices were programmed to record tri-axial acceleration at 50Hz. The devices were deployed dorsally using TESA marine tape and superglue, following Guilford et al. (2008), and were removed at the end of clock-shifting, prior to attachment of i-gotUs. Only 9 accelerometers produced sufficient data for use in analysis.

To extract measures of overall activity during the clock-shifting procedure, we first calculated the mean acceleration in each axis over a two-second rolling window. This acts as an estimate of static acceleration. We then calculated the difference between this rolling mean and raw acceleration in each axis for each timepoint at 50Hz. This represented dynamic acceleration and we summed it across the three axes to calculate overall dynamic body acceleration (ODBA). Finally, we calculated mean ODBA over 1-minute windows.

Activity in the burrow peaked at night, as expected for a species which is nocturnal at the colony. To extract data that might reveal the internal clock state of the shearwaters, we therefore split the duration of the deployment into periods from one midday to the next. Within these periods we calculated cumulative ODBA and identified at what timepoint within the period this value reached 10% and 90% of its maximum. These marked the onset and end of activity, respectively.

To test whether the clock-shift procedure generated changes in activity timings of incubating shearwaters, we constructed a linear mixed effects model using the *lmer* function from the package *lme4* (Bates et al., 2015). The response was relative timing of onset or end of activity. The fixed effects were treatment interacting with days since the start of clock-shifting, and individual was included as a random effect. This model resulted in singular fit, as individual explained no variation, so we refitted the model without the random effect. F-ratios and *P*-values were

calculated using type III ANOVA from the *car* package (Fox & Weisberg, 2019; Fox et al., 2019).

Although the onset and end of activity appear to have shifted progressively earlier in the fast treatment and later in the slow treatment, the timing of activity in the burrow was not significantly predicted by treatment ($F_{1,52}$ = 1.31, $P$ = 0.258), days since the start of clock-shifting ($F_{1,52}$ = 0.56, $P$ = 0.458), nor the interaction between them ($F_{1,52}$ = 1.39, $P$ = 0.244). These results should be interpreted with caution given the very small number of burrows (n = 9) for which accelerometer data were available.

## References

Agostinelli, C., & Lund, U. (2024). *R package 'circular': Circular Statistics*. R package version 0.5-1. https://CRAN.R-project.org/package=circular

Aschoff, J. (1951). Die 24-Stunden-Periodik der maus unter konstanten umgebungsbedingungen. *Naturwissenschaften*, *38*(21), 506-507. https://doi.org/10.1007/BF00628863

Aschoff, J. (1954). Zeitgeber der tierischen Tagesperiodik. *Naturwissenschaften*, *41*(3), 49-56. https://doi.org/10.1007/BF00634164

Barrett, T., Dowle, M., Srinivasan, A., Gorecki, J., Chirico, M., Hocking, T., Schwendinger, B., & Krylov, I. (2025). *data.table: Extension of 'data.frame'*. R package version 1.17.99. https://r-datatable.com

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1-48. https://doi.org/10.18637/jss.v067.i01

Benaglia, T., Chauveau, D., Hunter, D. R., & Young, D. S. (2009). mixtools: An R Package for Analyzing Mixture Models. *Journal of Statistical Software*, *32*(6), 1 - 29. https://doi.org/10.18637/jss.v032.i06

Bloch, G., Bar-Shai, N., Cytter, Y., & Green, R. (2017). Time is honey: circadian clocks of bees and flowers and how their interactions may influence ecological communities. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20160256. https://doi.org/10.1098/rstb.2016.0256

Challet, E. (2019). The circadian regulation of food intake. *Nature Reviews Endocrinology*, *15*(7), 393-405. https://doi.org/10.1038/s41574-019-0210-x

Chappell, J., & Guilford, T. (1995). Homing pigeons primarily use the sun compass rather than fixed directional visual cues in an open-field arena food-searching task. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *260*(1357), 59-63. https://doi.org/10.1098/rspb.1995.0059

Chen, C., Buhl, E., Xu, M., Croset, V., Rees, J. S., Lilley, K. S., Benton, R., Hodge, J. J. L., & Stanewsky, R. (2015). *Drosophila* Ionotropic Receptor 25a mediates circadian clock resetting by temperature. *Nature*, *527*(7579), 516-520. https://doi.org/10.1038/nature16148

Costa, G. (2003). Shift work and occupational medicine: an overview. *Occupational medicine*, *53*(2), 83-88. https://doi.org/10.1093/occmed/kqg045

Davidson, A. J., Sellix, M. T., Daniel, J., Yamazaki, S., Menaker, M., & Block, G. D. (2006). Chronic jet-lag increases mortality in aged mice. *Current Biology*, *16*(21), R914-R916. https://doi.org/10.1016/j.cub.2006.09.058

de Mairan, J. J. (1729). Observation botanique. Histoire de l'Academie Royale des Sciences. *Des Sciences (1729)*.

Dominoni, D. M., Helm, B., Lehmann, M., Dowse, H. B., & Partecke, J. (2013). Clocks for the city: circadian differences between forest and city songbirds.

*Proceedings of the Royal Society of London. Series B: Biological Sciences*, *280*(1763), 20130593. https://doi.org/10.1098/rspb.2013.0593

Duff, S. J., Brownlie, L. A., Sherry, D. F., & Sangster, M. (1998). Sun compass and landmark orientation by black-capped chickadees (*Parus atricapillus*). *Journal of Experimental Psychology: Animal Behavior Processes*, *24*(3), 243-253. https://doi.org/10.1037/0097-7403.24.3.243

Dunnington, D. (2025). *ggspatial: Spatial Data Framework for ggplot2*. R package version 1.1.9.9000. https://github.com/paleolimbot/ggspatial

Fluharty, S. L., Taylor, D. H., & Barrett, G. W. (1976). Sun-Compass Orientation in the Meadow Vole, *Microtus pennsylvanicus*. *Journal of Mammalogy*, *57*(1), 1-9. https://doi.org/10.2307/1379508

Fonken, L. K., Workman, J. L., Walton, J. C., Weil, Z. M., Morris, J. S., Haim, A., & Nelson, R. J. (2010). Light at night increases body mass by shifting the time of food intake. *Proceedings of the National Academy of Sciences*, *107*(43), 18664-18669. https://doi.org/10.1073/pnas.1008734107

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd ed.). Sage, Thousand Oaks, CA, United States. https://socialsciences.mcmaster.ca/jfox/Books/Companion/index.html, ISBN: 9781544336473

Fox, J., Weisberg, S., & Price, B. (2019). *carData: Companion to Applied Regression Data Sets*. R package version 3.0-3. https://CRAN.R-project.org/package=carData

Fuchikawa, T., Eban-Rothschild, A., Nagari, M., Shemesh, Y., & Bloch, G. (2016). Potent social synchronization can override photic entrainment of circadian rhythms. *Nature Communications*, *7*(1), 11662. https://doi.org/10.1038/ncomms11662

Gerkema, M. P., & van der Leest, F. (1991). Ongoing ultradian activity rhythms in the common vole, *Microtus arvalis*, during deprivations of food, water and rest. *Journal of Comparative Physiology A*, *168*(5), 591-597. https://doi.org/10.1007/BF00215081

Grolemund, G., & Wickham, H. (2011). Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, *40*(3), 1-25. https://doi.org/10.18637/jss.v040.i03

Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S., & Perrins, C. M. (2008). GPS tracking of the foraging movements of Manx Shearwaters Puffinus puffinus breeding on Skomer Island, Wales. *Ibis*, *150*(3), 462-473. https://doi.org/10.1111/j.1474-919X.2008.00805.x

Halle, S. (2000). Ecological Relevance of Daily Activity Patterns. In S. Halle & N. C. Stenseth (Eds.), *Activity Patterns in Small Mammals: An Ecological Approach* (pp. 67-90). Springer, Berlin, Germany. https://doi.org/10.1007/978-3-642-18264-8_5, ISBN: 978-3-642-18264-8

Harris, S. M., Bishop, C. M., Bond, S., Fernandes, P. G., Guilford, T., Lewin, P. J., Padget, O., Robins, P., Schneider, W. T., Waggitt, J. J., Wilmes, S. B., & Cordes, L. S.

(2025). Adjustable wind selectivity in shearwaters implies knowledge of the foraging landscape. *Current Biology*, *35*(4), 889-897.e883. https://doi.org/10.1016/j.cub.2024.12.017

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T., & Bloch, G. (2017). Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20160246. https://doi.org/10.1098/rstb.2016.0246

Hijmans, R. J. (2019). *geosphere: Spherical Trigonometry*. R package version 1.5-10. https://CRAN.R-project.org/package=geosphere

Hirschie Johnson, C., Elliott, J. A., & Foster, R. (2003). Entrainment of Circadian Programs. *Chronobiology international*, *20*(5), 741-774. https://doi.org/10.1081/CBI-120024211

Jaggers, P. E. (2023). *Causes and consequences of individual behavioural variability in a pelagic seabird.* [MPhil Thesis, University of Oxford]. Oxford, United Kingdom.

Kelly, D. M., Cheng, K., Balda, R., & Kamil, A. C. (2019). Effects of sun compass error on spatial search by Clark's nutcrackers. *Integrative Zoology*, *14*(2), 172-181. https://doi.org/10.1111/1749-4877.12302

Krittika, S., & and Yadav, P. (2020). Circadian clocks: an overview on its adaptive significance. *Biological Rhythm Research*, *51*(7), 1109-1132. https://doi.org/10.1080/09291016.2019.1581480

Levy, O., Dayan, T., Rotics, S., & Kronfeld-Schor, N. (2012). Foraging sequence, energy intake and torpor: an individual-based field study of energy balancing in desert golden spiny mice. *Ecology Letters*, *15*(11), 1240-1248. https://doi.org/10.1111/j.1461-0248.2012.01845.x

Merlin, C., Gegear, R. J., & Reppert, S. M. (2009). Antennal Circadian Clocks Coordinate Sun Compass Orientation in Migratory Monarch Butterflies. *Science*, *325*(5948), 1700-1704. https://doi.org/10.1126/science.1176221

Mistlberger, R. E., & Rusak, B. (2021). Biological Rhythms and Behavior. In J. J. Bolhuis, L.-A. Giraldeau, & J. A. Hogan (Eds.), *The Behavior of Animals: Mechanisms, Function, and Evolution* (2nd ed., pp. 78-110). John Wiley & Sons, Hoboken, NJ, United States. https://doi.org/10.1002/9781119109556.ch4, ISBN: 9781119109518

Montevecchi, W. A., Davoren, G. K., Regular, P. M., & Hedd, A. (2010). Crepuscular foraging by a pursuit-diving seabird: tactics of common murres in response to the diel vertical migration of capelin. *Marine Ecology Progress Series*, *415*, 295-304. https://doi.org/10.3354/meps08752

Mrosovsky, N. (1999). Masking: history, definitions, and measurement. *Chronobiology international*, *16*(4), 415-429. https://doi.org/10.3109/07420529908998717

Müller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences*, *85*(14), 5287-5290. https://doi.org/10.1073/pnas.85.14.5287

Padget, O., Bond, S. L., Kavelaars, M. M., van Loon, E., Bolton, M., Fayet, A. L., Syposz, M., Roberts, S., & Guilford, T. (2018). *In situ* clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology*, *28*(2), 275-279.e272. https://doi.org/10.1016/j.cub.2017.11.062

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M., & Guilford, T. (2019). Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the National Academy of Sciences*, *116*(43), 21629-21633. https://doi.org/10.1073/pnas.1903829116

Pardi, L. (1960). Innate components in the solar orientation of littoral amphipods. In *Cold Spring Harbour Symposia on Quantitative Biology* (25th ed., pp. 395-401). Biological Clocks 1960, Cold Spring Harbor, NY, United States. Cold Spring Harbor Laboratory Press, Cold Spring Harbour, NY, United States. https://doi.org/10.1101/sqb.1960.025.01.042

Pilorz, V., Helfrich-Förster, C., & Oster, H. (2018). The role of the circadian clock system in physiology. *Pflügers Archiv - European Journal of Physiology*, *470*(2), 227-239. https://doi.org/10.1007/s00424-017-2103-y

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rafnsson, V., Tulinius, H., Jónasson, J. G., & Hrafnkelsson, J. (2001). Risk of breast cancer in female flight attendants: a population-based study (Iceland). *Cancer Causes & Control*, *12*, 95-101. https://doi.org/10.1023/a:1008983416836

Rijnsdorp, A., Daan, S., & Dijkstra, C. (1981). Hunting in the kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. *Oecologia*, *50*(3), 391-406. https://doi.org/10.1007/BF00344982

Roenneberg, T., & Merrow, M. (2016). The Circadian Clock and Human Health. *Current Biology*, *26*(10), R432-R443. https://doi.org/10.1016/j.cub.2016.04.011

Schmidt-Koenig, K. (1990). The sun compass. *Experientia*, *46*, 336-342. https://doi.org/10.1007/BF01952166

Schwartz, W. J., Helm, B., & Gerkema, M. P. (2017). Wild clocks: preface and glossary. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20170211. https://doi.org/10.1098/rstb.2017.0211

Shoji, A., Dean, B., Kirk, H., Freeman, R., Perrins, C. M., & Guilford, T. (2016). The diving behaviour of the Manx Shearwater *Puffinus puffinus*. *Ibis*, *158*(3), 598-606. https://doi.org/10.1111/ibi.12381

Siddiqi-Davies, K., Lancaster-Reeves, L., Morford, J., Padget, O., Wynn, J., Bond, S., Lewin, P., Jaggers, P., & Guilford, T. (2025). Pre-laying sex differences in

reproductive roles can constrain foraging behaviour in a monomorphic seabird. *Marine Biology*, *172*(7), 103. https://doi.org/10.1007/s00227-025-04666-9

Signorell, A. (2025). *DescTools: Tools for Descriptive Statistics*. R package version 0.99.59. https://github.com/AndriSignorell/DescTools/

Strubbe, J. H., Keyser, J., Dijkstra, T., & Prins, A. J. A. (1986). Interaction between circadian and caloric control of feeding behavior in the rat. *Physiology & Behavior*, *36*(3), 489-493. https://doi.org/10.1016/0031-9384(86)90320-3

Sulzman, F. M., Ellman, D., Fuller, C. A., Moore-Ede, M. C., & Wassmer, G. (1984). *Neurospora* Circadian Rhythms in Space: a Reexamination of the Endogenous-Exogenous Question. *Science*, *225*(4658), 232-234. https://doi.org/10.1126/science.11540800

Tomotani, B. M., Straußß, A. F. T., Kishkinev, D., van de Haar, H., & Helm, B. (2024). Circadian clock period length is not consistently linked to chronotype in a wild songbird. *European Journal of Neuroscience*, *60*(7), 5522-5536. https://doi.org/10.1111/ejn.16535

Tomotani, B. M., Timpen, F., & Spoelstra, K. (2023). Ingrained city rhythms: flexible activity timing but more persistent circadian pace in urban birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *290*(1999), 20222605. https://doi.org/10.1098/rspb.2022.2605

Turek, F. W., Joshu, C., Kohsaka, A., Lin, E., Ivanova, G., McDearmon, E., Laposky, A., Losee-Olson, S., Easton, A., Jensen, D. R., Eckel, R. H., Takahashi, J. S., & Bass, J. (2005). Obesity and Metabolic Syndrome in Circadian *Clock* Mutant Mice. *Science*, *308*(5724), 1043-1045. https://doi.org/10.1126/science.1108750

von Frisch, K. (1974). Decoding the Language of the Bee. *Science*, *185*(4152), 663-668. https://doi.org/10.1126/science.185.4152.663

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, United States. https://ggplot2.tidyverse.org, ISBN: 978-3-319-24277-4

Wickham, H. (2023). *stringr: Simple, Consistent Wrappers for Common String Operations*. R package version 1.5.1. https://github.com/tidyverse/stringr

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A Grammar of Data Manipulation*. R package version 1.1.4. https://github.com/tidyverse/dplyr

Wiltschko, W., & Balda, R. P. (1989). Sun compass orientation in seed-caching scrub jays (Aphelocoma coerulescens). *Journal of Comparative Physiology A*, *164*(6), 717-721. https://doi.org/10.1007/BF00616744

Xu, K., Zheng, X., & Sehgal, A. (2008). Regulation of Feeding and Metabolism by Neuronal and Peripheral Clocks in *Drosophila*. *Cell Metabolism*, *8*(4), 289-300. https://doi.org/10.1016/j.cmet.2008.09.006

Yerushalmi, S., & Green, R. M. (2009). Evidence for the adaptive significance of circadian rhythms. *Ecology Letters*, *12*(9), 970-981. https://doi.org/10.1111/j.1461-0248.2009.01343.x

Zeileis, A., & Grothendieck, G. (2005). zoo: S3 Infrastructure for Regular and Irregular Time Series. *Journal of Statistical Software*, *14*(6), 1-27. https://doi.org/10.18637/jss.v014.i06.

Zimmerman, P. H., Pope, S. J., Guilford, T., & Nicol, C. J. (2009). Involvement of the sun and the magnetic compass of domestic fowl in its spatial orientation. *Applied Animal Behaviour Science*, *116*(2-4), 204-210. https://doi.org/10.1016/j.applanim.2008.09.006

# 5

# Free ranging shearwaters do not rely on magnetic maps or compasses

With contributions from Bond, S., Padget, O., Harris, S. M., Lancaster-Reeves, L., de Boer, M., Serafini, P. P., Hughes, G., Wynn, J., Morford, J. and Guilford, T.

## Contents

**5.1** Abstract....144

**5.2** Introduction....145

**5.3** Materials & Methods....148

**5.4** Results....154

**5.5** Discussion....158

*"The theory of a magnetic sensitivity is always cropping up [... ] It is to be hoped that we have heard the last of this theory."*

G. V. T. Matthews, *The Sensory Basis of Bird Navigation* (1951)

[and my supervisors, every time I mention compass calibration]

## 5.1 Abstract

The idea that animals might orient using the earth's magnetic field has been an enduring and alluring possibility since the earliest days of animal navigation research. This possibility has now become established scientific fact, with good evidence for geomagnetic orientation across a range of animal taxa. Among these taxa, migratory passerine birds are one of the best studied examples and use geomagnetic cues both as a compass (to sense heading direction) and as a map (to sense their location). Although the mechanism of magnetosensing remains unresolved, birds appear able to sense the inclination of the geomagnetic field, probably using a light-dependent chemical reaction in the retina. However, most passerine migrants travel at night and the evidence for geomagnetic navigation in diurnal avian taxa remains controversial. We report the results of the largest ever magnetic disruption experiment in wild birds, yielding no evidence for geomagnetic orientation in Manx shearwaters (*Puffinus puffinus*). Qualitative assessment of effect sizes suggests that, although our negative results do not exclude the possibility that shearwaters can use geomagnetic cues to navigate, these cues are highly unlikely to be an important element of shearwater navigation, unlike olfactory map cues and solar compass information.

## 5.2 Introduction

Many animals are thought to navigate using a two-step map-and-compass approach (Kramer, 1953). Under this framework, animals first estimate their location and thus the direction (and perhaps distance) to their goal, before orienting in that direction using a compass. The geomagnetic field has the potential to provide both positional and directional information on a global scale (Lohmann et al., 2022; Lohmann et al., 2007). Animals can use the north-south axis of the field to sense the approximate geographic direction of their heading. In addition, various parameters of the field – its total intensity, inclination (vertical angle relative to the earth's surface) and declination (horizontal angle between geographic and magnetic north) – vary relatively predictably over the earth's surface. The geomagnetic field, therefore, appears an almost perfect navigational reference. Indeed, there is now strong evidence for the use of geomagnetic information for orientation by a wide array of animals, from moths to sharks (Boles & Lohmann, 2003; Dreyer et al., 2018; Fleischmann et al., 2018; Keller et al., 2021; Phillips, 1986; Wiltschko & Wiltschko, 1972). Among vertebrates, perhaps the best-studied geomagnetic navigation models are sea turtles and night-migratory passerine birds, which appear to use the field for both their map and compass senses (Brothers & Lohmann, 2015; Chernetsov et al., 2017; Fuxjager et al., 2011; Goforth et al., 2025; Kishkinev et al., 2015; Kishkinev et al., 2021; Lohmann et al., 2004; Lohmann et al., 2001; Lohmann & Catherine, 1993; Wiltschko & Wiltschko, 1972).

Although magnetic cues are demonstrably important in avian navigation, controversy remains. The magnetoreceptor of birds has never been definitively identified, with candidates including biogenic magnetite in the upper mandible, electromagnetic induction in the inner ear and a light-dependent mechanism involving cryptochrome molecules in the retina (Hore & Mouritsen, 2016; Nimpf et al., 2019; Nordmann et al., 2017; Treiber et al., 2012; Walcott et al., 1979; Wiltschko

& Wiltschko, 2013; Wiltschko & Wiltschko, 2019; Wiltschko, Munro, et al., 2009). In addition, whilst the magnetic orientation abilities of passerine birds are well-established, evidence for use of magnetic cues in homing pigeons (*Columba livia*), the main model of avian navigation, is contradictory and contentious (Beacon et al., 1997; Gordon, 1948; Holland et al., 2013; Jandačka et al., 2022; Keeton et al., 1974; Lednor & Walcott, 1983; Matthews, 1951; Schiffner & Wiltschko, 2011; Walcott, 1977; Wallraff et al., 1986; Wiltschko, Schiffner, et al., 2009; Yeagley & Whitmore, 1947). Attempts have been made to conduct similar tests in wild birds, using magnetic sensory manipulation to test for use of magnetic cues. Whilst there are a small number of studies on other taxa including one passerine species (Holland et al., 2009; Wikelski et al., 2015), the vast majority of these experiments have taken place in Procellariiform seabirds, the best-studied wild avian navigators. These studies involved attachment of strong neodymium magnets to the birds' heads or wings to scramble geomagnetic information (Bonadonna et al., 2005; Bonadonna et al., 2003; Gagliardo et al., 2013; Massa et al., 1991; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015), an approach which has been validated in passerines known to rely heavily on a magnetic compass (Packmor et al., 2021). Nonetheless, these manipulations of wild birds have failed to detect any substantial impact of magnetic disruption on wild birds' navigation. However, these studies are limited by relatively small sample sizes (Bonadonna et al., 2005; Bonadonna et al., 2003; Gagliardo et al., 2013; Holland et al., 2009; Massa et al., 1991; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015), methodological issues such as failure to maintain magnetic disruption (Mouritsen et al., 2003; Padget et al., 2017) and perhaps targeting of the incorrect putative magnetoreceptor (Bonadonna & Gagliardo, 2021; Treiber et al., 2012; Wikelski et al., 2015; Zapka et al., 2009). Yet despite these issues, marginal differences appear in some cases between the control and magnetically disrupted groups, especially after a number of days under the treatment or when approaching the goal

(Bonadonna et al., 2005; Gagliardo et al., 2013; Massa et al., 1991; Padget et al., 2017).

These possible effects of magnetic treatment, appearing only after a longer period of disruption, point to a subtler possibility. Some birds are known to transfer information between celestial and geomagnetic compasses, effectively calibrating one against the other to provide a unified frame of reference (Muheim et al., 2006) and similar effects have been observed in shearwaters (Wynn et al., 2021). If birds calibrate their sun compass against their magnetic compass, possibly to keep track of changes in the visible sun arc resulting from latitudinal movements and seasonal progression, they should become increasingly disoriented with the passage of time or latitudinal movements, when denied magnetic information.

Here, we set out to provide a definitive test of geomagnetic orientation in Manx shearwaters, as a model of diurnal avian navigation in the wild, by conducting the largest magnetic disruption experiment to-date. During the breeding season, Manx shearwaters nest on coastal islands, with the largest numbers on the western coasts of the UK and Ireland. Pairs alternate incubation stints and long-distance foraging trips, travelling up to around 1,500 kilometres from the colony for a maximum of roughly two weeks (Dean et al., 2015; Guilford et al., 2008; Padget et al., 2019). After foraging, shearwaters home back to their colony during the day, orienting from out of sight of land using a large-scale grid map and fail to anticipate landmasses which they must orient around, suggesting this is not based on familiarity (Padget et al., 2019). Once in sight of land, shearwaters often follow the coast, perhaps via visual pilotage (Padget et al., 2017; Pollonara et al., 2015). Manx shearwaters appear to rely heavily on the sun as a compass cue (Chapters 2 and 3; Padget et al., 2018), whilst evidence from closely related species has implicated olfactory cues as the main source of map information. However, Manx shearwaters are known to be magnetosensitive and use geomagnetic inclination to re-find their natal colonies after first migration (Wynn et al., 2020). Other shearwaters appear to possess a

magnetic compass sense (Takahashi et al., 2022) and marginal effects of magnetic disruption are apparent in some experiments (Gagliardo et al., 2013; Padget et al., 2017). Nonetheless, the role of geomagnetic cues in the remarkable homing navigation of adult shearwaters is unclear and the possibility that reliance on calibration of the sun compass might underlie the marginal magnetic effects in other experiments has never been explored. We collected 131 tracks of foraging trips from shearwaters fitted with either a strong neodymium magnet designed to block access to geomagnetic information or a brass control. We find no evidence for impacts on any element of navigation or movement behaviour, including calibration effects or differences near the colony. Although this does not rule out that shearwaters and other diurnal avian navigators are able to use geomagnetic information, it suggests that they are not reliant on these cues and primarily use other sources of directional and positional information.

## 5.3 Materials & Methods

### 5.3.1 Site & subjects

This experiment took place across two breeding colonies of Manx shearwaters: Skomer Island, Pembrokeshire, Wales (51°44′15.7″N, 5°16′58.8″W) and Lighthouse Island, Copeland Islands, County Down, Northern Ireland (51° 41′ 38.5″N, 5°31′32.9″W) in 2023 and 2024. Shearwaters were monitored during egg laying and incubation in known study burrows accessible by hand either via the burrow entrance or a purpose-built access hatch.

### 5.3.2 Experimental protocol

From 24$^{th}$ May to 4$^{th}$ June 2023 and 31$^{st}$ May to 8$^{th}$ June 2024, the identity of the incubating partner in each burrow was recorded during the day and knock-down sticks were placed in the entrance of the burrow so that the entry or exit of birds could be monitored without disturbing the nest. On the following nights, burrows were visually checked at frequent intervals and if the sticks were knocked down, they were checked by hand. In cases where both partners were present, the

burrow was temporarily blocked with a towel to allow time for the behaviours associated with swapping incubation duties (e.g. allopreening and duetting calls). After 15-30 minutes, the towels were removed and the departing bird was captured. We then dorsally attached a SnapperGPS archival post-processing GNSS logger programmed to record satellite data every 2 minutes (Beuchert et al., 2023) to each bird using tape and superglue (see Guilford et al., 2008). The logger was sealed in heatshrink plastic, with a second chamber in the plastic housing containing the experimental treatment; either an 8 mm diameter N38 spherical neodymium magnet or a brass bearing of equal dimensions. The local geomagnetic field in the shearwaters' foraging range varies in intensity between roughly 48,000 nT and 52,000 nT. Using the equation for a dipole field from a uniformly magnetised sphere with remanence of 1.24 T, our magnets produced a field between 77,150 nT and 423,280 nT (1.5 to 8 times stronger than the local geomagnetic field) at the bird's eye, the site of the best-supported putative magnetoreceptor (50-70 mm from the magnet, at 0-90° from the axis of the magnetic field; Hore & Mouritsen, 2016). In contrast, using the equation for a dipole field created by a loop of wire (radius 15 mm, current 25 mA; Beuchert et al., 2023), the magnetic field produced by a SnapperGPS is estimated to be no more than approximately 10.3 nT; almost 6,000 times weaker than the local geomagnetic field at the eye (at 70 mm from the device, on the axis of the field). The magnets did not roll entirely freely within the housing due to the enclosed space. Nonetheless, the housing was designed to allow the magnet some movement independent of the bird, in addition to any movement of the entire attachment on the feathers or movement of the head relative to the body, and jostling movement is not required to disrupt magnetic orientation in other birds known to rely on a magnetic compass (Packmor et al., 2021). The total mass of the deployment, including device, housing, tape and treatment was 13.46 ± 0.28 g in the magnet group and 13.39 ± 0.24 g in the control group (mean ± standard deviation). On each night,

birds were alternately assigned to each treatment to avoid biases in deployment date. Birds were also weighed on deployment. After deployment, birds were returned to the entrance of their burrow to depart on a foraging trip. Device retrieval attempts began only after 7 days had elapsed and took place by checking the incubating partner each day, unless the breeding attempt showed signs of possible failure, in which case they were checked at night and the device was retrieved as soon as possible.

### 5.3.3 Data processing

All data processing and analysis was conducted in R version 4.4.2 (R Core Team, 2024), with packages *lubridate*, *raster*, *dplyr* and *data.table* (Barrett et al., 2025; Grolemund & Wickham, 2011; Hijmans, 2025; Wickham et al., 2023). Figures were created using the packages *effects*, *ggplot2*, *ggspatial*, *gridExtra*, *cowplot*, *sf*, *rnaturalearth*, *rnaturalearthdata* and *rnaturalearthhires* (Auguie, 2017; Dunnington, 2025; Fox & Weisberg, 2018, 2019; Massicotte & South, 2025; Pebesma, 2018; Pebesma & Bivand, 2023; South et al., 2025a; South et al., 2025b; Wickham, 2016; Wilke, 2024).

The raw data from SnapperGPS were processed using an open-source algorithm to generate location estimates with high accuracy and precision (Beuchert & Rogers, 2021). This algorithm assigns a confidence value in arbitrary units, where a missing value indicates a failed location estimate. These fixes were removed from the data. For each remaining fix, we calculated the great circle distance travelled from the previous fix and the distance from the colony using the *distHaversine* function from the *geosphere* package (Hijmans, 2019). We used distance from the colony to assess whether each fix was within the maximum visible distance of the colony. We also identified whether each fix was within 30 km of any landmass of at least 20 $km^2$. Using the distance between fixes we calculated travel speed and iteratively filtered to remove fixes with unrealistic speeds greater than 80 $kmh^{-1}$. For remaining fixes, we used a Gaussian mixture model (*normalmixEM* from *mixtools*; Benaglia et al.,

2009) on values of speed to identify a threshold of 19.33 $kmh^{-1}$ above which birds were considered to be predominantly in flight during the fix interval.

Using the *suncalc* package (Thieurmel & Elmarhraoui, 2025), we identified local sunrise and sunset time at each fix location, using this to assess whether the fix occurred during daylight and at which fix the bird experienced sunrise. For each fix, we calculated the time until local sunset occurred. To calculate the predicted orientation error if shearwaters rely on a geomagnetic compass to calibrate their sun compass, we calculated for each fix the time elapsed since the bird experienced sunrise. We then added this time to the time of sunrise at the colony on the day of deployment. We extracted the sun azimuth at the colony on the day of deployment at each of these times. This represented the azimuth the bird would expect if it had been unable to update its time-compensation programme due to lack of geomagnetic compass information. The difference between this angle and the sun's true azimuth angle visible from each fix was the predicted orientation error.

To identify homing behaviour, we first identified bouts of continuous flight lasting at least 10 minutes, ignoring gaps of up to 30 minutes, which represent periods of commuting towards, between or back from foraging areas. For each of these bouts, we recorded the distance from the colony at the start and end of each bout, and the bearing from start to end relative to the bearing towards the colony. Using these distances, we also calculated the proportional change in distance from the colony from the start to the end of the bout. Any bout which started at least 10 km from the colony, ended at least 50% closer to the colony and was oriented within 75° of the homeward direction was classed as homing. Within these bouts, only fixes representing flight were recorded as actively homing. For each homing fix, we recorded whether there were any landmasses blocking the beeline great circle route from the fix to the colony. To measure observed orientation error, we calculated the initial great circle bearing from each fix to the next using the *bearing* function from *geosphere* (Hijmans, 2019). We then calculated the difference

between this bearing and the homeward beeline direction. This was the observed angular deflection. Finally, we split each track into trips based on when the shearwater was more than 3 km from the colony for more than 6 hours.

For each trip, we calculated and recorded a number of variables:

- Colony (Copeland, Skomer)
- Individual ring number
- Treatment group (magnet, control)
- Trip duration (hours)
- Maximum displacement from the colony (km)
- Time between application of treatment and homing (days)
- Circular mean predicted compass calibration error during homing under daylight, either when more than 30 km from land or when there was a clear beeline to the colony and the colony was not visible (°, using the *mean.circular* function from *circular*; Agostinelli & Lund, 2024)
- Circular mean observed deflection from the homeward beeline during homing under the same conditions (°)
- Mean absolute observed deflection from the homeward beeline during homing at any time of day, either when more than 30 km from land or when there was a clear beeline to the colony and the colony was not visible (°)
- Mean absolute observed deflection from the homeward beeline during homing at night, either when more than 30 km from land or when there was a clear beeline to the colony and the colony was not visible (°)
- Mean absolute observed deflection from the homeward beeline during homing at any time of day when within 30 km of the colony (°)
- Distance from the colony at the start of homing (km)
- Distance from the colony at the end of homing (km)
- Distance travelled from fix to fix between the start and end of homing (km)
- Time from the start of homing to local sunset (hours)
- Proportion of fixes occurring within 30 km of land
- Proportion of fixes at night during which the bird was in flight

We divided the distance travelled between fixes during homing by the change in distance from the colony to generate the homing efficiency index. This is a measure

of tortuosity, relative to homewards movement. For all measures of mean absolute deflection, the means were calculated after a logarithmic transformation to impose normality and then back-transformed. In addition, we recorded each bird's change in mass from device deployment and retrieval.

### 5.3.4 Statistical analysis

To test for impacts of magnetic disruption on the general characteristics of foraging trips, we constructed two linear mixed effects models with log-transformed trip duration and maximum displacement as the dependent variables. The independent variables were treatment and colony, with individual as a random intercept term. In addition, we tested for impacts on foraging success using a linear model with mass change from deployment to retrieval as the response and colony and treatment as predictors. Models were fitted using the function *lmer* from *lme4* (Bates et al., 2015).

We next constructed a series of models to test whether magnetic disruption affected shearwaters' navigational abilities. All models included individual as a random intercept and the first four were linear mixed effects models. The response of the first model was mean absolute orientation error and the fixed effects were treatment interacting with day of homing, colony and distance from the colony at the start of homing. The second model was similar but the response was mean absolute deflection during homing at night and day of homing was not included in the fixed predictors. In the third model, the response was mean absolute deflection within 30 km of the colony but distance from the colony at the start of homing was not included as a fixed predictor. The next model was designed to test whether magnetic disruption affected distance estimation in shearwaters so the response was log-transformed time from start of homing to local sunset and the fixed effects were log-transformed first homing distance, treatment and colony. The final model was a mixed effects beta regression with a logit-link using the function *glmmTMB* from the package *glmmTMB* (Brooks et al., 2017; McGillycuddy et al., 2025). The

response was homing efficiency index. The predictors were treatment and colony. For all models, if the variance explained by individual was zero or very close to zero, we refitted the model without the random effect. This was the case for the model of homing efficiency, deflection at night and deflection within 30 km of the colony. The beta regression model was refitted using the function *betareg* from the package *betareg* (Cribari-Neto & Zeileis, 2010).

The final two models were logistic mixed effect models designed to test whether shearwaters compensated for any magnetic disruption by changing their movement patterns to rely on other cues using the function *glmer* from *lme4* (Bates et al., 2015). We therefore tested whether treatment and colony predicted the proportion of time shearwaters spent within 30 km of the coast and the proportion of time they spent in flight at night. Individual was included as a random intercept in both models but explained no variance in the night flight model so was dropped.

For all simple linear models, *P*-values were calculated using F-tests. For all other models, *P*-values were estimated using likelihood ratio tests on full and restricted models for each term, including via the *lrtest* function in the *lmtest* package (Zeileis & Hothorn, 2002). Coefficients are presented with 95% confidence bounds in square brackets. For each linear model, we calculated Cohen's d for the difference in coefficient between magnet and control groups, using the *eff_size* function from the *emmeans* package (Lenth, 2024).

## 5.4 Results

142 devices were deployed and 134 of these were successfully retrieved, with 131 producing sufficient data for analysis. The resulting tracks are shown in Fig. 5.1A.

Trips lasted 48 hours and shearwaters travelled up to 69 km from the colony, on average. Trip duration and maximum distance were significantly higher from Skomer Island than from Lighthouse Island (221% [162%, 292%] longer, $\chi^2_1 = 29.11$, $P < 0.001$ and 305% [195%, 457%] farther, $\chi^2_1 = 59.23$, $P < 0.001$, respectively) but

neither measure was affected by treatment ($\chi^2_1 = 0.41$, $P = 0.523$ and $\chi^2_1 = 1.45$, $P = 0.229$; Fig. 5.1B-C). Mass change did not differ significantly between either island or treatment ($F_{1,62} = 1.84$, $P = 0.179$ and $F_{1,62} = 0.02$, $P = 0.878$; Fig. 5.1D).

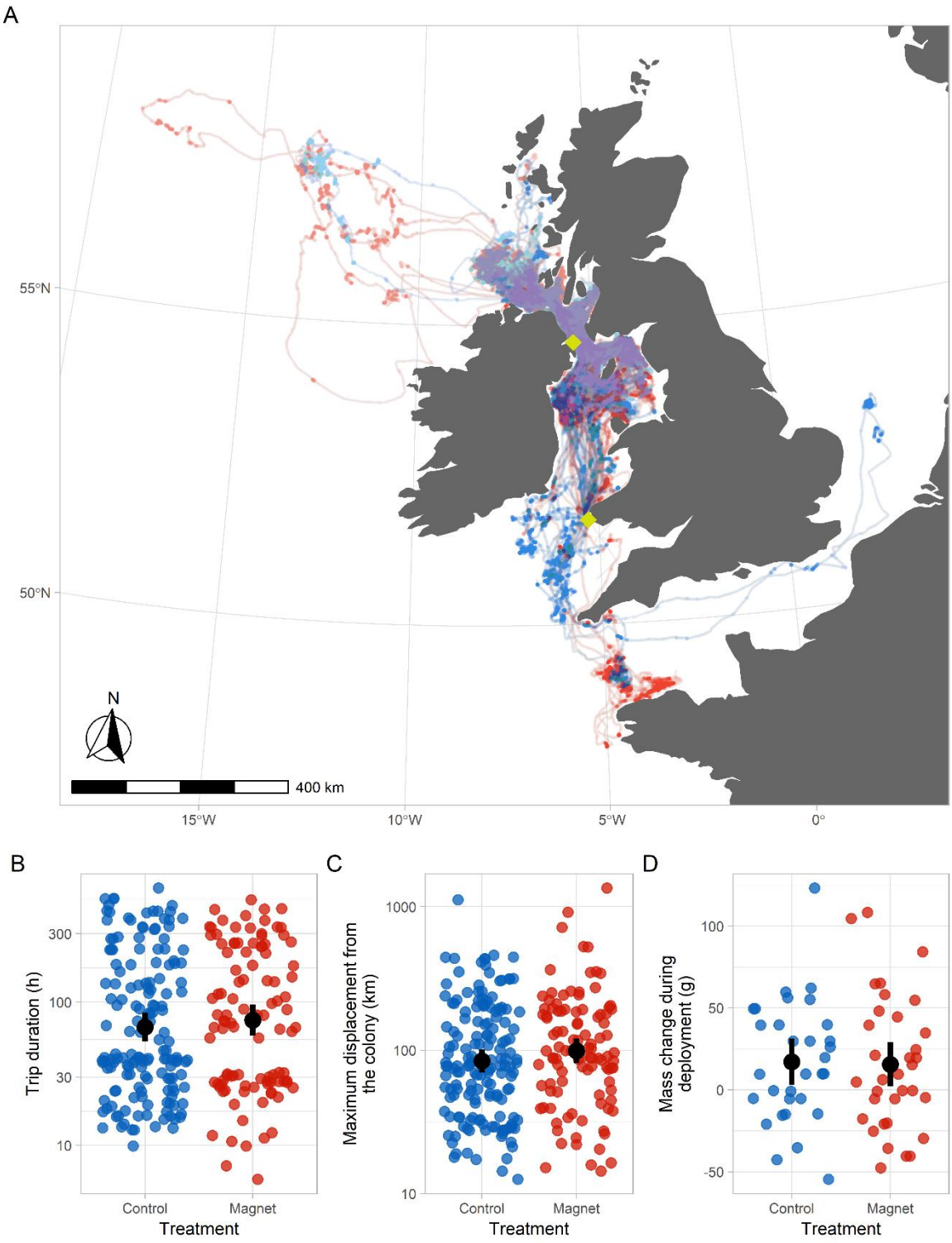



Fig. 5.1. Tracks and trip parameters of shearwaters in both magnetically disrupted (red) and control (blue) groups from Skomer (darker colours) and Copeland (lighter colours). In

B-D, the black dot and error bar shows the mean and 95% confidence interval derived from model coefficients and each point is the partial residual from a single trip. (A) Tracks from all birds, coloured by treatment group. Copeland and Skomer are shown by green diamonds. (B) Trip duration, in hours, for each treatment group. The y-axis is on a log-scale. (C) Maximum displacement from the colony (km) in each treatment, shown on a log-scale. (D) Mass change of the shearwater between deployment and retrieval, in grams.

Absolute deflection from the beeline during homing out of sight of land was no higher in the magnetic treatment group ($\chi^2_1 = 0.37$, $P = 0.545$), even when treatment was allowed to interact with day of homing ($\chi^2_1 = 0.54$, $P = 0.464$; Fig. 5.2A). No other covariates predicted absolute deflection (day of homing: $\chi^2_1 = 2.73$, $P = 0.099$; distance from the colony at the start of homing: $\chi^2_1 = 0.23$, $P = 0.635$; colony: $\chi^2_1 = 0.12$, $P = 0.725$). Whilst absolute deflection within 30 km of the colony was not significantly different in each treatment ($F_{1,152} = 0.33$, $P = 0.565$; Fig. 5.2B) it was 26% [1%, 57%] higher for birds from Skomer ($F_{1,62} = 4.22$, $P = 0.042$). Similarly, absolute deflection during homing at night was not affected by treatment or distance from the colony at the start of homing ($F_{1,87} = 0.05$, $P = 0.817$ and $F_{1,87} = 3.42$, $P = 0.068$, respectively; Fig. 5.2C) but was 38% [2%, 87%] higher among birds from Skomer ($F_{1,87} = 4.50$, $P = 0.037$). Conversely, homing efficiency index across all homing in a trip was significantly higher among birds from Skomer ($\chi^2_1 = 3.91$, $P = 0.048$) but did not differ between treatments ($\chi^2_1 = 0.24$, $P = 0.627$; Fig. 5.2D).

The time allocated to homing increased by 0.25% for each 1% increase of distance from the colony ($\chi^2_1 = 12.99$, $P < 0.001$) with no significant interaction with treatment ($\chi^2_1 = 1.15$, $P = 0.284$; Fig. 5.2E). The time allocated to homing was not affected by colony ($\chi^2_1 = 0.11$, $P = 0.746$) or an additive effect of treatment ($\chi^2_1 = 0.14$, $P = 0.711$).

Change in the sun's arc with latitude and season did not predict orientation error in either the control or magnet group ($\chi^2_1 = 0.69$, $P = 0.406$), with no significant interaction ($\chi^2_1 = 1.86$, $P = 0.173$; Fig. 5.2F). There was no additive effect of treatment ($\chi^2_1 = 2.35$, $P = 0.125$) but birds from Skomer oriented 12.54° [4.11°, 20.97°] further anticlockwise than those from Copeland ($\chi^2_1 = 8.11$, $P = 0.004$).

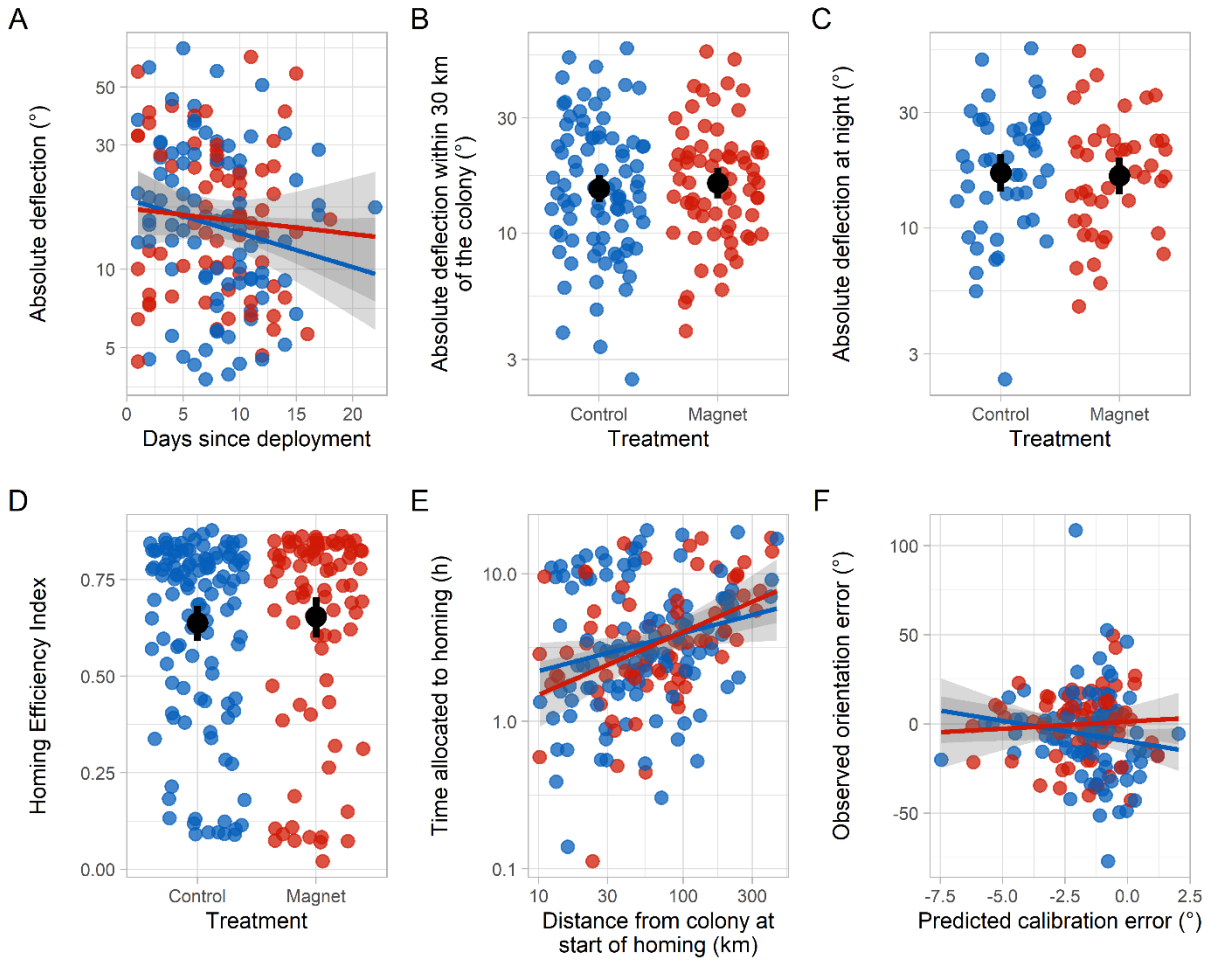



**Fig. 5.2. Navigational impacts of magnetic disruption on shearwater homing.** Fitted slopes, means and confidence intervals are derived from model coefficients, with points representing partial residuals. Each point is a single trip. (A-C) Absolute deflection from the homeward beeline, on a log-scale, as a measure of navigational error in both treatment groups (A) when homing beyond 30 km from land or with a clear beeline to the colony over the course of the deployment, (B) close to the colony and (C) during homing at night. (D) Homing efficiency index across all homing in both treatments. (E) Time allocated to homing against distance from the colony, both on log-scales. This represents distance estimation by shearwaters. (F) Relationship between observed deflection from the homeward beeline and predicted orientation error resulting from failure to calibrate the sun compass.

The probability of remaining within 30 km of the coast was 0.18 [0.05, 0.38] higher for birds from Copeland than Skomer ($\chi^2_1 = 10.43$, $P = 0.001$) but no different between treatments ($\chi^2_1 = 1.20$, $P = 0.273$; Fig. 5.3A). The probability of flying at night did not differ between either treatment or colony ($\chi^2_1 = 0.28$, $P = 0.594$ and $\chi^2_1 = 0.43$, $P = 0.510$, respectively; Fig. 5.3B).

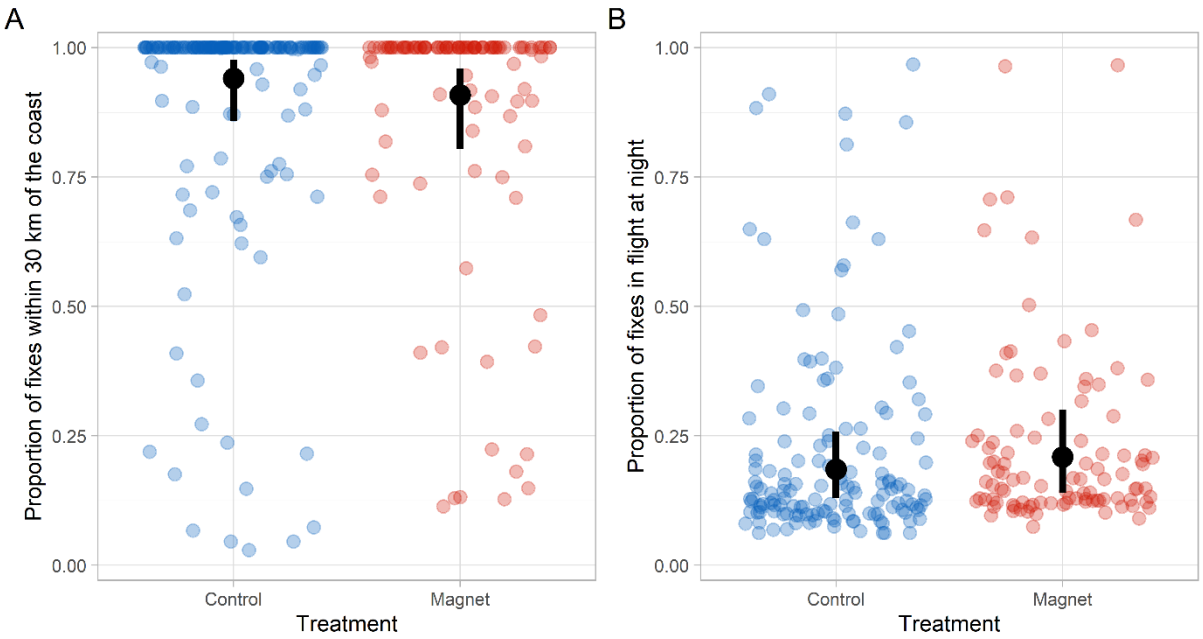



**Fig. 5.3. Potential compensatory changes in shearwater movement behaviour which might buffer navigational impacts.** Means and confidence intervals are derived from logistic models. (A) Proportion of each trip spent within 30 km of the coast, where shearwaters may be able to employ pilotage to home without reference to a map or compass. (B) Proportion of time spent in flight at night, when impacts of magnetic disruption on navigation may be strongest, due to lack of solar azimuth compass cues.

## 5.5 Discussion

The earth's magnetic field provides a wealth of spatial and directional information. Use of geomagnetic cues for orientation is widespread and has become a key focus of animal navigation research (Wiltschko & Wiltschko, 2022). Orientation of night-migratory passerines under artificial magnetic fields suggests that a magnetic inclination sense provides both map and compass information to guide their long-distance annual migrations (Chernetsov et al., 2017; Kishkinev et al., 2015; Kishkinev et al., 2021; Wiltschko & Wiltschko, 1972). When powerful neodymium magnets of the kind used here are attached to these birds to disrupt geomagnetic sensing, they are unable to orient (Packmor et al., 2021). However, the role of geomagnetic information in the navigation of other birds remains controversial. There is evidence that non-passerine birds possess a magnetic sense (Mora et al., 2004; Wynn et al., 2020; Zimmerman et al., 2009) but use of magnetic cues by homing pigeons and the sensory basis of magnetoreception remain contested

(Beacon et al., 1997; Gordon, 1948; Holland et al., 2013; Hore & Mouritsen, 2016; Jandačka et al., 2022; Keeton et al., 1974; Lednor & Walcott, 1983; Matthews, 1951; Mora et al., 2004; Nimpf et al., 2019; Nordmann et al., 2017; Schiffner & Wiltschko, 2011; Treiber et al., 2012; Walcott, 1977; Walcott et al., 1979; Wallraff et al., 1986; Wiltschko, Schiffner, et al., 2009; Wiltschko & Wiltschko, 2013; Wiltschko, Munro, et al., 2009; Yeagley & Whitmore, 1947). Further, a number of experiments using disruption of geomagnetic sensing in wild models of diurnal avian navigation have produced negative results (Bonadonna et al., 2005; Bonadonna et al., 2003; Gagliardo et al., 2013; Holland et al., 2009; Massa et al., 1991; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015; Wikelski et al., 2015), even if these studies were limited by sample size and methodological issues. Aiming to provide a definitive test of magnetic navigation in a model of avian navigation in the wild, we here conducted the largest ever magnetic disruption experiment in a wild bird and find no impact on the orientation or movement behaviour of Manx shearwaters.

The overall form of shearwaters' foraging trips was unaffected by treatment; shearwaters in each group remained at sea for similar duration and travelled a similar distance from the colony. Furthermore, the change in birds' mass over the course of each deployment was unaffected by treatment. This suggests that there were no general behavioural impacts of magnetic disruption and that shearwaters do not rely on geomagnetic information to find foraging grounds and feed successfully.

Magnetically disrupted birds did not show impaired navigational abilities. The absolute deflection of their orientation from the correct beeline direction when homing far from land was no higher than in controls, whilst their homing efficiency index throughout homing was no lower. In addition, unlike the marginal differences seen between magnetic and control groups in previous experiments (Gagliardo et al., 2013; Padget et al., 2017; Wikelski et al., 2015), no effects of

magnetic disruption were apparent either after many days or close to the colony. Absolute deflection remained consistent between groups even at night, when the sun compass is not available, limiting any potential redundancy. In addition, we found that the magnetically disrupted group were equally able to estimate the distance to the colony and allocate appropriate time to homing, indicating that they did not require magnetic map cues for distance estimation.

Inspired by the calibration between celestial and magnetic compasses seen in passerines and shearwaters (Muheim et al., 2006; Wynn et al., 2021) and small differences between magnetic and control groups in previous experiments that would be consistent with this mechanism, we aimed to test whether shearwaters rely on a geomagnetic compass to calibrate their sun compass. Under this mechanism, shearwaters would use a geomagnetic compass to measure solar azimuth at sunrise or sunset, thus disambiguating changes in photoperiod with latitudinal or seasonal change from changes in local solar time with longitude. They would then be able to predict the sun arc and adjust their time-compensation accordingly. However, we found that changes in the sun's arc during the deployment did not significantly predict orientation error in either group, with no significant difference between them, suggesting that shearwaters rely on other mechanisms to maintain accurate time-compensation during large-scale movements.

Finally, we investigated whether a lack of apparent impact on shearwater navigation resulted from compensatory changes in movement behaviour. Shearwaters denied magnetic information might resort to visual pilotage along coastlines, which can be achieved without reference to either a map or compass, whilst they might choose to travel less at night if they rely more on magnetic cues in the absence of the sun. However, we found no increase in time spent within 30 km of the coast nor a decrease in the proportion of time spent in flight at night.

Throughout our analyses, we found generally consistent and substantial differences between Skomer and Copeland. Shearwaters from Skomer embark on longer trips and travel further from the colony, whilst showing higher homing efficiency and an anticlockwise orientation bias, compared to those from Copeland. In contrast, birds from Skomer showed higher orientation error both at night and when homing within 30 km of the colony. The greater distance and longer duration of trips by birds on Skomer might result from the much higher population density on and around this colony, and its effect on food resource distributions (Ashmole, 1963; Weber et al., 2021). We suggest that the navigational differences are explained by the fact that Copeland is surrounded by land in closer proximity to the colony than Skomer and thus shearwaters from Copeland spent far more of their time at sea within 30 km of the coast. As shearwaters avoid flying over land, these obstacles likely reduced homing efficiency whilst the differing layout of obstacles around the colony likely altered orientation during homing.

Although negative results must be interpreted with caution, assessment of the effect sizes derived from our models suggests that it is highly unlikely that magnetic disruption has any major impact on the navigation of wild shearwaters (Fig. 5.4). This implies that, at the very least, there is a high level of redundancy in their navigational senses such that the removal of magnetic information can be compensated by other cues. This is in stark contrast to the removal or olfactory cues or the manipulation of sun compass orientation, which result in severe and easily detectable impacts on shearwater navigation (Gagliardo et al., 2013; Padget et al., 2018; Padget et al., 2017; Pollonara et al., 2015). In addition, we find no evidence for compensation in the behaviour of shearwaters. Consequently, we conclude that geomagnetic cues can only play a very small role, if any at all, in the navigational mechanisms of wild adult Manx shearwaters during normal wide-ranging foraging movements.

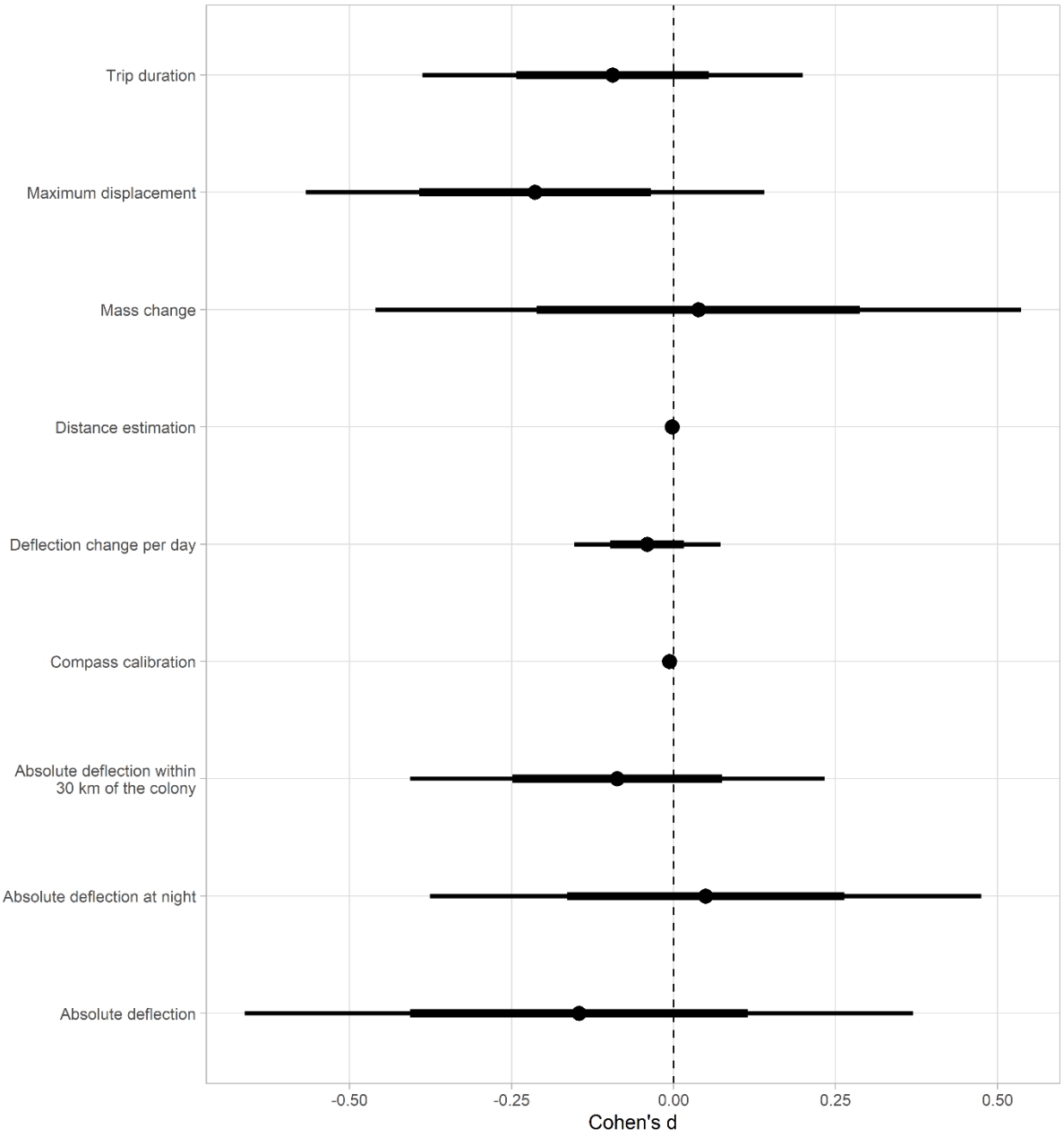



**Fig. 5.4. Cohen's d as a standardised measure of effect size for each potential navigational impact derived from linear model coefficients.** All but one of the mean estimates lie below the arbitrary value of 0.2 for a small effect size and only three 95% confidence intervals overlap the value of 0.5 for a medium effect size.

Our findings do not rule out the possibility that shearwaters use geomagnetic cues during migration. Their migratory movements span a scale at which variation in the geomagnetic field is more pronounced and might be more useful in providing coarse map information. Indeed, evidence suggests that immature shearwaters use geomagnetic inclination to guide their movements back to the colony after first migration (Wynn et al., 2020). Furthermore, shearwaters fly at night far more often

during migration than during the breeding season (Siddiqi-Davies et al., 2024). In the absence of the sun, and at a light levels where the radical pair mechanism of magnetoreception is more likely to operate (Wiltschko et al., 2000a, 2000b), a geomagnetic compass may be the most salient source of directional information. We suggest, therefore, that our results should only be interpreted in the context of shearwaters' diurnal homing navigation during foraging trips over scales of hundreds to thousands of kilometres.

Despite the apparent, almost universal utility of geomagnetic information for map-and-compass navigation and its prominence in animal navigation research, our findings demonstrate that one of the best-studied avian navigators does not rely on such cues for its remarkable feats of homing. With a large sample size and investigation of previously neglected navigational possibilities, we build on earlier studies of magnetic disruption in homing pigeons and wild birds which have provided little to no evidence for the use of geomagnetic cues (Bonadonna et al., 2005; Bonadonna et al., 2003; Gagliardo et al., 2013; Gordon, 1948; Holland et al., 2013; Holland et al., 2009; Massa et al., 1991; Matthews, 1951; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015; Wikelski et al., 2015). Instead, these diurnal travellers appear to require olfactory cues for positional information and a solar azimuth compass (Gagliardo, 2013; Gagliardo et al., 2013; Holland et al., 2009; Padget et al., 2018; Padget et al., 2017; Pollonara et al., 2015; Wikelski et al., 2015). We suggest, therefore, that whilst geomagnetic cues are clearly important for the navigation of many animals, their role in animal navigation is not universal and the phylogenetic, ontogenetic, mechanistic and adaptive factors shaping the evolution of the sensory mechanisms underlying navigation in different avian taxa require far greater study.

## References

Agostinelli, C., & Lund, U. (2024). *R package 'circular': Circular Statistics*. R package version 0.5-1. https://CRAN.R-project.org/package=circular

Ashmole, N. P. (1963). The regulation of numbers of oceanic tropical birds. *Ibis*, *103b*(3), 458-473. https://doi.org/10.1111/j.1474-919X.1963.tb06766.x

Auguie, B. (2017). *gridExtra: Miscellaneous Functions for "Grid" Graphics*. R package version 2.3. https://CRAN.R-project.org/package=gridExtra

Barrett, T., Dowle, M., Srinivasan, A., Gorecki, J., Chirico, M., Hocking, T., Schwendinger, B., & Krylov, I. (2025). *data.table: Extension of 'data.frame'*. R package version 1.17.99. https://r-datatable.com

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1-48. https://doi.org/10.18637/jss.v067.i01

Beacon, R. C., Wiltschko, R., & Wiltschko, W. (1997). Pigeon Homing: Effects of Magnetic Pulses on Initial Orientation. *The Auk*, *114*(3), 405-415. https://doi.org/10.2307/4089242

Benaglia, T., Chauveau, D., Hunter, D. R., & Young, D. S. (2009). mixtools: An R Package for Analyzing Mixture Models. *Journal of Statistical Software*, *32*(6), 1 - 29. https://doi.org/10.18637/jss.v032.i06

Beuchert, J., Matthes, A., & Rogers, A. (2023). SNAPPERGPS: open hardware for energy-efficient, low-cost wildlife location tracking with snapshot GNSS. *Journal of Open Hardware*, *7*(1), 1-13. https://doi.org/10.5334/joh.48

Beuchert, J., & Rogers, A. (2021). SnapperGPS: Algorithms for energy-efficient low-cost location estimation using GNSS signal snapshots. In *Proceedings of the 19th ACM Conference on Embedded Networked Sensor Systems* (pp. 165-177). The 19th ACM Conference on Embedded Networked Sensor Systems 2021, Coimbra, Portugal. Association for Computing Machinery, New York, NY, United States. https://doi.org/10.1145/3485730.3485931

Boles, L., & Lohmann, K. (2003). True Navigation and Magnetic Maps in Spiny Lobsters. *Nature*, *421*, 60-63. https://doi.org/10.1038/nature01226

Bonadonna, F., Bajzak, C., Benhamou, S., Igloi, K., Jouventin, P., Lipp, H.-P., & Dell'Omo, G. (2005). Orientation in the wandering albatross: Interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *272*, 489-495. https://doi.org/10.1098/rspb.2004.2984

Bonadonna, F., Chamaillé-Jammes, S., Pinaud, D., & Weimerskirch, H. (2003). Magnetic cues: are they important in Black-browed Albatross *Diomedea melanophris* orientation? *Ibis*, *145*(1), 152-155. https://doi.org/10.1046/j.1474-919X.2003.00117.x

Bonadonna, F., & Gagliardo, A. (2021). Not only pigeons: avian olfactory navigation studied by satellite telemetry. *Ethology Ecology & Evolution*, *33*(3), 273-289. https://doi.org/10.1080/03949370.2021.1871967

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378-400. https://doi.org/10.32614/RJ-2017-066

Brothers, J. R., & Lohmann, Kenneth J. (2015). Evidence for Geomagnetic Imprinting and Magnetic Navigation in the Natal Homing of Sea Turtles. *Current Biology*, *25*(3), 392-396. https://doi.org/10.1016/j.cub.2014.12.035

Chernetsov, N., Pakhomov, A., Kobylkov, D., Kishkinev, D., Holland, R. A., & Mouritsen, H. (2017). Migratory Eurasian Reed Warblers Can Use Magnetic Declination to Solve the Longitude Problem. *Current Biology*, *27*(17), 2647-2651.e2642. https://doi.org/10.1016/j.cub.2017.07.024

Cribari-Neto, F., & Zeileis, A. (2010). Beta Regression in R. *Journal of Statistical Software*, *34*(2), 1-24. https://doi.org/10.18637/jss.v034.i02

Dean, B., Kirk, H., Fayet, A., Shoji, A., Freeman, R., Leonard, K., Perrins, C. M., & Guilford, T. (2015). Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area. *Marine Ecology Progress Series*, *538*, 239-248. https://doi.org/10.3354/meps11443

Dreyer, D., Frost, B., Mouritsen, H., Günther, A., Green, K., Whitehouse, M., Johnsen, S., Heinze, S., & Warrant, E. (2018). The Earth's Magnetic Field and Visual Landmarks Steer Migratory Flight Behavior in the Nocturnal Australian Bogong Moth. *Current Biology*, *28*(13), 2160-2166.e2165. https://doi.org/10.1016/j.cub.2018.05.030

Dunnington, D. (2025). *ggspatial: Spatial Data Framework for ggplot2*. R package version 1.1.9.9000. https://github.com/paleolimbot/ggspatial

Fleischmann, P. N., Grob, R., Müller, V. L., Wehner, R., & Rössler, W. (2018). The Geomagnetic Field Is a Compass Cue in Cataglyphis Ant Navigation. *Current Biology*, *28*(9), 1440-1444.e1442. https://doi.org/10.1016/j.cub.2018.03.043

Fox, J., & Weisberg, S. (2018). Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. *Journal of Statistical Software*, *87*(9), 1-27. https://doi.org/10.18637/jss.v087.i09

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd ed.). Sage, Thousand Oaks, CA, United States. https://socialsciences.mcmaster.ca/jfox/Books/Companion/index.html, ISBN: 9781544336473

Fuxjager, M. J., Eastwood, B. S., & Lohmann, K. J. (2011). Orientation of hatchling loggerhead sea turtles to regional magnetic fields along a transoceanic migratory pathway. *The Journal of Experimental Biology*, *214*(15), 2504-2508. https://doi.org/10.1242/jeb.055921

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *The Journal of Experimental Biology*, *216*(12), 2165-2171. https://doi.org/10.1242/jeb.070250

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *The Journal of Experimental Biology*, *216*(15), 2798-2805. https://doi.org/10.1242/jeb.085738

Goforth, K. M., Lohmann, C. M. F., Gavin, A., Henning, R., Harvey, A., Hinton, T. L., Lim, D. S., & Lohmann, K. J. (2025). Learned magnetic map cues and two mechanisms of magnetoreception in turtles. *Nature*, *638*(8052), 1015-1022. https://doi.org/10.1038/s41586-024-08554-y

Gordon, D. A. (1948). Sensitivity of the Homing Pigeon to the Magnetic Field of the Earth. *Science*, *108*(2817), 710-711. https://doi.org/10.1126/science.108.2817.710

Grolemund, G., & Wickham, H. (2011). Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, *40*(3), 1-25. https://doi.org/10.18637/jss.v040.i03

Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S., & Perrins, C. M. (2008). GPS tracking of the foraging movements of Manx Shearwaters Puffinus puffinus breeding on Skomer Island, Wales. *Ibis*, *150*(3), 462-473. https://doi.org/10.1111/j.1474-919X.2008.00805.x

Hijmans, R. (2025). *raster: Geographic Data Analysis and Modeling*. R package version 3.6-32. https://rspatial.org/raster

Hijmans, R. J. (2019). *geosphere: Spherical Trigonometry*. R package version 1.5-10. https://CRAN.R-project.org/package=geosphere

Holland, R., Filannino, C., & Gagliardo, A. (2013). A magnetic pulse does not affect homing pigeon navigation: a GPS tracking experiment. *Journal of Experimental Biology*, *216*(12), 2192-2200. https://doi.org/10.1242/jeb.083543

Holland, R. A., Thorup, K., Gagliardo, A., Bisson, I. A., Knecht, E., Mizrahi, D., & Wikelski, M. (2009). Testing the role of sensory systems in the migratory heading of a songbird. *The Journal of Experimental Biology*, *212*(24), 4065-4071. https://doi.org/10.1242/jeb.034504

Hore, P. J., & Mouritsen, H. (2016). The radical-pair mechanism of magnetoreception. *Annual review of biophysics*, *45*, 299-344. https://doi.org/10.1146/annurev-biophys-032116-094545

Jandačka, P., Burda, H., & Ščučka, J. (2022). Investigating the impact of weak geomagnetic fluctuations on pigeon races. *Journal of Comparative Physiology A*, *208*(1), 177-184. https://doi.org/10.1007/s00359-021-01534-x

Keeton, W. T., Larkin, T. S., & Windsor, D. M. (1974). Normal fluctuations in the earth's magnetic field influence pigeon orientation. *Journal of comparative physiology*, *95*(2), 95-103. https://doi.org/10.1007/BF00610108

Keller, B. A., Putman, N. F., Grubbs, R. D., Portnoy, D. S., & Murphy, T. P. (2021). Map-like use of Earth's magnetic field in sharks. *Current Biology*, *31*(13), 2881-2886.e2883. https://doi.org/10.1016/j.cub.2021.03.103

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., & Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Current Biology*, *25*(19), R822-R824. https://doi.org/10.1016/j.cub.2015.08.012

Kishkinev, D., Packmor, F., Zechmeister, T., Winkler, H.-C., Chernetsov, N., Mouritsen, H., & Holland, R. A. (2021). Navigation by extrapolation of geomagnetic cues in a migratory songbird. *Current Biology*, *31*(7), 1563-1569.e1564. https://doi.org/10.1016/j.cub.2021.01.051

Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *Journal für Ornithologie*, *94*(3-4), 201-219. https://doi.org/10.1007/BF01922508

Lednor, A. J., & Walcott, C. (1983). Homing pigeon navigation: The effects of in-flight exposure to a varying magnetic field. *Comparative Biochemistry and Physiology Part A: Physiology*, *76*(4), 665-671. https://doi.org/10.1016/0300-9629(83)90127-5

Lenth, R. (2024). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.10.6. https://CRAN.R-project.org/package=emmeans

Lohmann, K., Lohmann, C., Ehrhart, L., Bagley, D., & Swing, T. (2004). Geomagnetic Map Used in Sea-Turtle Navigation. *Nature*, *428*, 909-910. https://doi.org/10.1038/428909a

Lohmann, K. J., Cain, S. D., Dodge, S. A., & Lohmann, C. M. (2001). Regional magnetic fields as navigational markers for sea turtles. *Science*, *294*(5541), 364-366. https://doi.org/10.1126/science.106455

Lohmann, K. J., & Catherine, M. F. L. (1993). A Light-Independent Magnetic Compass in the Leatherback Sea Turtle. *Biological Bulletin*, *185*(1), 149-151. https://doi.org/10.2307/1542138

Lohmann, K. J., Goforth, K. M., Mackiewicz, A. G., Lim, D. S., & Lohmann, C. M. F. (2022). Magnetic maps in animal navigation. *Journal of Comparative Physiology A*, *208*(1), 41-67. https://doi.org/10.1007/s00359-021-01529-8

Lohmann, K. J., Lohmann, C. M., & Putman, N. F. (2007). Magnetic maps in animals: nature's GPS. *Journal of Experimental Biology*, *210*(21), 3697-3705. https://doi.org/10.1242/jeb.001313

Massa, B., Ioalè, S. B. P., Lo Valvo, M., & Papi, F. (1991). Homing of Cory's shearwaters (*Calonectris diomedea*) carrying magnets. *Bollettino di zoologia*, *58*(3), 245-247. https://doi.org/10.1080/11250009109355760

Massicotte, P., & South, A. (2025). *rnaturalearth: World Map Data from Natural Earth*. R package version 1.1.0. https://docs.ropensci.org/rnaturalearth/

Matthews, G. V. T. (1951). The Experimental Investigation of Navigation in Homing Pigeons. *Journal of Experimental Biology*, *28*(4), 508-536. https://doi.org/10.1242/jeb.28.4.508

McGillycuddy, M., Warton, D. I., Popovic, G., & Bolker, B. M. (2025). Parsimoniously Fitting Large Multivariate Random Effects in glmmTMB. *Journal of Statistical Software*, *112*(1). https://doi.org/10.18637/jss.v112.i01

Mora, C. V., Davison, M., Wild, J. M., & Walker, M. M. (2004). Magnetoreception and its trigeminal mediation in the homing pigeon. *Nature*, *432*(7016), 508-511. https://doi.org/10.1038/nature03077

Mouritsen, H., Huyvaert, K. P., Frost, B. J., & Anderson, D. J. (2003). Waved albatrosses can navigate with strong magnets attached to their head. *Journal of Experimental Biology*, *206*(22), 4155-4166. https://doi.org/10.1242/jeb.00650

Muheim, R., Moore, F. R., & Phillips, J. B. (2006). Calibration of magnetic and celestial compass cues in migratory birds-a review of cue-conflict experiments. *Journal of Experimental Biology*, *209*(1), 2-17. https://doi.org/10.1242/jeb.01960

Nimpf, S., Nordmann, G. C., Kagerbauer, D., Malkemper, E. P., Landler, L., Papadaki-Anastasopoulou, A., Ushakova, L., Wenninger-Weinzierl, A., Novatchkova, M., Vincent, P., Lendl, T., Colombini, M., Mason, M. J., & Keays, D. A. (2019). A Putative Mechanism for Magnetoreception by Electromagnetic Induction in the Pigeon Inner Ear. *Current Biology*, *29*(23), 4052-4059.e4054. https://doi.org/10.1016/j.cub.2019.09.048

Nordmann, G. C., Hochstoeger, T., & Keays, D. A. (2017). Magnetoreception—A sense without a receptor. *PLoS biology*, *15*(10), e2003234. https://doi.org/10.1371/journal.pbio.2003234

Packmor, F., Kishkinev, D., Bittermann, F., Kofler, B., Machowetz, C., Zechmeister, T., Zawadzki, L. C., Guilford, T., & Holland, R. A. (2021). A magnet attached to the forehead disrupts magnetic compass orientation in a migratory songbird. *Journal of Experimental Biology*, *224*(22), jeb243337. https://doi.org/10.1242/jeb.243337

Padget, O., Bond, S. L., Kavelaars, M. M., van Loon, E., Bolton, M., Fayet, A. L., Syposz, M., Roberts, S., & Guilford, T. (2018). *In situ* clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology*, *28*(2), 275-279.e272. https://doi.org/10.1016/j.cub.2017.11.062

Padget, O., Dell'Ariccia, G., Gagliardo, A., González-Solís, J., & Guilford, T. (2017). Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. *Scientific Reports*, *7*(1), 9668. https://doi.org/10.1038/s41598-017-09738-5

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M., & Guilford, T. (2019). Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the National Academy of Sciences*, *116*(43), 21629-21633. https://doi.org/10.1073/pnas.1903829116

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, *10*(1), 439-446. https://doi.org/10.32614/RJ-2018-009

Pebesma, E., & Bivand, R. (2023). *Spatial Data Science: With applications in R*. Chapman and Hall/CRC, Boca Raton, FL, United States. https://doi.org/10.1201/9780429459016, ISBN: 0-429-45901-7

Phillips, J. B. (1986). Two magnetoreception pathways in a migratory salamander. *Science*, *233*(4765), 765-767. https://doi.org/10.1126/science.3738508

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., & Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific Reports*, *5*(1), 1-10. https://doi.org/10.1038/srep16486

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Schiffner, I., & Wiltschko, R. (2011). Temporal fluctuations of the geomagnetic field affect pigeons' entire homing flight. *Journal of Comparative Physiology A*, *197*(7), 765-772. https://doi.org/10.1007/s00359-011-0640-y

Siddiqi-Davies, K., Wynn, J., Padget, O., Bond, S., Danielsen, J., Fayet, A. L., Fisher-Reeves, L., Freeman, R., Gillies, N., Kirk, H., Maurice, L., Morgan, G., Syposz, M., Shoji, A., & Guilford, T. (2024). Night flight facilitates late breeding catch-up in a long-distance migratory seabird. *Scientific Reports*, *14*(1), 31792. https://doi.org/10.1038/s41598-024-82328-4

South, A., Michael, S., & Massicotte, P. (2025a). *rnaturalearthdata: World Vector Map Data from Natural Earth Used in 'rnaturalearth'*. R package version 1.0.0.9000. https://docs.ropensci.org/rnaturalearthdata/

South, A., Michael, S., & Massicotte, P. (2025b). *rnaturalearthhires: High Resolution World Vector Map Data from Natural Earth used in rnaturalearth*. R package version 1.0.0.9000. https://docs.ropensci.org/rnaturalearthhires

Takahashi, S., Hombe, T., Matsumoto, S., Ide, K., & Yoda, K. (2022). Head direction cells in a migratory bird prefer north. *Science Advances*, *8*(5), eabl6848. https://doi.org/10.1126/sciadv.abl6848

Thieurmel, B., & Elmarhraoui, A. (2025). *suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase*. R package version 0.5.2. https://github.com/datastorm-open/suncalc

Treiber, C. D., Salzer, M. C., Riegler, J., Edelman, N., Sugar, C., Breuss, M., Pichler, P., Cadiou, H., Saunders, M., Lythgoe, M., Shaw, J., & Keays, D. A. (2012). Clusters of iron-rich cells in the upper beak of pigeons are macrophages not magnetosensitive neurons. *Nature*, *484*(7394), 367-370. https://doi.org/10.1038/nature11046

Walcott, C. (1978). Anomalies in the Earth's Magnetic Field Increase the Scatter of Pigeons' Vanishing Bearings. In K. Schmidt-Koenig & W. T. Keeton (Eds.), *Animal Migration, Navigation, and Homing* (pp. 143-151). 1977, Tübingen, Germany. Springer, Berlin, Germany. https://doi.org/10.1007/978-3-662-11147-5_13

Walcott, C., Gould, J. L., & Kirschvink, J. L. (1979). Pigeons Have Magnets. *Science*, *205*(4410), 1027-1029. https://doi.org/10.1126/science.472725

Wallraff, H. G., Papi, F., Ioalè, P., & Benvenuti, S. (1986). Magnetic fields affect pigeon navigation only while the birds can smell atmospheric odors. *Naturwissenschaften*, *73*(4), 215-217. https://doi.org/10.1007/BF00417729

Weber, S. B., Richardson, A. J., Brown, J., Bolton, M., Clark, B. L., Godley, B. J., Leat, E., Oppel, S., Shearer, L., Soetaert, K. E. R., Weber, N., & Broderick, A. C. (2021). Direct evidence of a prey depletion “halo” surrounding a pelagic predator colony. *Proceedings of the National Academy of Sciences*, *118*(28), e2101325118. https://doi.org/10.1073/pnas.2101325118

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, United States. https://ggplot2.tidyverse.org, ISBN: 978-3-319-24277-4

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A Grammar of Data Manipulation*. R package version 1.1.4. https://github.com/tidyverse/dplyr

Wikelski, M., Arriero, E., Gagliardo, A., Holland, R. A., Huttunen, M. J., Juvaste, R., Mueller, I., Tertitski, G., Thorup, K., Wild, M., Alanko, M., Bairlein, F., Cherenkov, A., Cameron, A., Flatz, R., Hannila, J., Hüppop, O., Kangasniemi, M., Kranstauber, B.,...Wistbacka, R. (2015). True navigation in migrating gulls requires intact olfactory nerves. *Scientific Reports*, *5*(1), 17061. https://doi.org/10.1038/srep17061

Wilke, C. (2024). *cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'*. R package version 1.1.3. https://CRAN.R-project.org/package=cowplot

Wiltschko, R., Schiffner, I., & Wiltschko, W. (2009). A strong magnetic anomaly affects pigeon navigation. *Journal of Experimental Biology*, *212*(18), 2983-2990. https://doi.org/10.1242/jeb.032722

Wiltschko, R., & Wiltschko, W. (2013). The magnetite-based receptors in the beak of birds and their role in avian navigation. *Journal of Comparative Physiology A*, *199*(2), 89-98. https://doi.org/10.1007/s00359-012-0769-3

Wiltschko, R., & Wiltschko, W. (2019). Magnetoreception in birds. *Journal of The Royal Society Interface*, *16*(158), 20190295. https://doi.org/10.1098/rsif.2019.0295

Wiltschko, R., & Wiltschko, W. (2022). The discovery of the use of magnetic navigational information. *Journal of Comparative Physiology A*, *208*(1), 9-18. https://doi.org/10.1007/s00359-021-01507-0

Wiltschko, W., Munro, U., Ford, H., & Wiltschko, R. (2009). Avian orientation: the pulse effect is mediated by the magnetite receptors in the upper beak. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *276*(1665), 2227-2232. https://doi.org/10.1098/rspb.2009.0050

Wiltschko, W., & Wiltschko, R. (1972). Magnetic compass of European robins. *Science*, *176*(4030), 62-64. https://doi.org/10.1126/science.176.4030.62

Wiltschko, W., Wiltschko, R., & Munro, U. (2000a). Light-Dependent Magnetoreception in Birds: Does Directional Information Change with Light Intensity? *Naturwissenschaften*, *87*(1), 36-40. https://doi.org/10.1007/s001140050006

Wiltschko, W., Wiltschko, R., & Munro, U. (2000b). Light-dependent magnetoreception in birds: the effect of intensity of 565-nm green light. *Naturwissenschaften*, *87*(8), 366-369. https://doi.org/10.1007/s001140050742

Wynn, J., Padget, O., Mouritsen, H., Fayet, A. L., Kobylkov, D., Siddiqi-Davies, K., Syposz, M., Trapp, S., Gillies, N., & Guilford, T. (2021). *Twilight cue manipulation suggests a pelagic seabird uses a magnetic compass to calibrate its sun compass.* [Doctoral Thesis Chapter, University of Oxford]. Oxford, United Kingdom.

Wynn, J., Padget, O., Mouritsen, H., Perrins, C., & Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology*, *30*(14), 2869-2873.e2862. https://doi.org/10.1016/j.cub.2020.05.039

Yeagley, H. L., & Whitmore, F. C. (1947). A Preliminary Study of a Physical Basis of Bird Navigation. *Journal of Applied Physics*, *18*(12), 1035-1063. https://doi.org/10.1063/1.1697587

Zapka, M., Heyers, D., Hein, C. M., Engels, S., Schneider, N.-L., Hans, J., Weiler, S., Dreyer, D., Kishkinev, D., Wild, J. M., & Mouritsen, H. (2009). Visual but not trigeminal mediation of magnetic compass information in a migratory bird. *Nature*, *461*(7268), 1274-1277. https://doi.org/10.1038/nature08528

Zeileis, A., & Hothorn, T. (2002). Diagnostic Checking in Regression Relationships. *R News*, *2*(3), 7-10. https://CRAN.R-project.org/doc/Rnews/

Zimmerman, P. H., Pope, S. J., Guilford, T., & Nicol, C. J. (2009). Involvement of the sun and the magnetic compass of domestic fowl in its spatial orientation. *Applied Animal Behaviour Science*, *116*(2-4), 204-210. https://doi.org/10.1016/j.applanim.2008.09.006

# 6

# Climate change drives migratory range shift via individual plasticity

Adapted from Lewin, P., Wynn, J., Arcos, J. M., Austin, R. E., Blagrove, J., Bond, S., Carrasco, G., Delord, K., Lancaster-Reeves, L., García, D., Gillies, N., Guilford, T., Hawkins, I., Jaggers, P., Kirk, C., Louzao, M., Maurice, L., McMinn, M., Micol, T., Morford, J., Morgan, G., Moss, J., Miquel Riera, E., Rodriguez, A., Siddiqi-Davies, K., Weimerskirch, H., Wynn, R. B. and Padget, O. (2024) Climate change drives migratory range shift via individual plasticity in shearwaters. *PNAS* 121 (6) e2312438121.

## Contents


**6.1** Abstract ..... 174

**6.2** Introduction ..... 175

**6.3** Materials and Methods ..... 177

**6.4** Results ..... 186

**6.5** Discussion ..... 192

**6.6** Appendix ..... 197


*"One would be reluctant to credit [birds] with advanced reasoning powers."*

G. V. T. Matthews, *The sensory basis of bird navigation* (1951)

## 6.1 Abstract

How individual animals respond to climate change is key to whether populations will persist or go extinct. Shifts in the distributions of migratory animals can occur through adaptation in migratory behaviours, but there is little understanding of how selection and plasticity contribute to population-level range shifts. Here, we use long-term geolocator tracking of Balearic shearwaters (*Puffinus mauretanicus*) to investigate how year-to-year changes in individual birds' migrations underpin a range shift in the post-breeding migration. We demonstrate a northwards shift in the post-breeding range and show that this occurs through individual plasticity in migratory destination, with individuals migrating further north under rising sea-surface temperatures. Furthermore, we find that when individuals migrate further, they return faster, perhaps minimising delays in return to the breeding area. Birds apparently judge the increased distance that they will need to migrate via memory of the migration route, suggesting that spatial cognitive mechanisms may contribute to this plasticity and the resulting range shift. Our study exemplifies the role that individual behaviour plays in populations' responses to environmental change, and highlights some of the behavioural mechanisms that might be key to understanding and predicting species persistence in response to climate change.

## 6.2 Introduction

Understanding the biological impact of climate change is contingent upon understanding species' responses at every level: from population-level phenomena, through the processes of selection and plasticity, to the behavioural and cognitive mechanisms that underpin these changes. Adaptation in response to environmental change might occur within or between individuals (Chevin et al., 2010; Winkler et al., 2014). Adaptive genotypic evolution occurs through selection between individuals with different strategies. Developmental plasticity (*sensu* Piersma & Drent, 2003) involves limited periods of adaptation within individuals, producing adults with fixed strategies and generational changes at the population level. In contrast, within-individual phenotypic flexibility (Piersma & Drent, 2003) allows reversible adaptation within individual lifetimes. Range shift, usually viewed as a population-level result of climate change (Austin & Rehfisch, 2005; Parmesan & Yohe, 2003; Thomas & Lennon, 1999), can also be understood as the result of adaptation in spatial behaviours, including migration (Linssen et al., 2023; Verhoeven et al., 2018; Xu et al., 2021). In previous empirical work, range shift has mostly been found to result from turnover of individuals with fixed adult migratory routes and destinations (Gill et al., 2019; Linssen et al., 2023; Verhoeven et al., 2018). However, the potential role of phenotypic flexibility in contributing to migratory range shift remains little investigated, as do the potential navigational mechanisms that might underlie flexibility in migratory behaviours.

Balearic shearwaters are a Critically Endangered Procellariiform seabird. They breed exclusively on the Balearic Islands from March to early July, before the majority of the population migrates out of the Mediterranean Sea, into the North Atlantic, via the Strait of Gibraltar between April and September (Guilford et al., 2012; Le Mao & Yésou, 1993; Mouriño et al., 2003; Pérez-Roda et al., 2017). Individuals spend variable amounts of time along the western coasts of Europe and Morocco before returning between May and January for an extended pre-

breeding period in the western Mediterranean (Guilford et al., 2012; Le Mao & Yésou, 1993). Most individuals migrate either to the western and southwestern coasts of Iberia, or to a spatially separated area further north, in the Bay of Biscay and around Brittany (Astarloa et al., 2021; Guilford et al., 2012). Analysis of sightings data has suggested a rapid northwards shift in the species' Atlantic range in the mid-1990s, associated with rising Sea-Surface Temperatures (SST) and shifting clupeid fish stocks (Luczak et al., 2011; Wynn et al., 2007). However, this trend might be subject to bias, resulting from increased observer interest (Votier et al., 2008) due to the species' changing taxonomic status (Austin, 1996; Heidrich et al., 1998; Obiol et al., 2022; Sangster et al., 2002), or could result from other temporally correlated variables (Votier et al., 2008). Nonetheless, if there is an ongoing range shift in the species' post-breeding distribution, Balearic shearwaters might be particularly likely to exhibit flexibility in migratory destination. Like other seabirds, shearwaters can be extremely long-lived (Brooke, 1990; Harris et al., 2011), are capable of frequent long-distance movements (Meier et al., 2015; Padget et al., 2019) and are generally dependent on patchy and ephemeral resources which might shift rapidly with climate change (Davies et al., 2021; Dean et al., 2015). Furthermore, shearwaters have become a model system for the study of avian spatial cognition in the wild (Gagliardo et al., 2013; Padget et al., 2018; Padget et al., 2017; Padget et al., 2022; Padget et al., 2019; Pollonara et al., 2015; Wynn et al., 2020; Yoda et al., 2017). As a result, Balearic shearwaters provide an excellent opportunity to explore the processes generating range shift in migratory taxa and investigate the underlying behavioural and spatial cognitive mechanisms.

Here, we used light-level geolocators (274 migrations from 145 individuals) to track Balearic shearwaters breeding on the Balearic Islands of Ibiza and Mallorca over the course of a decade and investigate their response to climate change (**Fig. 6.1**). We demonstrate a northwards range shift in the species' post-breeding distribution, facilitated at least in part by phenotypic flexibility in migratory

destination, and show that shearwaters compensate for the resulting increase in migratory distance by travelling faster on return migration. Differences in return distance appear to be anticipated from the start of return migration, via route learning. Despite compensatory increases in speed, when shearwaters must return from further north, they return to the breeding area later.

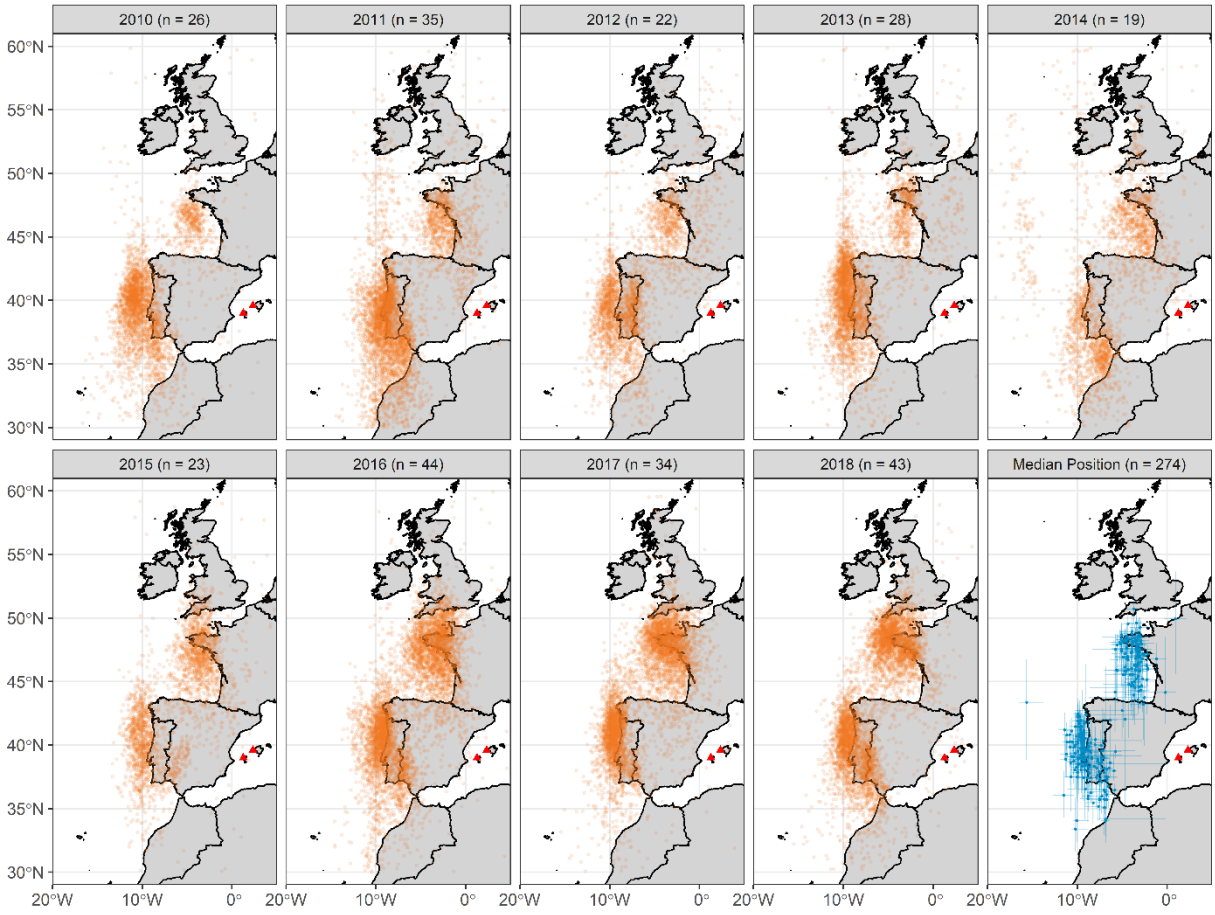



**Fig. 6.1. All location estimates for all birds in each year, which were identified as being part of a migration.** The final panel shows the median and interquartile range of latitude and longitude during each separate migration. Breeding locations are shown with red triangles; the Ibizan colonies of Sa Conillera and Es Bosc are to the west, the Mallorcan colonies of Sa Cella and Sa Dragonera are to the East.

## 6.3 Materials and Methods

### 6.3.1 Fieldwork and data collection

This study took place across four colonies of the Balearic shearwater: Sa Cella (39°36'N, 2°21'E) and Sa Dragonera (39°35'N, 2°19'E) on Mallorca, and Es Bosc (38°58'N, 1°13'E) and Sa Conillera (38°59'N, 1°13'E) on Ibiza, under permits issued

by the Government of the Balearic Islands (CAP03/2011, CAP31/2011, CEP04/2012, CEP26/2012, ENB347/12, CEP03/2013, CEP09/2013, CEP15/2014, CEP19/2014, CEP/2015, CEP09/2015, CEP/2016, CEP18/2016, SEN224/17, ANE23/2017, ANE16/2018, CEP21/2018) and permission from the Oxford University Animal Welfare Ethical Review Body. Geolocators were deployed on breeding birds between 2010 and 2018, using BAS MK15, MK18 and MK19, BioTrack MK3005, MK3006 and Migrate Tech C250, C330 and C65 loggers attached to a plastic leg ring, as per Guilford et al. (2012), or directly to the bird's permanent metal ring.

As a result of the inaccessibility of Balearic shearwater nesting sites, targeting of individual birds for geolocator deployments and retrievals was determined mostly by logistical constraints; nest sites were identified at the start of the study and returned to in future years, if access was still possible.

Monthly averaged SST data were accessed from the Copernicus ERA5 dataset (https://cds.climate.copernicus.eu/). There is a consistent latitudinal SST gradient in the eastern North Atlantic Ocean during the post-breeding migration period. Consequently, as average temperatures increase, the latitudes at which a given temperature occurs shift northwards. As a result, average temperature values over a fixed area during a fixed period in different years can act as a proxy for the latitudinal shift of climatic conditions. We defined a fixed area covering the core of the post-breeding distribution of Balearic shearwaters (12°W to 1°W and 38°N to 51°N) and calculated the mean July and August SST in each year, corresponding to when most Balearic shearwaters arrive in the Atlantic. This allowed us to set up the simple and testable prediction that as mean SST increases, shearwaters should shift northwards if there is a climate-driven range shift.

### 6.3.2 Geolocator processing and identification of migration

All processing and statistical analysis was conducted in R version 3.6.1 (R Core Team, 2020). Data are available at https://doi.org/10.6084/m9.figshare.22680283 (Lewin et al., 2024 [dataset]).

Geographic positions were estimated using the *geolight* package (Lisovski & Hahn, 2012), with a twilight threshold of 10 lux and an elevation angle of -4.5°. This elevation angle was chosen based on visual assessment of the location of breeding season fixes in the Western Mediterranean Sea in a random subset of 40 tracks. Further processing followed Austin et al. (2019), removing unreliable fixes around the equinoxes and those with unrealistic daily average speeds (> 55 $kmh^{-1}$). Unrealistic location estimates > 22°W, > 42°E, < 30°N or > 60°N were also removed. Tracks with fewer than 100 fixes or gaps of over 2 months within 8 months of tag deployment were excluded.

To isolate migratory behaviour, we specified the date each bird left the Mediterranean Sea (via the Straits of Gibraltar) and the date at which it returned using a rolling mean longitude and latitude over a window of three fixes and a buffer area across mainland Europe (see Appendix). When the rolling mean positions fell to the west of the buffer, they were identified as being in the Atlantic Ocean, on migration. When they fell east of the buffer, they were identified as being in the Mediterranean Sea. Those falling within the buffer were considered ambiguous and assigned the same value as the preceding location estimate, such that a change to or from migration was only identified when the rolling mean position fell unambiguously to one side of the buffer. The buffer is, at minimum, 170 km across, east to west, and 555 km across, north to south. Error in light-level geolocation is often high (Fudickar et al., 2012; Halpin et al., 2021; Lisovski et al., 2012; Phillips et al., 2004; Shaffer et al., 2005), especially in the latitudinal component (Fudickar et al., 2012). Given that Balearic shearwaters in the post-breeding migration are likely subject to only one of the three most significant causes of geolocator error in terrestrial settings (weather, topographical features and vegetation; Lisovski et al., 2012), it seems reasonable to assume that error in our location estimates, especially after filtering, is likely to be at the lower end of these published estimates. It may be similar to data from Scopoli's shearwaters

(*Calonectris diomedia*) in the Mediterranean Sea, in which similar methods yielded mean estimates of 139 ± 127 km absolute error relative to co-deployed GPS (Halpin et al., 2021). In addition, the use of a rolling mean longitude and latitude should further reduce error. We therefore believe that the chosen buffer is sufficient to rule out the vast majority of erroneously identified crossings.

Where a shearwater crossed into the Atlantic Ocean and back more than once in a single year, the longest period in the Atlantic Ocean was identified as the core period of migration and used for analyses of migratory behaviour. The midpoint in time between the fixes either side of the buffer was used to represent the date of crossing. This allowed us to estimate a date even if it occurred during a gap between fixes of more than one day. Seven tracks did not include any migration fixes by this measure and a further two tracks ended before return to the Mediterranean Sea, leaving 274 tracks by 145 individuals for analysis, including 127 tracks from Mallorca and 147 from Ibiza.

We aimed to split each migration into outbound and return sections. Balearic shearwaters show great variation in the extent of migration and many individuals do not spend a prolonged period in a single location during the post-breeding season. As a result, we could not use clear differences in the rate of travel to identify the end of outbound and the start of return migration. Instead, we used the latitudinal apex of each migration. We defined the apex as the fix closest to the 98th quantile of latitude (to exclude extreme outliers most likely to be the result geolocation error). All fixes before this were identified as part of the outbound migration and all fixes afterwards as the return.

### 6.3.3 Northwards range shift and phenotypic flexibility in migratory destination

To summarise the distribution of Balearic shearwaters in the post-breeding season, we calculated each individual's median latitude during migration. The distribution of median latitudes was highly bimodal, owing to the discrete areas occupied by

the shearwaters around Iberia in the south and Brittany in the north. We used mixture models to identify whether a median latitude belonged to the northern or southern area. Given northwards range shift, mixture models were not applied to the whole dataset. Conversely, single years provided too few tracks, with too incomplete a distribution to identify the two areas robustly. Instead, tracks were grouped into three batches of three consecutive years (2010-2012, 2013-2015 and 2016-2018) and a mixture model applied to the distribution of median latitudes in each batch. The results are seen in Fig. 6.2.

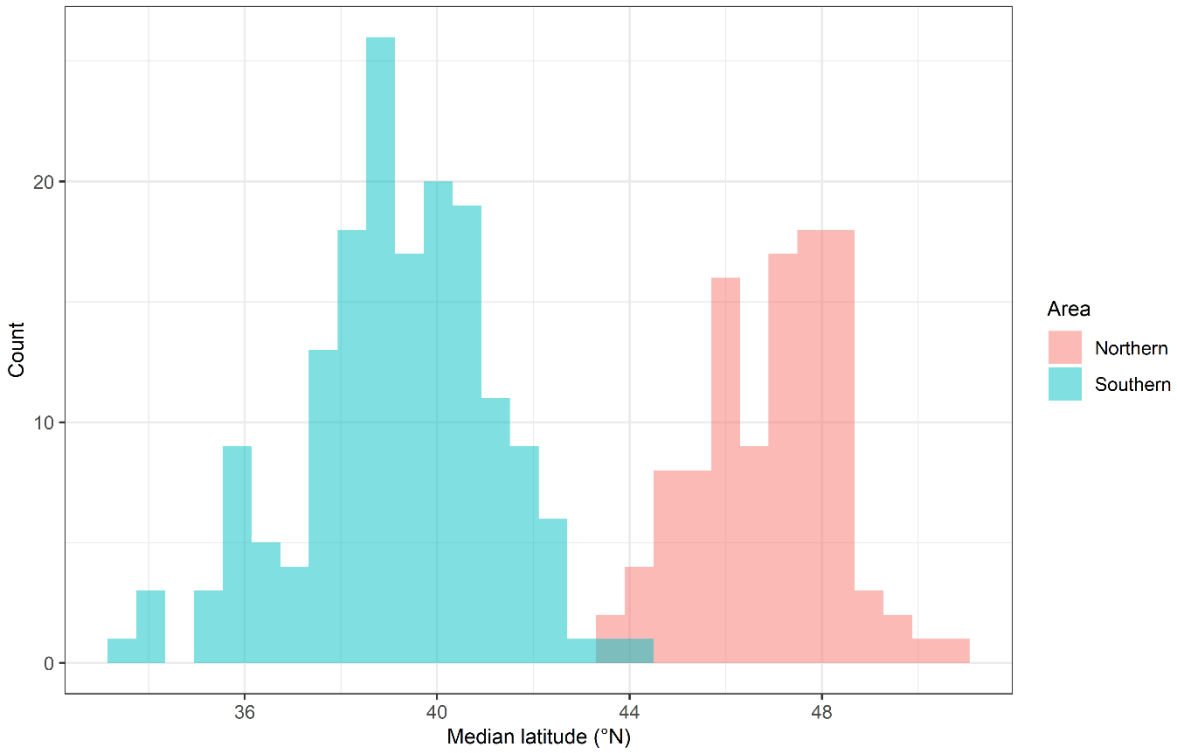



**Fig. 6.2. The distribution of median latitudes over all years of the study.** The distribution is coloured according to whether each latitude was identified as being part of the northern or southern area.

To test for range shift, we used a linear regression with median latitude as the response and year as the predictor, including only each bird's first track, to avoid pseudoreplication and age-related changes in latitude. In this model, we also accounted for the two separate areas (north/south), sex (male/female) and island (Mallorca/Ibiza).

To test whether this effect of year reflected climatic effects, we constructed an identical model but with mean SST as the predictor, instead of year. These models were compared to identify the best fitting model and thus determine whether SST, as a proxy for climate, better explained latitudinal shifts than time alone. Model comparisons were carried out using AICc, the small-sample corrected Akaike Information Criterion from the *AICcmodavg* package (Mazerolle, 2023).

To investigate range shift further, we constructed linear mixed effects models using the *lme4* package (Bates et al., 2015). For all mixed effects models, individual was included as a random intercept. Model construction followed the method of van de Pol and Wright (2009) to partition the relationship between median latitude and temperature into within-individual (phenotypic flexibility) and between-individual (turnover) effects, using subject-centring (Fig. 6.3). For each individual, we calculated the mean temperature over all the years it was tracked. For each year it was tracked, we then calculated the deviation from this individual mean. Differences between the mean temperatures experienced by different individuals express the variation in the predictor between individuals. Deviations from each individual's within-subject mean express the variation in the predictor within an individual. The relationship between the between-individual means and the behaviour of interest quantifies the population-level effect of the predictor, e.g. individuals in the study population experiencing different average temperatures have different average latitudes (Fig. 6.3B, E). The relationship between the within-individual variation and the behaviour of interest quantifies the within-individual flexible response, e.g. when a single individual experiences different temperatures, it changes its migratory latitude. Therefore, a significant effect of the within-individual component indicates an at least partially flexible response (Fig. 6.3C). If the effect of the between-individual component is significantly different to the within-individual effect, this suggests that the population-level change is not fully explained by within-individual responses. In this case, there must be turnover of

individuals with different average behaviours, in addition to any flexible response (Fig. 6.3F).

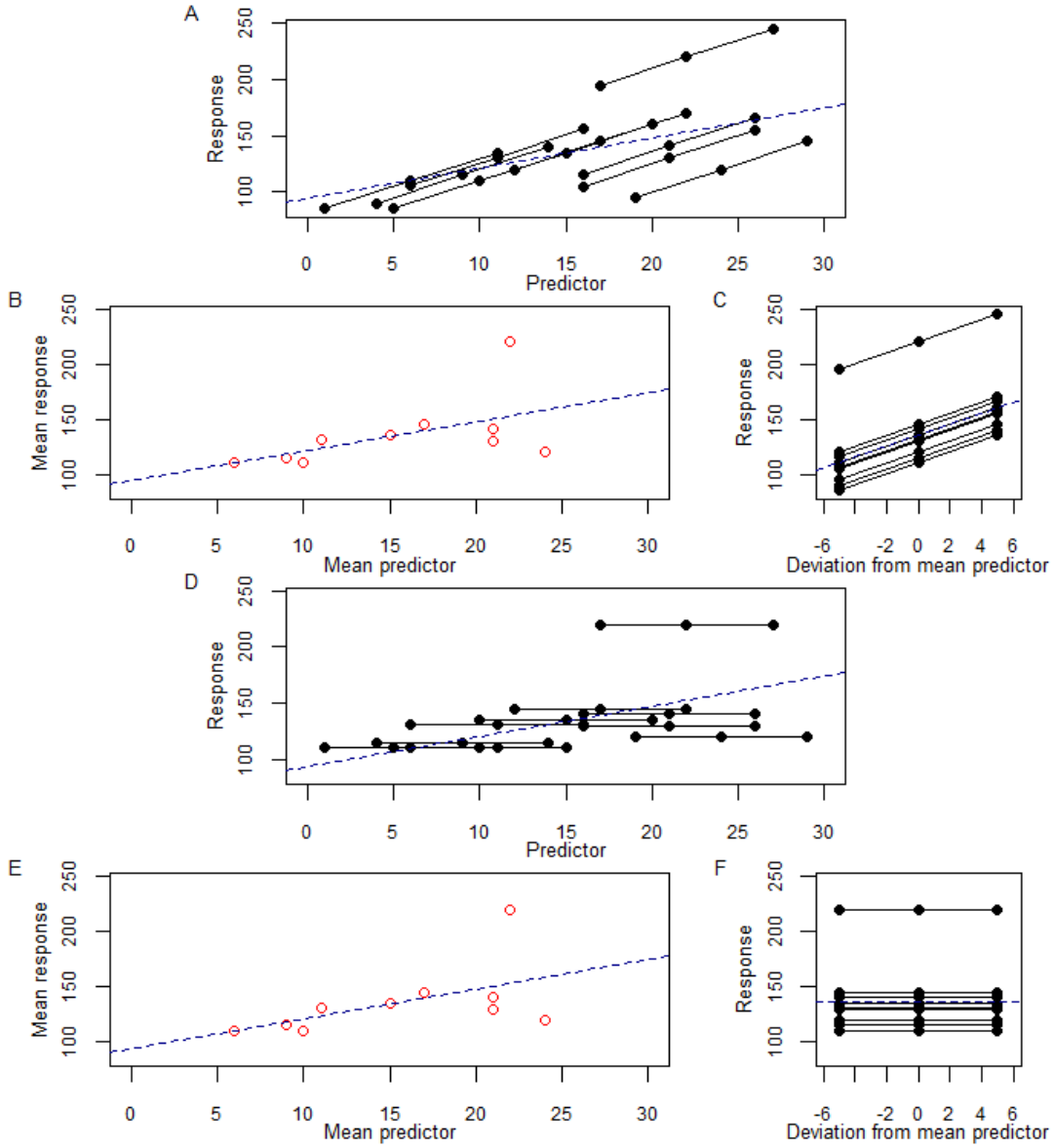



**Fig. 6.3. The subject centring method of van de Pol and Wright (2009).** The approach allows us to distinguish whether changes in behaviour observed at the population level are facilitated by individual flexibility or turnover of individuals with fixed strategies. (A) Hypothetical observations of a response to a predictor for 10 individuals, each with 3 observations. Each individual's observations are joined by the black lines. The overall relationship is shown with the blue dashed line. (B) The between-individual relationship can be estimated using the mean predictor and response for each individual; it is identical to the overall relationship. (C) The within-individual relationship can be estimated by expressing the predictor at each observation as a deviation from the mean predictor experienced by each individual. The relationship here is very similar to the overall relationship, indicating that the overall population-level change can be explained by within-individual flexibility. (D) Observations of a different response from 10 individuals,

as in panel A. (E) The relationship between individual's mean predictors and responses is the same as in B. (F) By expressing the predictor at each observation relative to the mean predictor experienced by each individual, it can be seen that the within-individual slope is 0. As the between-individual slope is much greater than 0, the population-level change in this response is facilitated by turnover between individuals, each of which has a fixed behaviour.

Given the two post-breeding areas occupied by Balearic shearwaters, the observed northwards range shift could reflect birds (a) changing destination from the southern to northern area, (b) shifting in latitude within each area or (c) both. We, therefore, applied the same subject-centring method to test whether the probability of migrating to the northern or southern area was associated with temperature, using a generalised linear mixed effects model with a logit-link function. In this model, the northern area was scored as 1 and the southern area as 0 and island and sex were included as fixed effects.

### 6.3.4 Differences in return speed based on route memory

To test whether daily speed during return migration was associated with maximum latitude, we used the latitude at the apex and calculated the average daily speed over all subsequent fixes before the bird first returned to the Mediterranean Sea. We then calculated the variation in maximum latitude both within- and between-individuals using the same subject-centring method from van de Pol and Wright (2009), and constructed a linear mixed effects model with between-individual maximum latitude, within-individual maximum latitude and area as fixed effects. To control for the possibility that faster birds inherently reach higher latitudes, we also included the mean outbound speed in our model, so that residual variation probably reflected decisions made by the bird.

We aimed to test whether shearwaters were aware of their increased return distance and increased their return speed from the start of migration. We calculated the average daily speed over the first 25% period of each return migration to test whether shearwaters could anticipate return distance from the start. In addition, we aimed to determine what kind of spatial representation they

used to estimate this distance. Exploiting the fact that shearwaters avoid flying far over land, we constructed two models based on different potential spatial representations. The first used the beeline distance directly back to the colony (regardless of any intervening land) which could be based on an extrapolated grid map representation (Padget et al., 2019). The second used the distance along the shortest sea route which could be based on route memory of previous migrations or the outbound migration. Both distances were calculated from the apex migration position to the colony. The beeline distance was calculated using the great circle distance via the Haversine function. The route distance was calculated as the shortest route from the apex fix to the colony without crossing over land. The variation in these distances is large and not perfectly correlated, and we used non-nested model comparisons to investigate which distance better explained changes in speed with migratory latitude. When defining the start of return migration using the latitudinal apex, there is a risk that the latitude identified will result from inaccurate geolocation which yields an extreme latitude estimate. Such erroneous estimates will inherently be associated with higher estimated speeds because, on average, they fall further from the preceding accurate location estimates than an accurate estimate would. We included a third model with maximum latitude as the predictor for this reason - if the speed-distance relationship were driven by the inherent link between erroneous latitudinal geolocation and estimated speed, latitude should be a better predictor of initial speed than either distance metric. We also constructed a model to rule out that differences in return speed were simply the result of a confound between maximum latitude and the area/habitat crossed during migration. To do this, we calculated average daily speed over a fixed latitudinal band (35°N to 45°N) where all shearwaters must be migrating over the same area.

### 6.3.5 Phenological shifts

To test for changes in phenology associated with changing migratory latitudes, we constructed two linear mixed effects models, one with departure date from the Mediterranean Sea and one with return date. Both models included within- and between-individual variation in maximum latitude, as well as area and island as fixed effects.

For all mixed effects models, significance was assessed with likelihood ratio tests on nested full and restricted models. Simulations were carried out using the *arm* package (Gelman & Su, 2024) to estimate bootstrapped 95% confidence intervals on coefficients and to estimate the 95% confidence intervals of the difference between within- and between-individual slopes (Moiron et al., 2020). Coefficients are reported ± their bootstrapped 95% confidence intervals. Full model results are reported in the Appendix.

## 6.4 Results

### 6.4.1 Northwards range shift and phenotypic flexibility in migratory destination

Across 274 tracks from 145 individuals spanning nine years, we found a significant northwards shift in birds' median migratory latitudes of 0.23° (± 0.07°) per year ($F_{4,93}$ = 108.55, $P < 1x10^{-15}$; Fig. 6.4A). A model with SST fitted substantially better than the model including just year (AICc = 383.08 and 393.93, respectively, ΔAICc = -10.85), indicating that climate-induced changes best explain this range shift.

We aimed to distinguish whether range shift resulted from phenotypic flexibility in migratory latitude within individuals or turnover of individuals with fixed migratory latitudes. Firstly, we found that the northwards range shift was at least partially explained by within-individual phenotypic flexibility in migratory latitude (within-individual slope: $\chi^2_1$ = 4.06, $P$ = 0.044; between-individual slope: $\chi^2_1$ = 12.07, $P$ = 0.001; Fig. 6.4C). The between-individual slope was larger

(1.42 ± 0.80° latitude per °C) than the within-individual slope (0.66 ± 0.65° latitude per °C), but there was no significant difference between these effect sizes (95% CI of difference: -0.26, 1.76); phenotypic flexibility in migratory latitude, but not turnover of individuals, has a detectable contribution to the population-level shift.

We also tested for changes in the probability that birds migrated to either the northern or southern area, using a binomial generalised linear mixed effects model with a logit link function. Island of origin had no significant effect, indicating that birds from different islands migrated to each area in similar proportions ($\chi^2_1 = 1.25$, $P = 0.264$). In contrast to changes in latitude within each area, we found that there was no significant within-individual effect of temperature on which area birds migrated to ($\chi^2_1 < 0.01$, $P = 0.988$). We found that, between individuals, the log odds of birds migrating to the northern area increased by 1.79 for every increase of 1 °C ($\chi^2_1 = 4.56$, $P = 0.033$; Fig. 6.4B-C). Despite the significance indicated by the likelihood ratio test, the bootstrapped confidence intervals of (a) the between-individual effect (-0.23, 3.89) and (b) the difference between the within- and between-individual effect sizes (-0.56, 0.54), overlapped with zero. Consequently, this result should be interpreted as inconclusive.

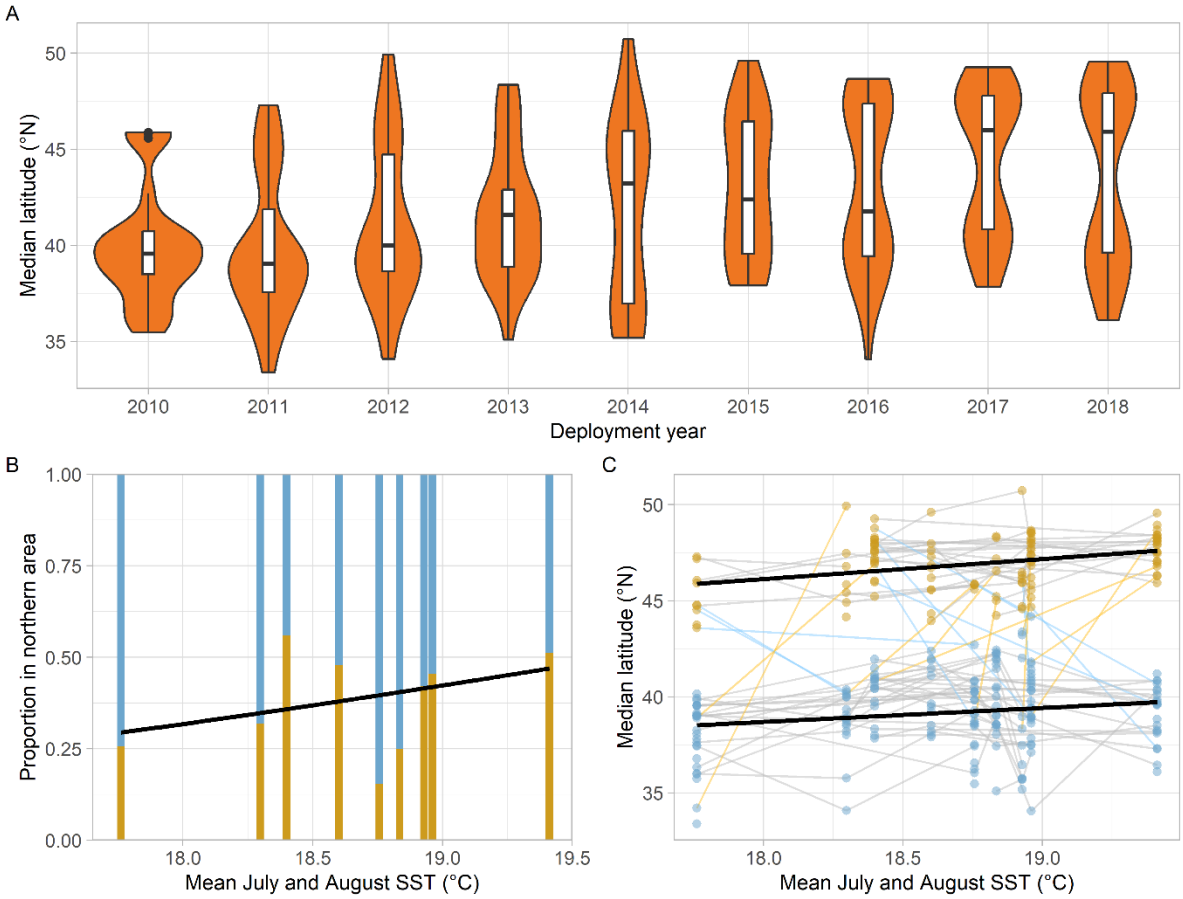



**Fig. 6.4. The northward range shift in Balearic shearwaters summarised through time and with respect to SST.** (A) The distribution of median latitudes over each deployment year of the study. (B) The proportion of birds migrating to the northern or southern area throughout the study, with respect to SST. The northern area (Biscay) is represented in gold. The fitted line is a logit-linked generalised linear regression between this proportion and SST in each year. (C) The relationship between average SST and median migratory latitude. The median latitude observed during each separate migration is represented as a single point; those identified as being in the northern area are gold and those in the southern area are blue. All observations relating to a single individual are joined by lines; gold lines indicate cases in which an individual has switched from the southern to the northern area between years and blue lines cases in which individuals have switched from the northern to southern area. The shift in migratory latitudes in each area is shown using a simple least-squares regression.

### 6.4.2 Differences in return speed based on route memory

If shearwaters migrate further north but their breeding sites remain fixed (Genovart et al., 2016; Oro et al., 2004), they must either migrate faster or spend longer migrating. We investigated whether shearwaters' return speed was related to the latitude they migrated to, and whether any change was explained by within-

individual phenotypic flexibility in migration speed or turnover of individuals with fixed speeds.

Return speed was not significantly related to outbound speed ($\chi^2_1$ = 2.66, $P$ = 0.103), suggesting that outbound and return speed are determined independently and are not simply under a joint biomechanical constraint. We found significant increases in return speed with maximum latitude; shearwaters which fly further north travel faster on return migration. The between- and within-individual slopes were almost identical (0.23 ± 0.15 $kmh^{-1}$ per 1° maximum latitude, $\chi^2_1$ = 8.52, $P$ = 0.004 and 0.21 ± 0.20 $kmh^{-1}$ per 1°, $\chi^2_1$ = 4.06, $P$ = 0.044, respectively; Fig. 6.5A) and there was no significant difference between these effect sizes (95% CI: -0.23, 0.26), suggesting that changes in speed in response to more northerly migratory destinations can be accounted for by individual flexibility alone.

Increases in migration speed could be facilitated by two mechanisms, with different cognitive implications: birds might estimate the distance of their return migration and increase their speed from the very start of the return, or they might only speed up reactively if they perceive that they have failed to reach their goal after a certain time. We calculated speed in the first 25% of return migration to test whether birds were estimating return distance and planning ahead by adjusting initial return speed accordingly.

We also investigated what kind of spatial representation might underlie estimates of the distance home from the start of return migration. We found that the model using the beeline distance fitted worse (AICc = 1117.64) than the model using route distance (AICc = 1112.64, ΔAICc = -5.00). Within the better fitting model, initial return speed increased by 0.07 $kmh^{-1}$ for every increase in distance of 100 km ($F_{1,272}$ = 8.93, $P$ = 0.003; Fig. 6.5B), suggesting that the shearwaters use an estimate of the route distance to adjust their speed from the start of return migration. Given this effect size, the furthest birds return two days earlier than they would have if

they flew at the same speed as the closest birds, on average. To rule out the possibility that this result is driven by the inherent relationship between latitudinal error in geolocation and the estimated speed, we also fitted a model predicting initial return speed from maximum latitude (AICc = 533.26). The model fit was marginally better than the beeline model (ΔAICc = -0.33) and substantially worse than the route distance model (ΔAICc = 4.67). This strongly suggests that this result is not an artefact of geolocation error. To ensure habitat differences were not driving the relationship between maximum latitude and return speed, we calculated the average speed for each track over a fixed latitudinal band (35°N to 45°N) through which all shearwaters must migrate. The positive effect of maximum latitude on return speed was still maintained over this fixed area (0.22 ± 0.17 $kmh^{-1}$ per °N, $\chi^2_1 = 6.36$, $P = 0.012$), ruling out the effect of differences in habitat. Hence, birds appear to learn about their route and use this memorised distance to anticipate how long their return journey will be.

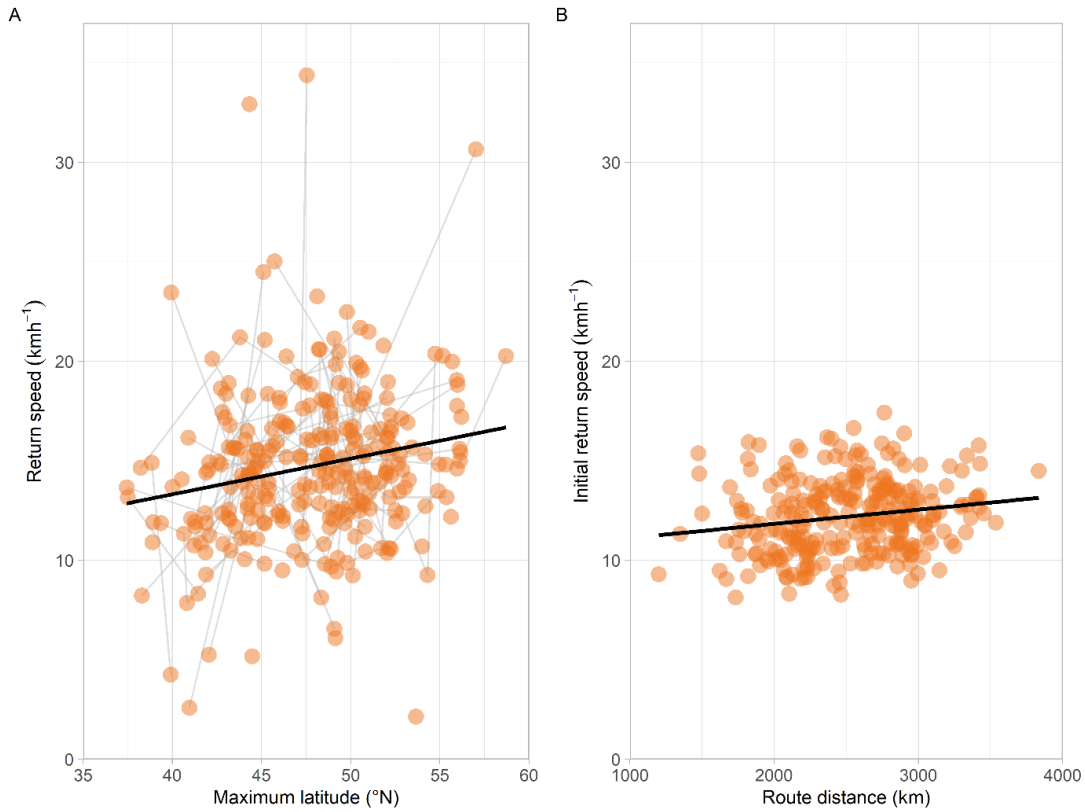



**Fig. 6.5. Relationships between the northerly extent of migration and return migration speed.** The overall and initial return speed from each migration is included as a single

point. (A) Overall return speed is regressed against maximum latitude for each migration and points are joined by lines for all observations of a single individual. (B) Average speed in the initial 25% of return migration against route distance, the best-fitting distance predictor.

### 6.4.3 Phenological shifts

Despite this compensatory increase in speed, migratory phenology might still be affected by the range shift or associated environmental changes. This could be because breeding phenology might advance under climate change (Charmantier et al., 2008; Parmesan & Yohe, 2003), because higher temperatures in post-breeding areas might prolong their suitability or because the increase in speed might not be sufficient to compensate for the increased migratory distance. There was no significant between- or within-individual relationship between maximum latitude and when shearwaters first left the Mediterranean Sea ($\chi^2_1 = 1.88$, $P = 0.171$ and $\chi^2_1 = 0.26$, $P = 0.611$, respectively; Fig. 6.6A), and there was no difference between breeding islands ($\chi^2_1 = 0.18$, $P = 0.672$). However, shearwaters migrating to the southern area left the Mediterranean Sea 11.4 ± 7.3 days later, on average ($\chi^2_1 = 6.50$, $P = 0.002$).

The date of return to the Mediterranean Sea was, however, significantly predicted by island of origin, whether birds migrated to the northern or southern area and maximum latitude. Mallorcan shearwaters returned to the Mediterranean Sea an average of 9.8 ± 6.787 days earlier than Ibizan shearwaters ($\chi^2_1 = 8.80$, $P = 0.003$) and those in the southern area returned an average of 38.5 ± 8.0 days later ($\chi^2_1 = 80.55$, $P < 1x10^{-15}$) than those from the north. Furthermore, within each area, shearwater return phenology was delayed as maximum latitude increased, with almost identical between- and within-individual slopes (5.4 ± 1.0 days per 1°, $\chi^2_1 = 81.78$, $P < 1x10^{-15}$; 4.4 ± 1.4 days per 1°, $\chi^2_1 = 42.53$, $P < 1x10^{-10}$; Fig. 6.6B), and no significant difference in effect size (95% CI: -0.64, 2.40).

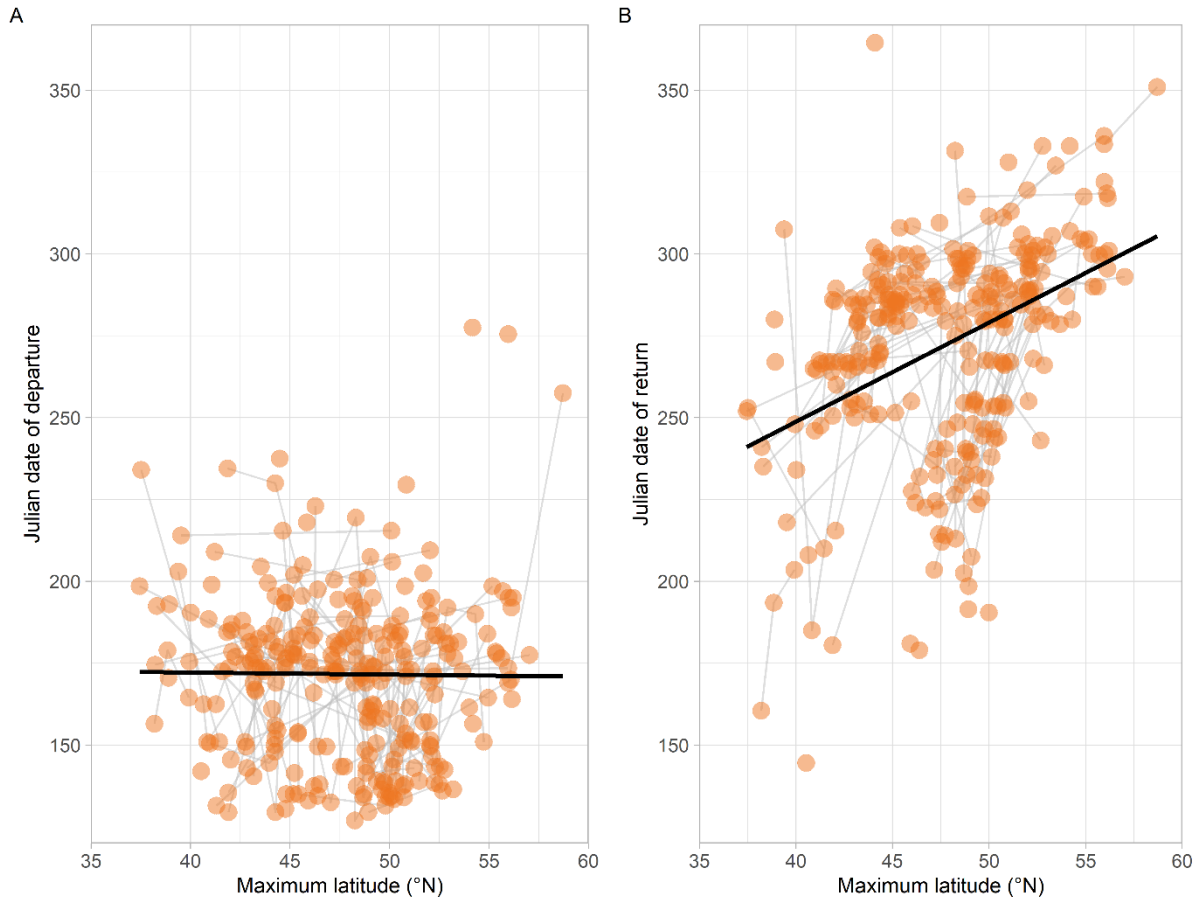



**Fig. 6.6. Relationships between northerly extent of migration and phenology.** The dates of these migratory departure and return are represented as single points for each migration, and the points belonging to single individuals are joined by the grey lines. The fitted lines are least-squares regressions between phenology and maximum migratory latitude. (**A**) Date of departure from the Mediterranean Sea against maximum latitude. (**B**) Date of return to the Mediterranean breeding area against maximum latitude.

## 6.5 Discussion

The post-breeding migration of Balearic shearwaters has shifted northwards over the course of a decade, under a changing climate. This shift appears to be facilitated by phenotypic flexibility in migratory destination and, in turn, increasing migration speeds based on memory of migratory route length. Whilst we use SST early in the migration season as a proxy for climate, it is unlikely that shearwaters are responding to temperature directly. Instead, Balearic shearwater distributions are probably determined by a number of environmental factors (Afán et al., 2021) and shearwaters may be responding more directly to food availability, as suggested by Luczak et al. (2011). We also acknowledge that analyses using geolocator data,

especially those relating location estimates to environmental conditions, are susceptible to artefacts caused by the effects of those environmental conditions on light levels (Lisovski et al., 2018). However, the observed range shift in this study is consistent with studies using other methods (Phillips et al., 2021; Wynn et al., 2007) and we consider a consistent bias towards more northerly error in geolocation with increasing temperature to be unlikely. We, therefore, suggest that although error in geolocation is necessarily high, it is likely to be unbiased in this study.

The range shift we detect at the population level is underpinned by two migratory changes. First, shearwaters are increasingly likely to migrate to the northernmost of two spatially separated areas and, second, the median latitudes reached by individuals migrating to each of these areas are moving north. The latter of these is consistent with phenotypic flexibility (*sensu* Piersma & Drent, 2003) in migratory destination; individual shearwaters alter their migratory destination as temperatures change. This is largely in contrast to previous investigations, most of which have identified turnover of individuals with fixed migratory strategies as an adaptive process underlying range shift (Gill et al., 2019; Linssen et al., 2023; Verhoeven et al., 2018). Phenotypic flexibility could allow individuals to track shifting resources under climate change and so remain in a constant thermal niche, despite changing conditions. This individual-level response might contribute to the population persistence crucial to the conservation of this Critically Endangered species. This interpretation is supported by apparently constant breeding success and survival of Balearic shearwaters throughout this study, despite the changing environmental conditions and individual migratory behaviour (see Appendix).

The mechanisms that underpin such plasticity are poorly understood. We find evidence that spatial cognition might influence the capacity for population-level range shift by shaping individual changes in behaviour in response to the environment; when migrating further north, shearwaters use memory of their migratory route distance to inform return migratory speed. This increase in speed

has the potential to compensate for increased migration distance whilst phenology is held constant. Previous studies in the closely related Manx shearwater have shown that irrespective of intervening geographic obstacles birds tend to time long-distance movements based upon the beeline distance to the colony, implying the use of a large-scale grid map (Padget et al., 2019). The use of route distance in Balearic shearwaters might instead reflect a cognitively simpler mechanism, where birds remember the length of return migration from previous years or from their outbound journey.

The second form of range shift is a change in the proportion of birds migrating to each area. This could be explained by turnover of individuals in the study population with changing temperature, as each individual consistently returns to one area every year (consistent with Meier, 2015), although the results were equivocal. This result would be consistent with the majority of previous investigations of the mechanism of migratory range shift (Gill et al., 2019; Verhoeven et al., 2018) and might be the result of developmental plasticity or selection. Rates of turnover in the study population were high (Fig. 6.9) but the constraints imposed on sampling by the inaccessibility of nest sites, along with inability to track juvenile and immature shearwaters before their first breeding attempts, makes it hard to distinguish selection from developmental plasticity because (a) we cannot definitively detect mortality, and (b) we cannot currently investigate when or how migration preferences might develop with age. Remote-download tracking of Balearic shearwaters' first migrations showed that birds appear to select areas with lower SST and higher marine productivity (Louzao et al., 2021) but these were incomplete migratory journeys and repeated tracking of entire migrations by young shearwaters would give important insight into the processes by which fixed migratory areas develop at the individual level and change through time at the population level.

Climatic changes frequently alter migratory phenology (Charmantier & Gienapp, 2014; Gordo, 2007; Parmesan & Yohe, 2003; Usui et al., 2017) and Conklin et al. (2021) showed for the first time that such changes could be explained entirely by phenotypic flexibility. Here, we also report a phenological change explained entirely by within-individual changes, but rather than an advancing departure, we see that birds are returning to the Mediterranean Sea later, as a result of longer migrations, despite increased return speeds. This might be interpreted in several ways. Higher temperatures might keep northern waters suitable for longer into the post-breeding period, allowing shearwaters to prolong their time there before return migration. Alternatively, it might be that the delay is simply a result of having to migrate further. In this case, the delay might be costly, reducing the amount of time shearwaters have to regain condition after migration, or coordinate with a mate at the colony before breeding, which may influence success (Guilford et al., 2012). Furthermore, breeding phenology is generally expected to advance under climate change, in conflict with a delayed return from migration, and lack of advancement appears to be associated with population decline in birds (Saino et al., 2011). Since Balearic shearwaters are Critically Endangered, future research should aim to investigate the effects of climate change on the pre-breeding period and their link to breeding success and survival.

Most previous studies have considered climate-driven range shifts only at the population-level (Austin & Rehfisch, 2005; Parmesan & Yohe, 2003; Thomas & Lennon, 1999) so have not investigated the underlying adaptive processes in spatial behaviour. Where studies have investigated these underlying processes, there has mostly been evidence for generational changes, indicative of selection or developmental plasticity (Gill et al., 2019; Linssen et al., 2023; Verhoeven et al., 2018). Our finding that a climate-driven range shift involves phenotypic flexibility in migratory destination demonstrates that life-long flexibility may play a role in some species and highlights the importance of considering range shifts not just as

population-level phenomena but as the result of adaptation in spatial behaviour. We clarify how this response is influenced by behavioural flexibility, itself underpinned by memory of migration routes, emphasising the importance of spatial cognitive mechanisms in mediating population-level range shift. Nonetheless, the considerable delays to return phenology associated with northwards range shift indicate that such flexibility could be insufficient to keep pace with climate change, for a species facing global extinction.

## 6.6 Appendix

### 6.6.1 Geolocator processing and identification of migration

The buffer designed to account for geolocator error when identifying crossings through the Strait of Gibraltar, in or out of the Mediterranean Sea, ran between 6.6°W 3°0N, 6.6°W 45°N, 1°W 45°N, 1°W 60°N, 90°E 60°N, 90°E 43°N, 1°W 43°N, 1°W 40°N, 4.6°W 40°N and 4.6°W 30°N (Fig. 6.7). Crossings of this buffer, indicating the initiation or end of migration, were identified when the rolling mean longitude and latitude position over a window of three fixes crossed from one side of the buffer to the other, as shown in Fig. 6.8.

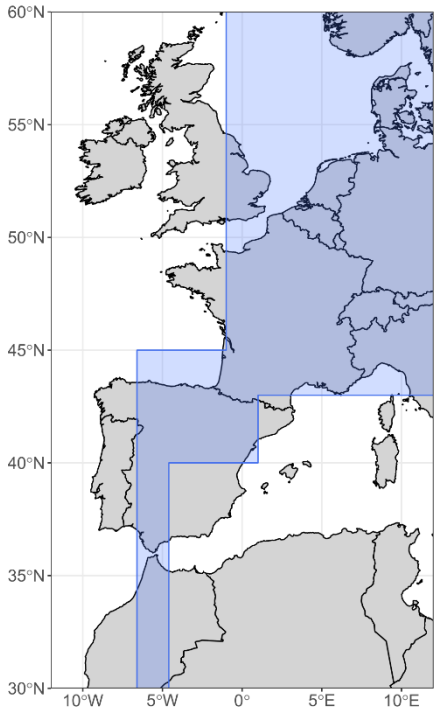



Fig. 6.7. The buffer area used to mitigate against geolocator error when identify crossings from the Mediterranean Sea to the Atlantic Ocean.

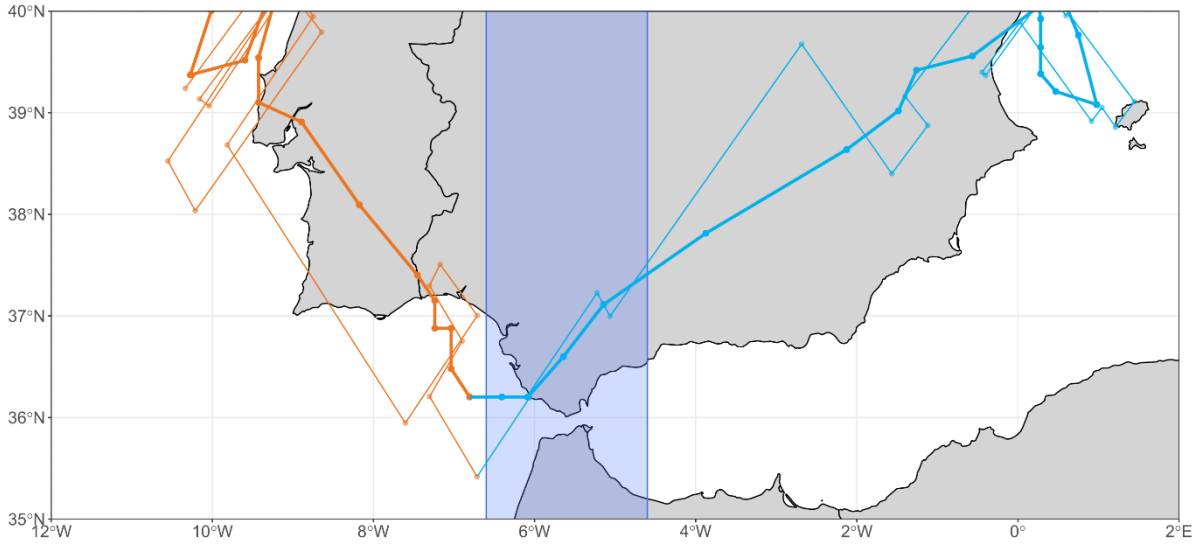



**Fig. 6.8. An example of a single crossing from the Mediterranean Sea (fixes shown in blue), over the buffer area, to the Atlantic Ocean (fixes shown in orange).** The thinner lines and points are raw location estimates, the thicker lines and points are the smoothed positions used to identify crossings and reduce the effect of geolocator error.

### 6.6.2 Survival and breeding success

To assess whether climatic changes in the post-breeding area and associated changes in migratory behaviour were affecting the demographic rates of Balearic shearwaters, we conducted a survival analysis of tracked birds and an analysis of breeding success at the population and individual levels.

To conduct a survival analysis, we made the assumption that the probability of geolocator retrieval (and so continued presence in the study population) was correlated with the probability of survival. The entry and disappearance of birds from the geolocator tracking is shown in **Fig. 6.9**. We implemented a Cox proportional hazard model using the *coxph* function from the *survival* package (Therneau, 2024; Therneau & Grambsch, 2000). The predictor was each bird's median latitude in the first year it was tracked, relative to the population average in that year, and the response was the number of years from the bird's first track to its last, censored at the end of the study in 2018. We found that relative median

latitude did not predict longevity in the study: the estimated hazard ratio was 0.999 (n = 145, SE = 0.03, $P$ = 0.690).

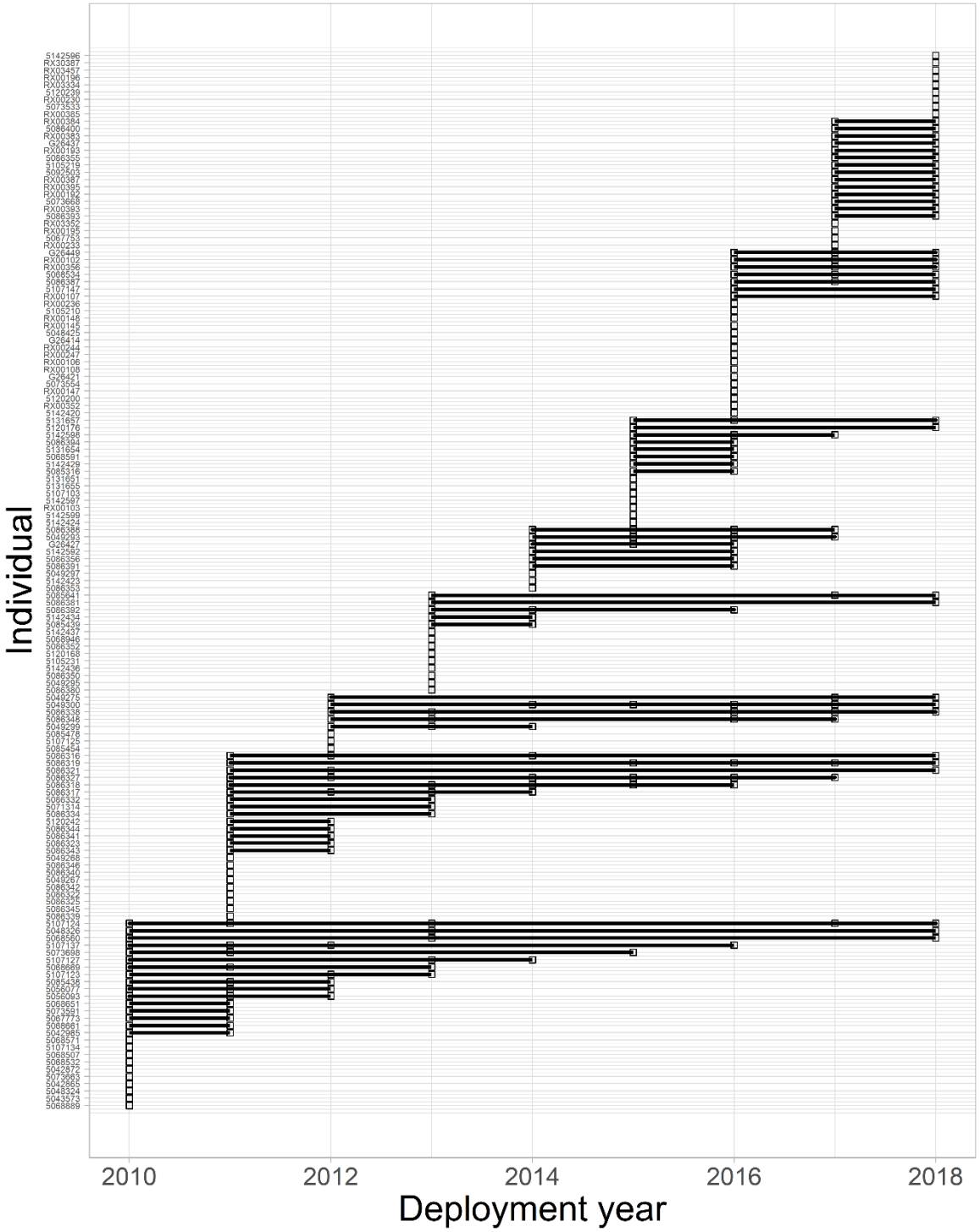



**Fig. 6.9. A visualisation of turnover in the study population.** Individuals are arranged along the y-axis and points represent years in which they are tracked. The points, from the year each bird was first tracked to the year each bird was last tracked, are connected by horizontal black lines.

Our analysis of breeding success involved data from Mallorca between 2011 and 2015. At the population level, we analysed the probability of egg laying in annually monitored study nests. Among those nests in which a chick hatched, we also conducted an analysis of the probability of fledging. Both outcomes were analysed in relation to the mean July and August SST in the post-breeding area in the previous year using a generalised linear model with a logit link. There was no effect of climate in the migratory area on either of these outcomes (egg-laying: n = 406, log odds change = 0.25 per °C, SE = 0.25, $P = 0.311$; fledging: n = 185, log odds change = 0.67 per °C, SE = 0.60, $P = 0.263$). Since geolocators were only retrieved from active breeders, it was not possible to analyse the relationship between individual migratory behaviour and egg-laying. However, we were able to investigate fledging success at the individual level in relation to the individuals' migratory latitudes in the previous migration. We again used a generalised linear model with a logit link and found that migratory behaviour did not significantly affect subsequent fledging success (n = 39, log odds change = 0.20 per °N, SE = 0.26, $P = 0.445$).

### 6.6.3 Full model results

**Table 6.1. Full results for all mixed effects models.** The confidence intervals were estimated using bootstrapping and the Chi-square and *P*-values were estimated from likelihood ratio tests on full and null models for each term. Significant predictors are highlighted in bold and the level of significance is indicated by asterisks: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

| Response | Predictor | Coefficient [95% CI] | $\chi^2_1$ | *P*-value |
|---|---|---|---|---|
| Median latitude (°N) | Intercept | 20.07 [ 5.89, 34.96] | - | - |
| | **Between-individual SST** (°C) | 1.42 [ 0.64, 2.27] | 12.12 | **<0.001*** ** |
| | **Within-individual SST** (°C) | 0.66 [ 0.02, 1.33] | 4.05 | **0.044*** |
| | **Area** (southern) | -7.18 [− 7.79, −6.56] | 225.04 | **<1x10$^{-15}$*** ** |
| | **Sex** (male) | −0.68 [− 1.24, −0.11] | 5.04 | **0.025*** |
| Area (log odds of migrating to northern area) | Intercept | -0.89 [− 4.93, 2.85] | - | - |
| | **Between-individual SST** (°C) | 1.79 [− 0.23, 3.89] | 4.56 | **0.033*** |
| | Within-individual SST (°C) | 0.00 [− 0.53, 0.58] | 0.00 | 0.988 |
| | Island (Mallorca) | 2.01 [− 2.41, 6.68] | 1.25 | 0.264 |
| | **Sex** (male) | −6.88 [−11.73, −2.20] | 6.18 | **0.013*** |
| Return speed (kmh$^{-1}$) | Intercept | 2.09 [− 6.30, 10.34] | - | - |
| | **Between-individual max. lat.** (°N) | 0.22 [ 0.06, 0.39] | 8.12 | **0.004**** |
| | **Within-individual max. lat.** (°N) | 0.22 [ 0.02, 0.41] | 4.54 | **0.033*** |
| | Outbound speed (kmh$^{-1}$) | 0.18 [− 0.03, 0.26] | 2.50 | 0.114 |
| | Area (southern) | 0.96 [− 0.22, 2.22] | 2.63 | 0.105 |
| Departure date (Julian date) | Intercept | 131.05 [ 77.88, 174.30] | - | - |
| | Between-individual max. lat. (°N) | 0.70 [− 0.18, 1.73] | 1.98 | 0.159 |

| | | | | |
|---|---|---|---|---|
| | Within-individual max. lat. (°N) | 0.27 [− 0.91, 1.46] | 0.19 | 0.664 |
| | **Area** (southern) | 11.66 [ 4.10, 18.63] | 9.61 | **0.002**** |
| | Island (Mallorca) | 1.42 [− 4.97, 7.62] | 0.20 | 0.659 |
| **Return date (Julian date)** | Intercept | −3.01 [−52.08, 45.58] | - | - |
| | **Between-individual max. lat.** (°N) | 5.37 [ 4.39, 6.28] | 82.09 | **$<1x10^{-15}$*** ** |
| | **Within-individual max. lat.** (°N) | 4.35 [ 3.18, 5.61] | 41.50 | **$<1x10^{-10}$*** ** |
| | **Area** (southern) | 38.75 [ 31.73, 46.76] | 81.44 | **$<1x10^{-15}$*** ** |
| | **Island** (Mallorca) | −9.79 [ −16.99, −3.67] | 8.52 | **0.004**** |

## References

Afán, I., Arcos, J. M., Ramírez, F., García, D., Rodríguez, B., Delord, K., Boué, A., Micol, T., Weimerskirch, H., & Louzao, M. (2021). Where to head: environmental conditions shape foraging destinations in a critically endangered seabird. *Marine Biology*, *168*(3), 23.

Astarloa, A., Glennie, R., Chust, G., Garca-Baron, I., Boyra, G., Martnez, U., Rubio, A., & Louzao, M. (2021). Niche segregation mechanisms in marine apex predators inhabiting dynamic environments. *Diversity and Distributions*, *27*(5), 799-815. https://doi.org/10.1111/ddi.13229

Austin, G. E., & Rehfisch, M. M. (2005). Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Global change biology*, *11*(1), 31-38. https://doi.org/10.1111/j.1529-8817.2003.00876.x

Austin, J. J. (1996). Molecular Phylogenetics of *Puffinus* Shearwaters: Preliminary Evidence from Mitochondrial Cytochrome b Gene Sequences. *Molecular Phylogenetics and Evolution*, *6*(1), 77-88. https://doi.org/10.1006/mpev.1996.0060

Austin, R. E., Wynn, R. B., Votier, S. C., Trueman, C., McMinn, M., Rodríguez, A., Suberg, L., Maurice, L., Newton, J., Genovart, M., Péron, C., Grémillet, D., & Guilford, T. (2019). Patterns of at-sea behaviour at a hybrid zone between two threatened seabirds. *Scientific Reports*, *9*(1), 14720. https://doi.org/10.1038/s41598-019-51188-8

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1-48. https://doi.org/10.18637/jss.v067.i01

Brooke, M. (1990). *The Manx shearwater*. T. & A. D. Poyser, London, United Kingdom. ISBN: 9780856610578

Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary applications*, *7*(1), 15-28. https://doi.org/10.1111/eva.12126

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C. M., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population. *Science*, *320*(5877), 800-803. https://doi.org/10.1126/science.1157174

Chevin, L. M., Lande, R., & Mace, G. M. (2010). Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. *PLoS biology*, *8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Conklin, J. R., Lisovski, S., & Battley, P. F. (2021). Advancement in long-distance bird migration through individual plasticity in departure. *Nature Communications*, *12*, 4780. https://doi.org/10.1038/s41467-021-25022-7

Davies, T. E., Carneiro, A. P. B., Tarzia, M., Wakefield, E., Hennicke, J. C., Frederikse, M., Hansen, E. S., Campos, B., Hazin, C., Lascelles, B., & et al. (2021).

Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conservation Letters*, *14*(5), e12824. https://doi.org/10.1111/conl.12824

Dean, B., Kirk, H., Fayet, A. L., Shoji, A., Freeman, R., Leonard, K., Perrins, C. M., & Guilford, T. (2015). Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area. *Marine Ecology Progress Series*, *538*, 239-248. https://doi.org/10.3354/meps11443

Fudickar, A. M., Wikelski, M., & Partecke, J. (2012). Tracking migratory songbirds: Accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution*, *3*(1), 47-52. https://doi.org/10.1111/j.2041-210X.2011.00136.x

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *Journal of Experimental Biology*, *216*(15), 2798-2805. https://doi.org/10.1242/jeb.085738

Gelman, A., & Su, Y.-S. (2024). *arm: Data Analysis Using Regression and Multilevel/Hierarchical Models*. R package version 1.14-4. https://CRAN.R-project.org/package=arm

Genovart, M., Arcos, J. M., Álvarez, D., McMinn, M., Meier, R. E., Wynn, R. B., Guilford, T., & Oro, D. (2016). Demography of the critically endangered Balearic shearwater: the impact of fisheries and time to extinction. *Journal of Applied Ecology*, *53*(4), 1158-1168. https://doi.org/10.1111/1365-2664.12622

Gill, J. A., Alves, J. A., & Gunnarsson, T. G. (2019). Mechanisms driving phenological and range change in migratory species. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *374*(1781), 20180047. https://doi.org/10.1098/rstb.2018.0047

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, *35*(1-2), 37-58. https://doi.org/10.3354/cr00713

Guilford, T., Wynn, R. B., McMinn, M., Rodrguez, A., Fayet, A. L., Maurice, L., Jones, A., & Meier, R. E. (2012). Geolocators reveal migration and pre-breeding behaviour of the critically endangered Balearic shearwater *Puffinus mauretanicus*. *PLoS One*, *7*(3), e33753. https://doi.org/10.1371/journal.pone.0033753

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., & Clarke, R. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods in Ecology and Evolution*, *12*(11), 2243-2255. https://doi.org/10.1111/2041-210X.13698

Harris, M. P., Wanless, S., & Brockie, K. (2011). *The puffin*. T. & A. D. Poyser, London, United Kingdom. ISBN: 1-283-47865-X

Heidrich, P., Amengual, J., & Wink, M. (1998). Phylogenetic relationships in Mediterranean and North Atlantic shearwaters (Aves: Procellariidae) based on nucleotide sequences of mtDNA. *Biochemical Systematics and Ecology*, *26*(2), 145-170 https://doi.org/10.1016/S0305-1978(97)00085-9

Le Mao, P., & Yésou, P. (1993). The annual cycle of Balearic shearwaters and western Mediterranean Yellow-legged gulls: some ecological considerations. In *Status and Conservation of Seabirds* (pp. 135-145). 2nd Mediterranean Seabird Symposium 1993, Madrid, Spain. SEO/Birdlife, Madrid, Spain.

[Dataset] Lewin, P. J., Wynn, J., Arcos, J. M., Austin, R. E., Blagrove, J., Bond, S., Carrasco, G., Delord, K., Fisher-Reeves, L., Garca, D., Gillies, N., Guilford, T., Hawkins, I., Jaggers, P., Kirk, C., Louzao, M., Maurice, L., McMinn, M., Micol, T.,...Padget, O. (2024). *Individual plasticity in migratory destination contributes to climate-driven range shift in a Critically Endangered seabird* (https://doi.org/10.6084/m9.figshare.22680283)

Linssen, H., van Loon, E. E., Shamoun-Baranes, J. Z., Nuijten, R. J. M., & Nolet, B. A. (2023). Migratory swans individually adjust their autumn migration and winter range to a warming climate. *Global change biology*, *29*, 6888-6899. https://doi.org/10.1111/gcb.16953

Lisovski, S., & Hahn, S. (2012). GeoLight - processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution*, *3*, 1055-1059. https://doi.org/10.1111/j.2041-210X.2012.00248.x

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W., & Hahn, S. (2012). Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, *3*(3), 603-612. https://doi.org/10.1111/j.2041-210X.2012.00185.x

Lisovski, S., Schmaljohann, H., Bridge, E. S., Bauer, S., Farnsworth, A., Gauthreaux, S. A., Hahn, S., Hallworth, M. T., Hewson, C. M., Kelly, J. F., Liechti, F., Marra, P. P., Rakhimberdiev, E., Ross, J. D., Seavy, N. E., Sumner, M. D., Taylor, C. M., Winkler, D. W., Wotherspoon, S. J., & Wunder, M. B. (2018). Inherent limits of light-level geolocation may lead to over-interpretation. *Current Biology*, *28*(3), R99-R100. https://doi.org/10.1016/j.cub.2017.11.072

Louzao, M., Delord, K., García, D., Afán, I., Arcos, J. M., & Weimerskirch, H. (2021). First days at sea: depicting migration patterns of juvenile seabirds in highly impacted seascapes. *PeerJ*, *9*, e11054. https://doi.org/10.7717/peerj.11054

Luczak, C., Beaugrand, G., Jaffré, M., & Lenoir, S. (2011). Climate change impact on Balearic shearwater through a trophic cascade. *Biology Letters*, *7*(5), 702-705. https://doi.org/10.1098/rsbl.2011.0225

Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3.3. https://cran.r-project.org/package=AICcmodavg

Meier, R. E. (2015). *The at-sea behaviour and ecology of the critically endangered Balearic shearwater.* [Doctoral thesis, University of Southampton]. Southampton, United Kingdom.

Meier, R. E., Wynn, R. B., Votier, S. C., McMinn, M., Rodríguez, A., Maurice, L., van Loon, E. E., Jones, A. R., Suberg, L., & Arcos, J. M. (2015). Consistent foraging areas and commuting corridors of the critically endangered Balearic shearwater *Puffinus mauretanicus* in the northwestern Mediterranean. *Biological Conservation*, *190*, 87-97. https://doi.org/10.1016/j.biocon.2015.05.012

Moiron, M., Araya-Ajoy, Y. G., Teplitsky, C., Bouwhuis, S., & Charmantier, A. (2020). Understanding the Social Dynamics of Breeding Phenology: Indirect Genetic Effects and Assortative Mating in a Long-Distance Migrant. *The American Naturalist*, *196*(5), 566-576. https://doi.org/10.1086/711045

Mouriño, J., Arcos, F., Salvadores, R., Sandoval, A., & Vidal, C. (2003). Status of the Balearic shearwater (*Puffinus mauretanicus*) on the Galician coast (NW Iberian Peninsula). *Scientia Marina*, *67*(S2), 135-142. https://doi.org/10.3989/scimar.2003.67s2135

Obiol, J. F., Herranz, J. M., Paris, J. R., Whiting, J. R., Rozas, J., Riutort, M., & González-Solís, J. (2022). Species delimitation using genomic data to resolve taxonomic uncertainties in a speciation continuum of pelagic seabirds. *Molecular Phylogenetics and Evolution*, *179*, 107671. https://doi.org/10.1016/j.ympev.2022.107671

Oro, D., Aguilar, J. S., Igual, J. M., & Louzao, M. (2004). Modelling demography and extinction risk in the endangered Balearic shearwater. *Biological Conservation*, *116*(1), 93-102. https://doi.org/10.1016/S0006-3207(03)00180-0

Padget, O., Bond, S. L., Kavelaars, M. M., van Loon, E., Bolton, M., Fayet, A. L., Syposz, M., Roberts, S., & Guilford, T. (2018). *In situ* clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology*, *28*(2), 275-279. https://doi.org/10.1016/j.cub.2017.11.062

Padget, O., Dell'Ariccia, G., Gagliardo, A., González-Solís, J., & Guilford, T. (2017). Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. *Scientific Reports*, *7*(1), 9668. https://doi.org/10.1038/s41598-017-09738-5

Padget, O., Gillies, N., Syposz, M., Lockley, E., & Guilford, T. (2022). Shearwaters sometimes take long homing detours when denied natural outward journey information. *Biology Letters*, *18*(2), 20210503. https://doi.org/10.1098/rsbl.2021.0503

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M., & Guilford, T. (2019). Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the*

*National Academy of Sciences*, *116*(43), 21629-21633. https://doi.org/10.1073/pnas.1903829116

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37-42. https://doi.org/10.1038/nature01286

Pérez-Roda, A., Delord, K., Boué, A., Arcos, J. M., García, D., Micol, T., Weimerskirch, H., Pinaud, D., & Louzao, M. (2017). Identifying Important Atlantic Areas for the conservation of Balearic shearwaters: Spatial overlap with conservation areas. *Deep Sea Research Part II: Topical Studies in Oceanography*, *141*, 285-293. https://doi.org/10.1016/j.dsr2.2016.11.011

Phillips, J. A., Banks, A. N., Bolton, M., Brereton, T., Cazenave, P., Gillies, N., Padget, O., van der Kooij, J., Waggitt, J., & Guilford, T. (2021). Consistent concentrations of critically endangered Balearic shearwaters in UK waters revealed by at-sea surveys. *Ecology and evolution*, *11*(4), 1544-1557. https://doi.org/10.1002/ece3.7059

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V., & Briggs, D. R. (2004). Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series*, *266*, 265-272. https://doi.org/10.3354/meps266265

Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, *18*(5), 228-233. https://doi.org/10.1016/S0169-5347(03)00036-3

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., & Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific Reports*, *5*(1), 16486. https://doi.org/10.1038/srep16486

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M., & Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *278*(1707), 835-842. https://doi.org/10.1098/rspb.2010.1778

Sangster, G., Collinson, J. M., Helbig, A. J., Knox, A. G., & Parkin, D. T. (2002). The specific status of Balearic and yelkouan shearwaters. *British Birds*, *95*(12), 636-639.

Shaffer, S. A., Tremblay, Y., Awkerman, J. A., Henry, R. W., Teo, S. L. H., Anderson, D. J., Croll, D. A., Block, B. A., & Costa, D. P. (2005). Comparison of light-and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology*, *147*(4), 833-843. https://doi.org/10.1007/s00227-005-1631-8

Therneau, T. (2024). *A Package for Survival Analysis in R*. R package version 3.7-0. https://CRAN.R-project.org/package=survival

Therneau, T., & Grambsch, P. M. (2000). *Modeling Survival Data: Extending the Cox Model*. Springer, New York, United States. ISBN: 0-387-98784-3

Thomas, C. D., & Lennon, J. J. (1999). Birds extend their ranges northwards. *Nature*, *399*(6733), 213. https://doi.org/10.1038/20335

Usui, T., Butchart, S. H. M., & Phillimore, A. B. (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. *Journal of Animal Ecology*, *86*(2), 250-261. https://doi.org/10.1111/1365-2656.12612

van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, *77*(3), 753-758. https://doi.org/10.1016/j.anbehav.2008.11.006

Verhoeven, M. A., Loonstra, A. H. J., Hooijmeijer, J. C. E. W., Masero, J. A., Piersma, T., & Senner, N. R. (2018). Generational shift in spring staging site use by a long-distance migratory bird. *Biology Letters*, *14*(2), 20170663. https://doi.org/10.1098/rsbl.2017.0663

Votier, S., Bearhop, S., Attrill, M., & Oro, D. (2008). Is climate change the most likely driver of range expansion for a critically endangered top predator in Northeast Atlantic waters? *Biology Letters*, *4*, 204-205. https://doi.org/10.1098/rsbl.2007.0558

Winkler, D. W., Jøgensen, C., Both, C., Houston, A. I., McNamara, J. M., Levey, D. J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D., & Piersma, T. (2014). Cues, strategies, and outcomes: how migrating vertebrates track environmental change. *Movement Ecology*, *2*(1), 10. https://doi.org/10.1186/2051-3933-2-10

Wynn, J., Padget, O., Mouritsen, H., Perrins, C. M., & Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology*, *30*(14), 2869-2873.e2862. https://doi.org/10.1016/j.cub.2020.05.039

Wynn, R. B., Josey, S. M., Martin, A. P., Johns, D. G., & Yésou, P. (2007). Climate-driven range expansion of a critically endangered top predator in northeast Atlantic waters. *Biology Letters*, *3*(5), 529-532. https://doi.org/10.1098/rsbl.2007.0162

Xu, W., Barker, K., Shawler, A., Van Scoyoc, A., Smith, J. A., Mueller, T., Sawyer, H., Andreozzi, C., Bidder, O. R., Karandikar, H., Mumme, S., Templin, E., & Middleton, A. D. (2021). The plasticity of ungulate migration in a changing world. *Ecology*, *102*(4). https://doi.org/10.1002/ecy.3293

Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Mller, M., & Yamamoto, M. (2017). Compass orientation drives naïve pelagic seabirds to cross mountain ranges. *Current Biology*, *27*(21), R1152-R1153. https://doi.org/10.1016/j.cub.2017.09.009

# 7
# General Discussion

## Contents


**7.1** Methodological advances, opportunities and limitations....210

**7.2** The place of this thesis within the navigation literature....218

**7.2.1** The sun compass....219

**7.2.2** Outward journey information....225

**7.2.3** Compass calibration....228

**7.2.4** Magnetic navigation....232

**7.3** Future directions....235

**7.3.1** The sun compass and its potential for map research....236

**7.3.2** Outward journey information....239

**7.3.3** Compass calibration....240

**7.3.4** The behavioural ecology of navigation....241

**7.3.5** A major direction: chronobiology....243

**7.4** Concluding remarks....244


*"It would take a lot of the fun out of science if we really knew how things worked."*

Rupert Sheldrake, *Paranormal Pigeons* (2006)

Navigation provides an unparalleled window onto the exquisite adaptations of animals to the fundamental mechanics of our planet and solar system. Animals contain endogenous clocks which track the rotation of our planet and its orbit around the sun; they use these clocks to organise their annual migrations and direct their movements relative to the axis of the earth's rotation; and whether by smell, sensitivity to the earth's magnetic field or some other means, animals are able to position themselves on the globe with a precision that human navigators have never achieved without the aid of modern satellite technology.

## 7.1 Methodological advances, opportunities and limitations

Towards the aim of furthering our understanding of animal navigation, I have studied the migration, foraging and homing movements of shearwaters: remarkable ocean travellers. In particular, the work presented in this thesis attempts to leverage tracking data from free-ranging birds to reveal the cues and navigational strategies by which shearwaters navigate during their natural movements. Although attempts were made early in the study of navigation to draw inference from the natural movements of birds via ringing recoveries or direct observation (Dobben, 1953; Tinbergen, 1941), and this has never completely abated (Alerstam et al., 2008; Alerstam et al., 2001; Alerstam & Pettersson, 1991; Mouritsen, 1998; Wynn et al., 2022; Wynn, Padget, et al., 2020), the vast majority of avian navigation research has relied on either artificial displacement of animals (Wallraff, 2005; sometimes simulated, e.g. Kishkinev et al., 2015) or the directional restlessness of caged migratory birds (Emlen & Emlen, 1966; Kramer, 1949). These approaches often require the close control or removal of potential sources of navigational information, beyond one or two cues of interest, whilst generating an orientation response that might not closely reflect any navigational challenge faced by these animals in the real world (e.g. displaced birds entirely lack any information from their outward journey, and caged songbirds lack any interaction with con- or heterospecifics, in contrast to normal migratory conditions; Van Doren

et al., 2025). The reliance on displacement also limits the study of navigation only to those mechanisms involved in homing. Outside taxa where an individual's entire movement or an isolated task takes place over a small enough scale for direct observation (e.g. Chappell & Guilford, 1995; Collett, 2010; Collett et al., 1992; Duff et al., 1998; Kelly et al., 2019; Tello-Ramos et al., 2015; Wehner et al., 2006; Zimmerman et al., 2009), we have almost no knowledge of how animals navigate efficiently towards and between multiple goals. This is not to say that these established paradigms offer us no insight into the navigational mechanisms of animals – far from it. Almost all of the considerable understanding we have of avian navigation is derived from these paradigms and they have proved incredibly powerful in yielding insight into the cues birds use to navigate. However, they are necessarily far less powerful when it comes to questions of *how* animals use these cues. These questions are now being addressed using the growing body of biotelemetry data from wild animals, including shearwaters (Goto et al., 2017; Harten et al., 2020; Padget et al., 2019; Shiomi et al., 2012; Toledo et al., 2020; Yoda et al., 2021; Yoda et al., 2017).

To further this approach, we have focused on free-ranging movement throughout this thesis, relying on precise predictions of navigational error expected to result from a given mechanism or strategy. In Chapters 4 and 5, we used established sensory manipulations to induce errors in controlled experimental designs, whilst in Chapters 2, 3 and 4, we generated novel predictions of naturally occurring errors imposed by the constraints of shearwaters' conjectured navigational mechanisms. Through this work, we have revealed the spatial cognition by which shearwaters estimate the distance of their return migration and regulate their travel speed, the compass cues by which they both find foraging areas and return from them, the manner in which they combine these cues with compass-independent information, the role (or lack thereof) of geomagnetic cues, and the control of the endogenous clock on the directions and timing of foraging movements.

Nonetheless, use of tracking data from free-ranging movements has its own limitations, each of which we have attempted to overcome or otherwise acknowledge.

The first difficulty is robustly identifying the behaviour of interest. In general, to draw specific navigational inferences requires that the researcher know the 'correct' orientation. This necessitates knowledge of where or in what direction the animal is aiming and whether or not it is actively attempting to move in that direction at a given moment. In migratory birds this is relatively easy – the population-level migratory direction can be measured from ringing recoveries or simply assumed to be that shown by birds in a control group (Emlen & Emlen, 1966; Kramer, 1949) and migratory restlessness appears a reliable indicator of motivation, with suppression of other behaviours (Berthold, 1984, 1990). In displaced birds it is even easier – the capture point is assumed to be the goal (this appears to hold even on surprisingly small scales in birds (Dayananda et al., 2021); apart from in birds displaced during migration which may orient towards the capture location, the end point of the migration or somewhere in between (Chernetsov et al., 2017; Kishkinev et al., 2015; Kishkinev et al., 2021) and motivation is generated by the very act of displacement. In contrast, birds moving naturally outside of migration will transition between various behaviours and in each of these they may be oriented towards different directions or goals, or not oriented at all (e.g. during rest). Thus, the first step of navigation research using free-ranging movements is to identify distinctive behavioural patterns associated with orientation towards a particular goal or direction.

In the case of shearwaters, the most obvious goal is the colony and homing behaviour is readily identifiable in most cases (Goto et al., 2017; Padget et al., 2017; Padget et al., 2019; Shiomi et al., 2012). The start of homing is characterised by a sudden increase in the rate of movement towards the colony after a period at sea, and this rate generally remains high until the shearwater is within a few

kilometres of the breeding island. Nonetheless, even in this relatively straightforward case, the great variability of free-ranging behaviour can cause issues, as noted in the General methods. In this thesis, we have developed a new algorithmic approach to homing identification in shearwaters, applied and modified in each chapter to suit the requirements of those analyses. Though there must necessarily be some false positives and negatives (of an unknown proportion), this approach allows for repeatable and objective identification of homing, and thus of goal-oriented behaviour in shearwaters.

A greater problem is presented by navigation towards other goals. Before shearwaters can return to their colony, they first have to leave it, and they do so in search of food. We would expect, therefore, that there must be periods during each foraging trip when they are actively orienting towards a foraging area. We reasoned that this is effectively homing in reverse and could, therefore, be identified by the same means, with the key difference that bouts of foraging commute should be oriented away (or at least obliquely) to the colony. We applied this approach with some success in Chapters 3 and 4.

Nonetheless, an issue remains: where is the shearwater aiming for? To define a goal during foraging commute, we used the next location at which the shearwater foraged, based on behavioural state identification derived from Hidden Markov Models. Definition of the goal as the endpoint reached is, of course, rather circular but we designed an analysis in which the shape of the trajectory rather than error from the goal per se, might yield information about the navigational mechanism. The success of this approach is unclear and we suggest that this may result from misidentification of the goal, for instance if shearwaters change foraging goal during commute, or frequently stop to forage opportunistically en route to a more distant goal (cf. the opportunistic, non-goal-directed foraging strategies of *Pterodroma* petrels; Ventura et al., 2020). Instead, we rely on a measure of navigational error which is blind to the intended goal – only the rough direction of

travel need be known *a priori*. As shearwaters follow coasts, they appear to combine information from their sun compass. As a result, sun compass errors lead to lateral shifts towards or away from land. This allowed us to investigate use of the sun compass during foraging commutes without having to identify a goal.

Once motivated orientation and the 'correct' direction have been identified, the next step is to quantify orientation error. Broadly speaking, measures of navigational performance can be broken down into measures of directedness (e.g. tortuosity), measures of directedness relative to a goal direction (e.g. homing efficiency and absolute angular deflection) or a measure of movement direction relative to a goal direction (e.g. signed angular deflection). The latter, containing information about the direction as well as magnitude of orientation error, can be most precisely compared to exact navigational predictions (i.e. reorientation predictions, as attempted in Chapters 2, 3, 4 and 5). Nonetheless, the other metrics can act as useful quantification of disorientation effects (see Chapter 5) and the exact geometric nature of absolute deflection can be used to test precise hypotheses (see section 7.4 for an example). However, a key and relatively under-appreciated aspect of each of these measures is that they depend not only on the temporal frequency of GPS position estimates but also on the relative frequency at which an animal reorients towards its goal (Wynn, Collet, et al., 2020). This issue applies even to vanishing bearings but is exacerbated by the use of tracking data.

This can be demonstrated by two extreme cases. Consider a clock-shifted pigeon allowed to home from a release site with the assumption that the correct direction is towards the loft, and its error measured via a vanishing bearing and GPS tracking. If the pigeon were to orient by vector navigation, which offers no opportunity for correction, it will depart on a constant geographic bearing with a certain angular error, $\theta$, from the homeward direction corresponding to the full expected error. Measured by vanishing bearing, the estimate, $\varphi$, of orientation error will be accurate. However, if tracked by GPS, the difference between the homeward

direction and the movement direction increases monotonically at each successive GPS fix (Fig. 7.1B). Consequently, mean measured deflection will be an overestimate of orientation error; $\varphi >> \theta$. If, on the other hand, the pigeon is navigating via a map-and-compass mechanism, it has the opportunity to reorient by re-estimating its location. If it does so continuously, it will fly with the loft constantly held at $\theta$ from the direction of travel, forming a logarithmic spiral towards the goal (assuming $\theta < \pi/2$). However, GPS fixes are not recorded continuously and, as a result, the implied straight-line path between fixes will form a shallower spiral than the true route, leading to under-estimates of orientation error: $\varphi << \theta$ (Fig. 7.1A). This is also the case with vanishing bearings; if the bird reorients at least once before it leaves the observer's visual limit, its measured error, $\varphi$, will be less than $\theta$. If the bird reorients only periodically, $\varphi$ will lie somewhere between these extremes and the exact ratio of $\varphi$:$\theta$ will depend on the relative frequency of reorientation and GPS fixes. If fixes are taken more frequently than the bird reorients, $\varphi > \theta$, whilst $\varphi < \theta$ if the reverse is true. Orientation error is only measured accurately if the frequencies are equal. Furthermore, decreasing distance from the goal exacerbates disparity between $\varphi$ and $\theta$ in both directions because, for a given distance travelled, the angle subtended from the goal between two GPS fixes is much greater when the goal is closer. This leads to more rapid increase in apparent error while the bird travels without reorientation but also to more extreme reorientation (so smaller measured error) every time it re-estimates its location (Fig. 7.1C-D).

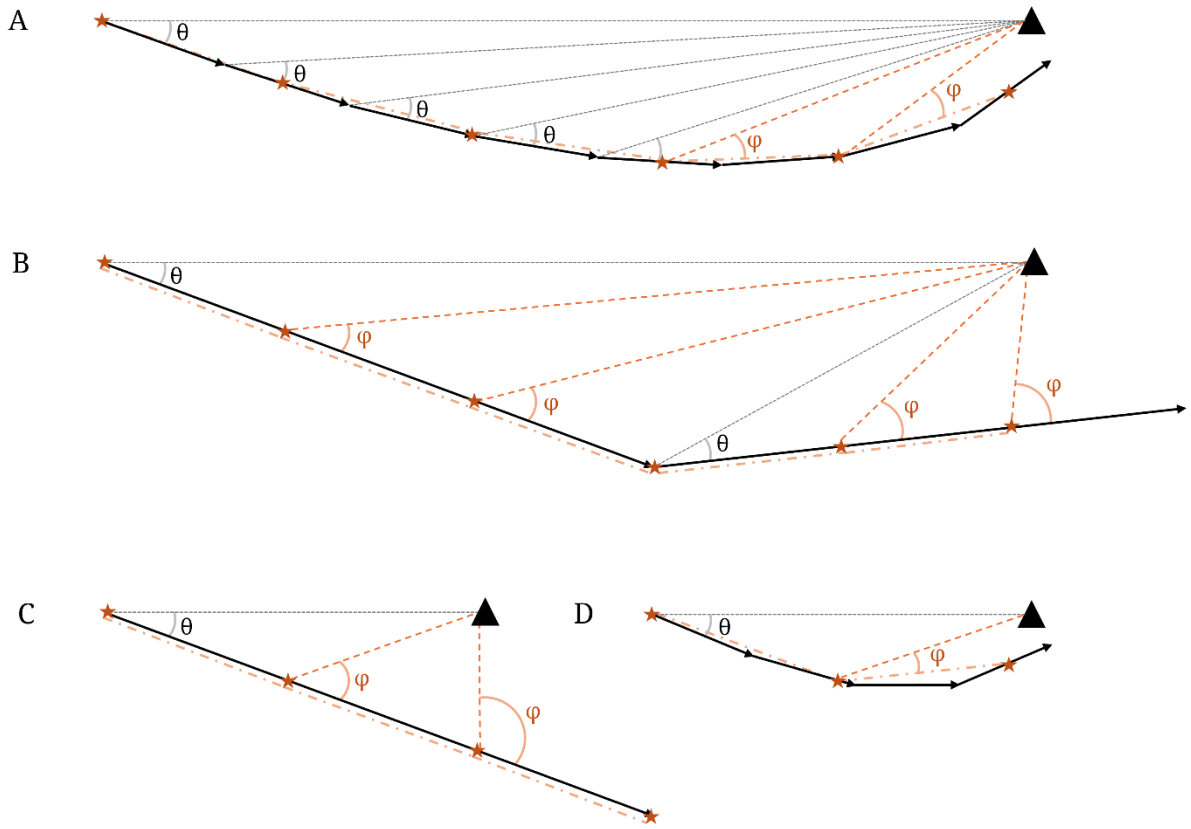



**Fig. 7.1. The relationship between reorientation, GPS temporal resolution and measured angular error.** An animal's true path (black arrows) and the implied path (pale orange dotted line) from successive GPS fixes (orange stars) to a goal (black triangle) are shown. For a fixed error, θ, the measured error, φ, depends on the relative frequency of GPS fixes and reorientation. (A) Reorientation occurs more frequently than GPS fixes; the angle between the correct direction and the implied path is shallower than between the correct direction and the true path, $\varphi < \theta$. (B) Reorientation occurs less frequently than GPS fixes. The angular error between the recorded true path and the correct direction increases monotonically between reorientations, so $\varphi > \theta$. (C-D) the effect is exacerbated in both directions when the bird is closer to the goal.

In cases where the frequency of reorientation is unknown (which is perhaps true in every example to-date), the exact magnitude of orientation error cannot be estimated. Instead, only relative measures of orientation error between individuals which are assumed to reorient equally frequently or where the expected impact of manipulation is on the location estimates themselves are useful. Exact values of coefficients should not be overinterpreted. Yet the impacts of this phenomenon go further. As a result of this phenomenon, changes in measured orientation error could result equally from changes in true orientation error or changes in the

frequency of reorientation. To take just one example, the reduced effect of clock-shift in pigeons over repeated releases at a site has traditionally been interpreted as resulting from a transition to compass-independent pilotage (Biro et al., 2007). However, it could, in principle, result from an increase in the resolution of the pigeon's map, even if the pigeon still relies fully on an error-prone compass to orient from those sites. See section 7.3 for suggestions as to how this ambiguity could be resolved and how the frequency of reorientation by birds might be estimated.

These issues highlight a key trade-off in tracking studies designed for navigation research. The temporal resolution possible using GPS loggers and other forms of biotelemetry has only increased. This offers insight into increasingly fine scale behaviours and more precise estimates of behavioural transitions, such as the initiation of homing. However, it does not necessarily improve estimates of navigational performance, given the issues above and the apparently high autocorrelation in navigational error in shearwaters, even at fix intervals in the order of tens of minutes. This high autocorrelation suggests that either shearwaters are not reorienting as frequently as every 5-30 minutes or that error in successive location estimates is highly non-independent, which will have a similar effect as infrequent reorientation. This is perhaps supported by the wildly inaccurate directions sometimes taken by shearwaters after displacement, with or without manipulation, and continued sometimes for hours (Padget et al., 2018; personal observations).

Despite these methodological challenges, our approaches have provided novel insights into the navigation of shearwaters and, by extension of other animals. In the next section, I will discuss our findings in relation to existing literature on the navigation of shearwaters.

## 7.2 The place of this thesis within the navigation literature

I will first provide a very brief overview of the current state of knowledge on the navigation of Procellariiforms generally, and shearwaters specifically. A more detailed summary can be found in the General Introduction. Procellariiforms rely on olfactory cues for position-finding (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015), likely as part of an extrapolated grid map (Padget et al., 2019). This map supports not only orientation but estimation of distance from the colony, which is used to adjust the timing of return to the colony (Padget et al., 2017; Padget et al., 2019; Shiomi et al., 2012). Despite evidence that geomagnetic inclination plays a role in natal philopatry (Wynn, Padget, et al., 2020), adult Procellariiforms mostly appear insensitive to magnetic disruption (Bonadonna et al., 2005; Bonadonna et al., 2003; Gagliardo et al., 2013; Massa et al., 1991; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015). Experimental evidence suggests that they combine their olfactory map with a time-compensated sun compass to achieve accurate homewards orientation (Padget et al., 2018), although they may also possess a geomagnetic compass (Takahashi et al., 2022), and might use this to calibrate their sun compass (Wynn et al., 2021). If denied olfactory information, shearwaters are still able to home, though less efficiently, by following coastlines (Padget et al., 2017; Pollonara et al., 2015). Whether this represents map-and-compass navigation via spatial memory of landmarks along the coast or compass independent pilotage via following of a linear feature is unclear. Interestingly, though shearwaters' extrapolated map-and-compass navigation appears blind to intervening obstacles, shearwaters accurately choose the shortest route around these obstacles (Lancaster-Reeves et al., unpublished-a; Padget et al., 2019), except in some cases after displacement (Padget et al., 2022). The mechanism by which this is possible (e.g. simple heuristics such as turning in the direction of least departure from the homewards beeline, recognition of familiar landmarks, reliance on memory of the outward journey etc.) remains unresolved – the poorer performance after

displacement might imply reliance on outward journey information or simply the non-specific effects of experimental disturbance.

The work presented in this thesis provides insight into aspects of shearwater navigation from position finding to compass systems, and even the role of the endogenous clock. A particular emphasis is placed on the time-compensated sun compass and its interaction with other elements of a shearwater's navigational toolkit. The focus on free-ranging movements allows us to infer not only what cues shearwaters are sensitive to but how they use and combine these cues in their everyday navigation.

### 7.2.1 The sun compass

In Chapter 2, we use the relationship between the endogenous clock and accurate sun compass orientation, as well as the conserved mechanisms of entrainment in endogenous circadian clocks to show that (a) shearwaters experience clock-shift as they travel longitudinally, and (b) they use the sun compass to guide homing after natural foraging trips. Whilst similar effects have been predicted for migratory birds (Alerstam & Pettersson, 1991) with some circumstantial evidence (Alerstam et al., 2008; Alerstam et al., 2001), this is, to my knowledge, the first direct evidence for sun compass orientation in any free-ranging animal. Whilst use of the sun compass has been demonstrated in a wide diversity of captive or displaced animals through artificial clock-shifting, this finding cements the importance of the sun compass to the navigation of wild diurnal animals. Although with great caution given the discussion of exact measures of orientation error derived from GPS data above, the very steep slope (5:1) of observed to expected deflection suggests that the sun is the dominant cue for shearwaters orienting via map-and-compass navigation out of sight of land. This corresponds well with findings from clock-shifted homing pigeons where observed orientation error from unfamiliar release sites is often equal or close to the full expected deflection (even when measured with vanishing bearings in which reorientation can lead to under- but not over-

estimated error; Schmidt-Koenig, 1990). This suggests that, though a magnetic compass might provide an accessory cue, diurnal birds do not routinely combine information from both compasses during homing and the sun is the primary compass cue.

A more intriguing element of this finding is that this error exists at all. Given that to explain the orientation ability of shearwaters in the first place we must invoke a rather precise sense of place, it would seem relatively trivial for the bird to track its longitudinal movements and update its time-compensation programme accordingly. Indeed, this could probably be achieved through simple associative learning – if shearwaters homing eastwards sometimes oriented a little further anticlockwise, they would home more quickly and presumably be reinforced for doing so. Equally, an innate, specifically evolved strategy could facilitate the same compensation. Alternatively, shearwaters might use other zeitgebers by which to reset their clock between dawn and dusk; temperature and solar elevation seem obvious candidates. Yet despite the availability of this temporal information to most animals, and some evidence for use of temperature (e.g. Chen et al., 2015), most animals seem to rely primarily on dawn and dusk (Hirschie Johnson et al., 2003). Extensive research in homing pigeons has shown that their time-compensation programme is entirely unaffected by solar elevation (Schmidt-Koenig, 1990).

There seem to be two reasonable, though rather imprecise explanations for this lack of correction. These suggestions offer little in the way of testable hypotheses but rely instead on their biological plausibility. The first is that that there is simply too small a cost for this error to be ‘noticed’ by natural selection or associative mechanisms. Given that shearwaters are able to reorient, the end goal of reaching the colony is never really in doubt and given that these orientation errors are in almost all cases relatively small (over 95% of homing bouts out of sight of land have an average predicted error < 3°), the actual increase in distance travelled is negligible. From 100 km, a shearwater homing to within 5 km of the colony with a

constant error of 3° would travel only 0.13 km further than the straight-line route. Even the most extreme cases of shearwaters homing over 1,000 km with 7° error only result in an increase of 0.5%. Further, this assumes that compass error is not mitigated at all by any compass-independent mechanisms within sight of land. For a bird which can travel at a groundspeed of around 70 $kmh^{-1}$ (Miller et al., 2025), and can do so with very little energetic expenditure (Harris et al., 2025; Kempton et al., 2022), these deviations are likely of negligible cost. On the other hand, there is no theoretical framework or empirical evidence for what might constitute a sufficient cost to drive solutions via natural selection or associative learning in the context of large-scale navigation. We can, therefore, only speculate. The second potential explanation is that of constraint or pleiotropy. Animals' endogenous circadian clocks are involved in myriad processes, often in complex ways (Mistlberger & Rusak, 2021). Changes to the clock mechanism which would allow entrainment against cues of local time as shearwaters fly east-west (e.g. solar elevation) might disrupt the functioning of the clock in other ways far more costly than the small navigational errors observed here. The highly conserved machinery of the endogenous clock is suggestive of strong constraint on these timekeeping mechanisms, perhaps due to pleiotropic effects. These two explanations are not mutually exclusive and, indeed, it is likely the balance between constraint or pleiotropic costs and the limited benefits of correction that underly the maintenance of this small but revealing navigational error.

Pigeons show reduced effects of clock-shift from familiar release sites and, particularly when following linear features such as roads, show only very small lateral shifts to the side of their habitual route (Biro et al., 2007). This has been taken as evidence of pilotage navigation (though see the alternative explanation in section 7.1), with some residual use of compass information. We find a remarkably similar phenomenon in the coast-following behaviour of shearwaters. Though shearwaters were observed to follow the coast regardless, they showed small

lateral shifts towards or away from the coast, depending on the direction and magnitude of their expected self-clock-shift relative to the coast. This suggests that shearwaters combine landmark information from the coast with directional information from their sun compass. As noted above, the large-scale extrapolated maps by which shearwaters orient from out of sight of land appear not to integrate information about landmasses yet shearwaters can accurately choose the shortest route around an obstacle once they reach it (Lancaster-Reeves et al., unpublished-a; Padget et al., 2022; Padget et al., 2019). This supports the idea that shearwaters might possess an extrapolated map-and-compass system by which they navigate from distant oceanic locations and a separate mechanism by which they navigate their familiar area. However, whether the second stage involves compass-independent pilotage with some residual input from the map-and-compass system, as is assumed in homing pigeons (Biro et al., 2007), or a full landmark-based map representation is unclear. In the next section, we suggest approaches which might be used to tackle this question, both in pigeons and shearwaters.

One of the most exciting elements of the effect of sun compass error on coast-following is that the navigational impact is measured not as deflection from a known goal but as distance from the coast. All one needs to know is which of the two possible directions along the coastline the shearwater is travelling. The implication is that this approach can be applied even when the shearwater's goal cannot be reliably identified *a priori*, such as during commutes towards foraging areas. In Chapter 3, we do just this. The mechanisms by which animals navigate towards memorised foraging patches (without relying on direct sensory contact) are poorly understood outside species with relatively small foraging ranges (e.g. Duff et al., 1998; Kelly et al., 2019; Tello-Ramos et al., 2015; Wiltschko & Balda, 1989; Zimmerman et al., 2009), particularly Hymenopterans (Collett, 2010; Collett et al., 1992; Wehner et al., 2006). Some recent studies have begun to address the spatial cognition of foraging in free-ranging bats (Harten et al., 2020; Toledo et al., 2020)

but still over a relatively small scale. Shearwaters might provide a valuable model for longer-distance foraging navigation. They appear to anticipate the distance to their foraging patches (Guilford et al., 2008), trade-off energetic costs of travel against returning to known areas (Harris et al., 2025) and show high individual foraging site fidelity (Jaggers, 2023). This suggests that they are actively navigating towards a known goal or in a known direction but the underlying navigational cues and strategies are entirely unknown. Use of the sun compass to find food has been demonstrated in caching birds (Duff et al., 1998; Kelly et al., 2019; Wiltschko & Balda, 1989), pigeons (Chappell & Guilford, 1995) and fowl (Zimmerman et al., 2009) over just metres. Using our coast-following framework, we provide the first evidence that animals use the sun compass to navigate towards foraging grounds over hundreds of kilometres. The relationship between predicted sun compass error and coast-following distance is identical to that seen in homing, suggesting that the same mechanisms might underpin both navigational tasks. Obviously only very limited general inference can be made from a single example but the similarity of navigation in foraging and homing commutes suggests that these tasks might rely on a unified navigational system. This would imply that the spatial representations of pigeons, shearwaters and other birds might accommodate multiple goals and facilitate flexible navigation between them, in a manner reminiscent of mammalian cognitive maps (O'Keefe & Nadel, 1978; Tolman, 1948), including in the free-ranging foraging movements of bats (Harten et al., 2020; Toledo et al., 2020). This line of inquiry requires far more extensive and intensive study of the mechanisms involved in navigating between goals other than the home location or migratory area. In contrast to coast-following, we find no effect of predicted sun compass error on foraging movements out of sight of land. For this latter analysis, however, we had to attempt the identification of the shearwater’s goal and resolved to use the next foraging patch visited for this

purpose. Whether the apparent lack of sun compass use holds any water in this case depends entirely on whether this assumption is valid.

In Chapter 4, we attempted to address the role of the sun compass in outward commuting further using an experimental clock-shift approach. The results are somewhat equivocal as to whether the sun compass is involved in determining the departure directions of shearwaters from the colony. If this were taken as weak evidence for sun compass orientation, it would imply that shearwaters do not rely entirely on pilotage for this task, despite the abundance of highly familiar landmarks and linear coastlines in the vicinity of the colony. Whether this is the case and whether any effect of the sun compass reflects vector or map-and-compass navigation requires further study, as outlined in section 7.3.

Although the role of time-compensated sun compass orientation in the foraging movements of Manx shearwaters is unclear, the more general role of the endogenous circadian clock has proved less resistant to experimental study. In Chapter 4 an artificial clock-shifting experiment demonstrates that the timing of foraging movements is under endogenous control in shearwaters. The role of the endogenous clock in governing behaviour and physiology in the wild is poorly understood due to the practical difficulty of clock-shifting procedures in most free-living animals (see section 7.1). However, fast-shifted shearwaters were active on average 1.5 hours earlier than slow-shifted shearwaters, whose endogenous clocks were expected to be eight hours behind, commuted less intensively and travelled less far on the first day of the outward journey. Despite these differences, fast-shifted birds were no more likely to return to the colony after only one day, suggesting that the impact of clock-shift was not on the decision to travel to foraging areas at all but rather on the decision of when to do so. Given that the difference in distance travelled was much greater than expected based purely on the 1.5-hour difference in activity timings, as a result of the lower speed of commuting flights, I suggest that this likely reflects not just an earlier termination of commuting activity

but a strategic decision by the shearwater not to initiate long-distance commuting on the first day. This would imply a mechanism similar to that of time allocation to homing, whereby they estimate the distance they need to travel and allot the appropriate time to commuting; if that time is greater than the time they perceive to be available before dusk, they delay commuting until the next day. These findings provide evidence on the important role of endogenous circadian clocks in governing the behaviour of wild animals, even when numerous external environmental are apparently more salient. This lack of 'masking' (Mrosovsky, 1999) by external cues suggests a strong, conserved reliance on the endogenous clock which might reflect its as yet unknown adaptive value in free-living animals (Helm et al., 2017).

### 7.2.2 Outward journey information

The presence of detectable orientation error during shearwaters' outward commuting flights creates an opportunity to explore whether cues perceived during the outward journey contribute to homewards orientation. Outward journey information contributes to the navigation of various animals (Mittelstaedt & Mittelstaedt, 1980; Seyfarth & Barth, 1972; Sibeaux et al., 2024; von Saint Paul, 1981; Wehner & Srinivasan, 2003; Zeil, 1998) and is understood in precise detail as part of the path integration systems of Hymenopterans. *Cataglyphis* ants foraging in featureless desert environments and honeybees searching for patches of nectar-rich flowers track their own movements from the nest to update a homewards vector continuously during their foraging excursions (Wehner & Srinivasan, 2003). Once they locate food, they use this vector to return directly to the nest. In ants, distance estimation is achieved by step-counting, as demonstrated by an elegant experiment manipulating the length of their legs (Wittlinger et al., 2006), whilst in flying bees distance estimation relies on optic flow (Srinivasan, 2014). The distances travelled are associated with a direction in order to compute the vector. This could be achieved entirely through proprioception (an idiothetic system) or

by reference to external direction cues (allothetic system; Heinze et al., 2018). Furthermore, use of allothetic cues could involve measurement of the insect's turning angles (egocentric system) or measurement of movement direction within an external frame of reference (allocentric system; Cheung & Vickerstaff, 2010). An allothetic and allocentric system is most robust to noise (Cheung & Vickerstaff, 2010) and is the best supported model empirically (Heinze et al., 2018). The possible role of outward journey information has generally been neglected in the avian navigation literature, partly due to the focus either on migratory orientation (where there is no outward journey for first time migrants or a long interval for adult migrants) and homing via true navigation, where cues from the outward journey are explicitly excluded, sometimes through extraordinary means (Kluijver, 1935; Matthews, 1951a; Walcott & Schmidt-Koenig, 1973; Wallraff, 1965). In addition, the feasibility of precise path integration whilst moving tens, hundreds or even thousands of kilometres through a fluid medium is questionable. This is exacerbated further in seabirds flying over a second fluid and visually quite homogenous medium, which may not provide reliable optic flow (Padget et al., 2019). However, if shearwaters were to rely, in some way like ants, on memory of the compass directions taken during their outward journey, then misperceptions of those directions would result in misorientation during homing. In Chapter 3, we explore this possibility but find no support.

On the basis of this analysis it would certainly be easy to dismiss the role of outward journey information in shearwaters and other birds entirely. However, there are myriad cues available during outward journeys other than compass directions, and numerous ways these cues might be used other than precise path integration. For instance, memory of the route taken around an obstacle on the way from the colony to the foraging grounds might support accurate choice of the shortest return route around the same obstacle on the return journey and might explain why shearwaters only seem to choose incorrectly when artificially

displaced (Padget et al., 2022). Alternatively, memory of grid-map location estimates during the outward journey might create a prior probability distribution for location estimates made at the start of homing, effectively improving the accuracy of location estimates by constant resampling. This might explain the poorer performance of displaced birds not just in deciding which way to travel around an obstacle but also in beeline orientation (Padget et al., 2018; personal observations). Further, recent research has suggested that path-integration-like mechanisms might contribute to shearwater navigation in subtler ways, helping track movements only when shearwaters move beyond sight of land (Lancaster-Reeves et al., unpublished-b).

There remains the possibility that outward journey information might contribute to some elements of shearwater navigation but not others. One such possibility is that outward journey information is involved in distance estimation but not orientation. This might explain the lack of evidence for distance estimation in displaced homing pigeons (Gagliardo, 2013). To my knowledge, the mechanisms of distance estimation have never been investigated in birds. After foraging trips, Manx shearwaters adjust the initiation of homing to allow sufficient time for return to the colony by dusk, with timing related most strongly to the beeline homewards distance, regardless of intervening obstacles (Padget et al., 2019). If this were based on outward journey information it would seem to suggest a path integration mechanism by which the homeward beeline vector is calculated, regardless of the complexity of the outward route. Alternatively, as posited by Padget et al. (2019), this distance estimation might be facilitated by an extrapolated grid map. In contrast, in Chapter 6, we find that estimates of the return migration distance in Balearic shearwaters correspond to the distance of the actual route, which requires detours around Iberia and through the Strait of Gibraltar. This is despite the distances involved being in the same order of magnitude. Anticipation of distance is evident in Balearic shearwaters' travel speed at the very beginning of return

migration. This must be based on experience and familiarity with the route – the shape of the Iberian coast cannot be extrapolated from more limited experience. This could be supported by two alternative mechanisms. The first is memory of the outward migration route. The second is learning from previous return migrations. These mechanisms are quite different in their implications for spatial cognition and for shearwaters' ability to accommodate increasingly northerly migrations whilst maintaining constant phenology. Estimates of the return migration distance based on the outward journey allow for flexibility in return speed specific to the focal migration, whereas learning based on previous migrations only allows shearwaters to adjust their speed in relation to the distance they have previously travelled, on average. The difference in the form of distance estimation between species might reflect differences in spatial representations – perhaps Balearic shearwaters do not possess an extrapolated grid map. It could also result from ecological differences. Certainly, the disparity between the beeline orientation and the direction of the shortest route is much greater in Balearic shearwater migration than in Manx shearwater foraging trips. This might favour use of route memory even if Balearic shearwaters are capable of beeline estimation using an extrapolated map. Whatever the mechanism, speed adjustment in shearwaters is clearly insufficient to compensate fully for more northerly migrations – shearwaters return roughly 2.5 days later to the pre-breeding area for every 100 km further north they travel on migration. Nonetheless, spatial cognition is clearly an important consideration in animals' flexibility of space-use and, therefore, in the climate responses of long-lived animals.

### 7.2.3 Compass calibration

The daily azimuthal change of the sun is not the only part of the solar arc that a shearwater must be able to predict. For a bird which remains at a constant longitude (and relatively far from the equator), solar azimuth can be accurately predicted by a well-entrained endogenous clock. This is true even over the

changing seasons and if the bird moves latitudinally (as long as it remains far from the equator) because the changes in solar ephemerides are only small and the change in photoperiod alters only when the sun is visible, not its azimuthal position at a certain time. For a bird which remains at the same latitude but moves longitudinally, the change in photoperiod is only seasonal so departures from an approximately 24-hour interval between successive dawns or dusks must result from longitudinal movement and can be used to reset the circadian clock to local time. However, for a bird which moves both longitudinally and latitudinally, these changes in the timing and length of the day with longitude and latitude, respectively, become ambiguous. Consider a shearwater at sea during a foraging trip at dawn on the summer solstice. Due to rapid movement during the preceding day, only 23 hours have passed since the shearwater last experienced dawn. Is this because it has moved 800 km eastwards or because it has moved 800 km northwards, or somewhere in between? If the answer is eastwards, it must advance its endogenous clock by an hour but the expected solar azimuth is the same as at last dawn. If the answer is northwards, it must not adjust its clock but must now assume the sun at dawn is roughly 10° further anticlockwise than at the last dawn the shearwater observed. This is a complex problem but there are a number of possible solutions.

In this thesis, I explored one particular solution: calibration via the magnetic compass. Numerous cue conflict experiments (involving the rotation of one or the other compass at dawn or dusk) have investigated the interaction between the celestial and magnetic compasses both during ontogeny (Pakhomov & Chernetsov, 2020) and during active orientation (Muheim et al., 2006; Sjöberg & Muheim, 2016) of migratory passerines. The results have been very mixed, with some experiments showing dominance of geomagnetic cues whilst others show dominance of celestial cues (Muheim et al., 2006), and the findings have generally defied obvious functional explanations. The most commonly cited explanation for compass

calibration is that birds use both celestial and magnetic compass senses at different times during their migrations and due to their different reference frames, this leads to inconsistent travel bearings and inefficient paths, especially near the poles where the reference frames are most disparate (Muheim et al., 2006). Compass calibration has also been investigated in Manx shearwaters (Wynn et al., 2021), with apparent correction of the sun compass to match the magnetic reference frame. This at first seems quite baffling, given that the sun appears to be the primary compass cue in shearwaters (Padget et al., 2018). In light of Wynn et al.'s findings, we posited that shearwaters might be using a geomagnetic compass to monitor changes in the sun arc with season and latitude, disambiguating these from changes in local time with longitudinal movement. The proposed mechanism is that shearwaters measure the azimuth of the sun at dawn or dusk and thus fix this point in the sun's arc at a known moment in the light-dark cycle (Fig. 7.2A). This mechanism would still retain some inherent error if shearwaters failed to account for changes in geomagnetic declination which varies by about 10° across their foraging range. A more complex mechanism would eliminate this error. If, as proposed by Muheim (2011), birds measure solar azimuth at dusk and at the following dawn, whilst remaining in the same location overnight, the midpoint between these two geomagnetic bearings is almost exactly true north (Fig. 7.2B). Muheim (2011) proposes that passerines use this mechanism to correct for changes in magnetic declination, bringing the magnetic compass into a geographic frame of reference. However, if the same process were used to adjust the time-compensation programme by measuring solar azimuth at dawn (whilst simultaneously correcting for magnetic declination), this would generate some interesting predictions. In this case, rotation of either compass during cue conflict experiments would produce a shift in orientation when birds subsequently use either compass, with the magnitude in both cases equal to half the cue conflict rotation. However, the direction of deflection would depend on the compass being

used to orient after cue conflict and on time of day. Birds orienting using the sun compass at dusk would show identical error to birds using the magnetic compass and it would appear that they had recalibrated their magnetic compass. However, birds orienting using the sun at dawn would show a deflection of equal magnitude in the opposite direction, appearing to have recalibrated their sun compass (Fig. 7.2C-E). This is because both compasses are effectively cross referenced to calibrate each other, perhaps explaining some of the inconsistencies in previous cue conflict experiments, as the direction of shift would depend on which compass cue the birds used to orient during testing.

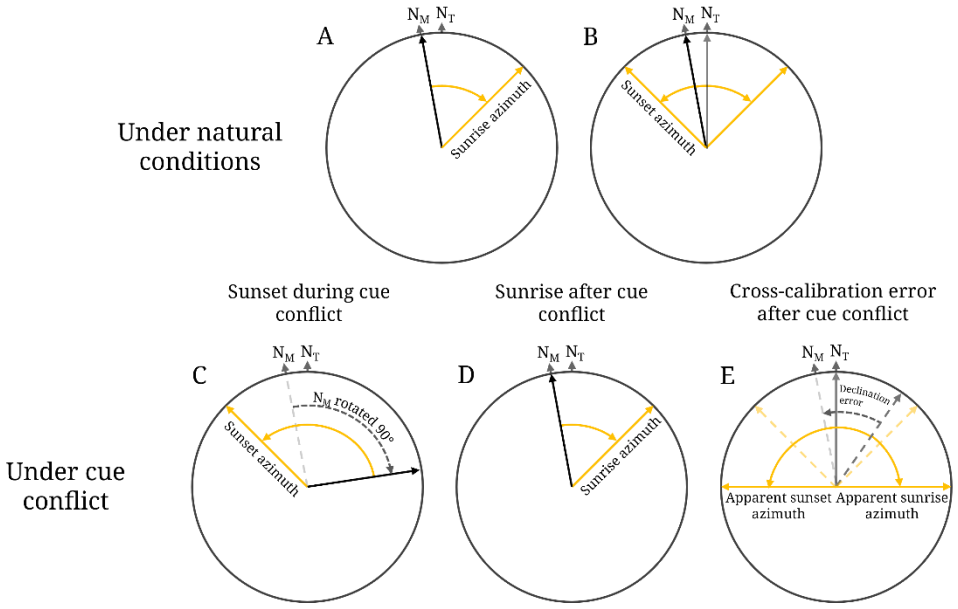



Fig. 7.2. Candidate mechanisms of sun compass calibration. (A) in the simplest scenario, birds might simply measure solar azimuth at sunrise using their magnetic compass and use this to adjust their time-compensation programme. This mechanism would retain error due to changes in geomagnetic declination. (B) Alternatively, birds might use the inherent symmetry of sunrise and sunset azimuth to derive the direction of true north and correct for declination. If this corrected magnetic compass were then used to adjust time-compensation, there might be unexpected results of cue conflict experiments. (C-E) If birds measure the azimuth at sunset whilst under an artificially clockwise rotated magnetic field (C), they would misestimate the azimuth of sunset relative to magnetic north. By the following sunrise, a normal magnetic field is restored (D). This change leads to misestimation of the direction of true north equal to half the magnetic field rotation in the anticlockwise direction (E). As a result, the birds estimate declination as 35° clockwise, when it is, in fact, 10° anticlockwise. Consequently, magnetic orientation is deflected by half the original rotation in the anticlockwise direction, whilst sun compass orientation is

similarly deflected near sunset but deflected by the same magnitude in the opposite direction at sunrise.

This mechanism would represent a neat, if somewhat convoluted solution to a complex problem faced by free-ranging animals. However, evidence that any bird relies on compass calibration during its natural movements (rather than merely showing directional shift after extreme cue conflict) is entirely lacking. In Chapter 5, we aimed to address this gap by disrupting shearwaters' magnetoreception even as they experienced changes in sun arc with latitude and season. Ultimately, we found no evidence that geomagnetic cues are important for tracking these changes in sun arc. The mechanism by which shearwaters disambiguate latitudinal, longitudinal and seasonal changes in sun arc remains unclear. The most likely candidate remains the circadian clock. Due to shearwaters' rapid longitudinal and latitudinal movements, they must experience warped photoperiods, which differ in period and phase from the local cycle at any single location. Nonetheless, the experienced light-dark cycle might be used to provide approximate entrainment which would be correct for a location near the mid-point of their day's travels. Additionally, shearwaters tend not to move far at night during foraging trips so if they can rapidly entrain their clock using a single dark period, it will always be well-matched to local time at dawn. Finally, the errors in time-compensation resulting from warped light-dark cycles might actually matter very little because when shearwaters use the sun compass to travel long distances, they travel to areas where their entrained circadian clock is poorly synchronised to local time anyway (see Chapters 2 and 3). Though the calibration mechanism tested here appears to have no place in the real world, the problem of tracking changing sun arcs requires a solution and, whatever the mechanism, it is worthy of study.

### 7.2.4 Magnetic navigation

Testing compass calibration through disruption of magnetoreception also provided the opportunity to investigate the role of magnetic cues in the navigation of shearwaters more generally. Given the ferocity that has traditionally defined

debates in this field, I will tread with care and try to provide what I consider to be a balanced perspective. The geomagnetic field presents a trove of potential navigational information and it is undeniable that many organisms exploit this information. The use of either geomagnetic polarity or inclination as a compass sense is both widespread and well-established, spanning Hymenopteran and Lepidopteran insects (Dreyer et al., 2018; Fleischmann et al., 2018; Guerra et al., 2014), crustaceans (Ugolini, 2001), fish (Quinn, 1980), amphibians (Phillips, 1986; Phillips & Borland, 1992), reptiles (Lohmann & Catherine, 1993), birds (Wiltschko & Wiltschko, 1972) and mammals (Burda et al., 1990). Use of the geomagnetic field as a bicoordinate map is more controversial both in its physical feasibility (Boström et al., 2012; Lohmann et al., 2024; Schneider, Packmor, et al., 2023; Schneider et al., 2024) and in the behavioural evidence (Gagliardo, 2013; Jorge et al., 2009; Jorge et al., 2010). Whilst evidence has accumulated for the role of magnetic cues in both steps of map-and-compass navigation among night-migratory passerine birds (Chernetsov et al., 2017; Kishkinev et al., 2015; Kishkinev et al., 2021; Wiltschko & Wiltschko, 2003) and other, non-avian taxa (Lohmann et al., 2022), the evidence in homing pigeons, the main model of diurnal avian navigation, has remained contradictory (Gordon, 1948; Holland et al., 2013; Jandačka et al., 2022; Keeton et al., 1974; Lednor & Walcott, 1983; Matthews, 1951a; Schiffner & Wiltschko, 2011; Walcott, 1977; Walcott et al., 1979; Wallraff et al., 1986; Wiltschko et al., 2009). This is in contrast to the extreme disorientation of anosmic pigeons (Gagliardo, 2013) and complete or near-complete reorientation of clock-shifted pigeons (Schmidt-Koenig, 1990). These findings are paralleled in Procellariiform seabirds; magnetic disruption has no clear effect (Bonadonna et al., 2005; Bonadonna et al., 2003; Gagliardo et al., 2013; Massa et al., 1991; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015) but anosmia and clock-shift have a major and specific impact on homing (Gagliardo et al., 2013; Padget et al., 2018; Padget et al., 2017; Pollonara et al., 2015). Our analysis yields similar results, though with a much larger sample

size than any previous experiment and having corrected some methodological flaws. The caveat that absence of evidence is not evidence of absence notwithstanding, quantitative assessment of the coefficients and confidence intervals in our analysis suggests that if geomagnetic cues play any role in the navigation of foraging adult shearwaters at all, that role is very minor.

Far from being the final word on this topic, these findings raise an important and relatively neglected question in navigation research: what drives the large variation apparent in the navigational mechanisms of different birds? Birds seem to fall into two navigational camps: the olfactory map and solar compass using non-passerines (Bonadonna & Gagliardo, 2021; Gagliardo, 2013; Wikelski et al., 2015) and the magnetic map and compass passerines (Kishkinev et al., 2021; Wiltschko & Wiltschko, 2003). If we are to accept that Galliforms and Passeriforms both have and use a magnetic sense for navigation (Wiltschko & Wiltschko, 1972; Zimmerman et al., 2009), that the light-dependent mechanism of magnetoreception seems shared also with reptiles and amphibians (Goforth et al., 2025; Phillips & Borland, 1992) and that even shearwaters seem to have access to magnetic information (Takahashi et al., 2022; Wynn, Padget, et al., 2020), then we must explain why adult Procellariiforms, some of the world's greatest navigators, seem totally indifferent to the magnetic field. Equally, despite their dominance in Procellariiforms and pigeons, passerines seem not to rely on an olfactory cues but use instead a geomagnetic map (Kishkinev et al., 2020), even though the capacity for olfactory navigation is present (Holland et al., 2009). These differences might reflect mechanistic constraints such as the relative abundance of geomagnetic anomalies in the home regions of different species, or limits of magnetic sensitivity which might not meet the greater demand for precision in homing tasks than in migration. Such constraints might also interact with phylogenetic history, for instance if Procellariiforms first radiated in regions where magnetic cues were less suitable as a bicoordinate map (Boström et al., 2012). The difference seems unlikely

to be ontogenetic – although pigeons and Procellariiforms are comparatively long-lived so might have greater opportunity to learn complex solar or olfactory information, where the sensitive learning phases for these cues have been investigated they have tended to occur very early in life and last only a short time (Gagliardo et al., 2001; Wiltschko & Wiltschko, 1981; Wiltschko et al., 1976). Ecological or adaptive drivers of different navigational systems must also be considered. For instance, passerine birds often live in dense vegetation, where the visibility of celestial compass cues (even via polarisation patterns) may be limited, compared to the open ocean environment of Procellariiforms, whilst atmospheric olfactants may form more reliable long-distance gradients over ocean-land boundaries than in terrestrial continental areas. These ecological drivers might themselves interact with mechanistic constraints. Most obviously, light-dependent magnetoreception may only function under certain light conditions. Passerines appear to rely on relatively dim light (in certain parts of the visible spectrum) for magnetoreception and appropriate orientation responses (Wiltschko et al., 2007; Wiltschko & Wiltschko, 2001; Wiltschko et al., 2000a, 2000b). As a result, navigation using a geomagnetic map or compass might only be possible in crepuscular or nocturnal species, not in diurnally active birds like homing pigeons and foraging shearwaters. An important step in answering these questions will be decoding the sensory and cognitive mechanisms of diverse avian taxa, beyond the traditional models and bringing a navigational lens to the vast accumulation of free-ranging movement data in birds.

## 7.3 Future directions

Interrogation of tracking data from free-ranging animals has the potential to be a powerful tool in navigational research. In the broadest possible terms, this approach allows far greater advances to be made towards understanding how animals use various cues, sometimes in combination, to navigate within their natural environments. The possibilities are likely endless – certainly within my

own research, I have repeatedly thought that we must have exhausted all the navigational inferences possible from shearwater tracking data and have repeatedly been proven wrong. Equally, there are still abundant insights to be gained from use of artificial displacement and, in other avian taxa, from orientation cage experiments. Here, I will focus on a few avenues which might prove fruitful in extending and expanding on the work presented in this thesis.

### 7.3.1 The sun compass and its potential for map research

Shearwaters provide a uniquely tractable model of sun compass orientation among wild birds. Their reliance on the sun compass is clear both after artificial displacement (Padget et al., 2018) and in their free-ranging movements (see Chapters 2 and 3) but what makes them more remarkable is their suitability for clock-shifting experiments. Few wild animals could be confined for up to a week under a continuous artificial light regime without major disturbance to their usual patterns of behaviour. In contrast, shearwaters naturally spend days or even weeks at a time inside an underground burrow partially shielded from external light (Brooke, 1990). A particularly intriguing element of shearwaters' sun compass use is its relation to coast-following. Distinguishing whether the small impacts of sun compass error on distance from land during coast-following reflects map-and-compass navigation using coastal landmarks or incomplete pilotage will require sensory manipulation experiments. Based on the ambiguity between map resolution and magnitude of sun compass error, I would argue that this question also remains open in the idiosyncratic routes of homing pigeons. A potential resolution lies in the disparate expectations of visual preview experiments. If reduced effects of clock-shifting on familiar routes results from increased reliance on visual pilotage then a bird able to see its surroundings should show reduced deflections. In contrast, if the reduced effect results from increasing map resolution, then increased certainty in the current location should not affect orientation error. As a result, clock-shifted birds offered a visual preview should

show reduced orientation error if they rely on visual pilotage but not if they are utilising a visual map-and-compass system. This approach could be used in both pigeons and shearwaters. Displacement of clock-shifted shearwaters to release sites along coastlines offers additional insights. The balance between pilotage and map-and-compass navigation might be further elucidated by clock-shifted shearwaters' behaviour when in sight of the colony and in how they navigate obstacles. The apparent dissociation between shearwaters' large-scale extrapolated maps and the mechanisms by which they orient around landmasses (Padget et al., 2022; Padget et al., 2019) suggests that these stages of homing might rely on different mechanisms. Whether shearwaters' choice of which way to orient around an obstacle is determined by pilotage or map-and-compass navigation could be revealed by the impact of clock-shifting on the proportion of correct choices in displaced shearwaters. Even without artificial clock-shifting and displacement, this might be possible using the self-generated clock-shifts seen in the natural movements of shearwaters.

Although in most cases, the relationship between GPS resolution, reorientation frequency and orientation error is a nuisance to researchers, it might also provide opportunities. We can, in some cases, make reasonably robust *a priori* predictions for the magnitude of sun compass error. For instance, naïve pigeons raised under an artificially shifted light-dark cycle before release at a distant release site (perhaps fitted with a disruptive neodymium magnet for good measure) are not expected to have any ability to compensate for sun compass error, other than through reorientation. Using very high resolution GPS tracking (e.g. 1Hz) to follow such a bird's trajectory would, therefore, allow an estimate of the frequency of reorientation, since both GPS resolution and sun compass error are known. Analytically, this might be as simple as iteratively down-sampling the GPS data until the measured orientation error is equal to that expected by the full clock-shift effect. In theory, this could also be achieved in shearwaters but it is harder to be

certain that a shifted light regime will have produced the full expected shift of the internal clock or that the shearwater is definitely unfamiliar with the release location.

In contrast, shearwaters make much better models than pigeons for the study of foraging navigation. Unlike pigeons, shearwaters do not show orientation responses only after artificial displacement – instead they navigate continuously through a complex resource environment in which the colony is only one of many important locations. Chapters 3 and 4 provide a tantalising glimpse of what might be possible in this area with the demonstration that shearwaters use the sun compass during foraging commutes, at least whilst following land and possibly in their initial departure directions from the colony. Further artificial clock-shifting of shearwaters before free-ranging foraging trips might help resolve this question. This might be aided by focusing effort on slow-shifted and unshifted control birds which remain active long enough after release to commute whilst under the shifted state, and on colonies where outward movement is less obstructed by nearby landmasses, such as those in South Wales, West Ireland and the Outer Hebrides. As well as revealing whether the sun compass is involved in outward orientation, this might generate insight into the strategy of which the sun compass is a part; if clock-shifted shearwaters show angular deflections yet reorient to reach the same foraging areas as unshifted birds, this would imply that shearwaters use a map-and-compass system to reach foraging goals, rather than vector navigation. Investigation of navigation during complex foraging movements could help bridge the gulf between studies of large-scale navigation, especially in wild birds, and the detailed mechanistic understanding of small-scale cognitive maps, primarily in mammals (Harten et al., 2020; O'Keefe & Nadel, 1978; Toledo et al., 2020; Tolman, 1948). There is one complication to consider which would make a failure to compensate difficult to interpret; if shearwaters are initially deflected, the net energy landscape surrounding their resulting location might mean that reaching

the same foraging areas as control birds is not the optimal choice, even if they are capable of doing so (Harris et al., 2025). Equally, if the energy landscape can be accurately predicted, this effect might actually yield insight into how shearwaters make dynamic decisions about where to forage to optimise net energy gain.

### 7.3.2 Outward journey information

Any compass errors during the outward journey might be used to investigate the role of outward journey information in shearwater homing. Although we attempt this in Chapter 3, recent findings (Lancaster-Reeves et al., unpublished-b) suggest that shearwaters might rely on outward journey information to track movements only during parts of their foraging trips, specifically when out of sight of land. Our results might, therefore, be based on misguided assumptions and further analyses should be conducted to resolve the role of the sun compass in any path-integration-like system in shearwaters. This could be achieved using both the self-generated clock-shifts seen in the natural movements of shearwaters and artificial clock-shifts before free-ranging foraging trips, ideally at the colonies mentioned above where most movements occur far from land. Although outward journey information is clearly not essential for accurate navigation by birds (Matthews, 1951b), as painstakingly shown by a number of extreme experimental treatments (Kluijver, 1935; Matthews, 1951a; Walcott & Schmidt-Koenig, 1973; Wallraff, 1965), it might play an essential role in the ontogeny of map representations (Morford et al., 2025). Indeed, it is actually quite hard to imagine how the spatial relationships between locations could be learned and encoded without an allocentric path integration system by which to first estimate the vectors between them.

The contribution of outward journey information to distance estimation, in addition to orientation, also requires investigation. Whilst Manx shearwaters are able to estimate the beeline distance to their colony after foraging trips (Padget et al., 2017; Padget et al., 2019; Shiomi et al., 2012) and Balearic shearwaters estimate the route distance of their return migration (Chapter 6), the underlying

mechanisms are unclear. In Manx shearwaters, use of data from previous displacement experiments might be used to test whether shearwaters show similar time allocation to homing as they do during free-ranging movement. Given that displaced shearwaters lack an outward journey, or even a measure of travel duration, any distance estimation among these birds would have to be based on a map representation. Displacement to the migratory destination of Balearic shearwaters is not feasible but use of the existing tracking data might provide some evidence as to the mechanism of route distance estimation. If Balearic shearwaters learn to adjust their travel speed in relation to their past experience of migrations, their speeds should relate most strongly to their average migration distance but not to variation in migration distance between years. In contrast, if they rely on outward journey information, the travel speed should change from year to year, as predicted by annual changes in migration distance. Given the high spatial error of light-level geolocation, it was not possible to conduct this analysis using the existing data presented in Chapter 6. However, with additional data or improvements in geolocation accuracy, this analysis might become feasible.

### 7.3.3 Compass calibration

The suggestions made so far rely on a mix of free-ranging tracking and displacement experiments with sensory manipulation. However, the question of compass calibration and how birds account for changes in sun arc during long-distance movements is a prime example of where analysis of free-ranging movements is desperately needed. We now have ample evidence that birds misorient after extreme artificial conflicts between celestial and magnetic compass cues (Muheim et al., 2006; Sjöberg & Muheim, 2016). However, whether this apparent transfer of information between compass systems represents a functional mechanism is entirely unknown. Whilst it is entirely possible to come up with reasons why birds might, in principle, calibrate their compasses and elegant mechanisms by which they might do so, these tempting theories must be

put to empirical tests. In passerine species where apparent compass calibration has been demonstrated via cue conflict, similar approaches might be taken to those reported in Chapter 5; when denied geomagnetic information do passerines subsequently show misorientation during diurnal movement and when denied celestial cues at sunrise and sunset do they misorient at night? In birds like shearwaters, the errors in estimated sun arc resulting from different candidate mechanisms (entrainment on the previous day and night, entrainment on the previous night, calibration by a magnetic compass or cross-calibration of both magnetic and sun compasses) could be mapped to free-ranging tracking data and compared to the observed orientation error during homing. These approaches might reveal whether birds really do require compass calibration for efficient navigation and, if not, how they solve the ambiguity of changes in sun arc with latitude, longitude and season. From a mechanistic perspective, the question of compass calibration might be more tractably addressed using a neurological approach in those models of navigation where the neural representations of compass direction are increasingly well-understood (Beetz & el Jundi, 2023; Beetz et al., 2023; Collett et al., 2025; Dreyer et al., 2025). Changes in the directional preference of neurons after cue-conflict might provide a more exact picture of how animals calibrate their compasses than is possible using behavioural outputs. Whilst this is currently limited mostly to insect navigators, it is conceivable that these methods might soon be applied to mammals (Lindecke et al., 2019; Rubin et al., 2014; Schneider, Holland, et al., 2023) and possibly even shearwaters (Takahashi et al., 2022; Wynn et al., 2021).

### 7.3.4 The behavioural ecology of navigation

Perhaps the element of navigation most inaccessible to traditional paradigms is not mechanistic but functional. Despite the clear intuitive importance of efficient navigation to dispersal, foraging, migration and almost every aspect of the movement that defines animal life, very little work has bridged the gap between

navigation, spatial cognition and ecology. Again, this perhaps results in part from reliance on captive or incarcerated model organisms, rather than the investigation of navigation in the natural movements of animals. In Chapter 5, we show in a small way how spatial cognition might mediate the flexibility of individuals' responses to changing environments and thus determine population-level trends under climate change. Indeed, the role of navigation in influencing climate responses might be quite ubiquitous; navigation will shape dispersal patterns and the possibility for colonisation of shifting habitats (Dufour et al., 2024) and determine whether animals are able to track shifting food distributions flexibly, for instance. In general, the individual-level processes underlying spatial responses to climate change are very poorly understood compared to, for example, phenological change, and they warrant far greater study. This requires long-term tracking datasets of animals which are, by the nature of the question, shifting in space. This presents a challenge but one which is being addressed by advances in tracking technology, allowing increasingly reliable remote transmission of increasingly accurate spatial data.

Even beyond contemporary environmental change, the adaptive value of navigational abilities is poorly understood. A number of recent studies have shown strong mortality selection on migratory birds' abilities to compensate for wind drift, which might be based on navigational mechanisms (Sergio et al., 2022; Wynn et al., 2025). In shearwaters, efficient navigation underpins the ability to find food and return to the colony to resume incubation or feed the chick in a timely manner, as well as the ability to migrate successfully and return to the colony to breed in the first place. Investigations of how variation in navigational abilities impact breeding success and survival are, therefore, long overdue. Such studies might be possible in Manx shearwaters, where long-term tracking data are paired with life history information in a large part of the dataset.

### 7.3.5 A major direction: chronobiology

Although I had no conception of it when I started working towards this thesis (nor even for the first three years of that work), the endogenous circadian clocks which underpin sun compass navigation in shearwaters and many other animals have emerged as a secondary theme of my research. The sun compass has long been identified as a particularly powerful link between observable behaviour and the invisible clock (DeCoursey, 2004). This is certainly the case in Chapters 2 and 3, where rapid longitudinal flights jointly reveal the constraints of clock entrainment and use of the sun compass in free-living shearwaters. This phenomenon circumvents the enormous practical challenges ordinarily facing any attempt to manipulate the endogenous clock of free-living animals and thus study its role in their behaviour or physiology. In addition, shearwaters are well-suited to artificial clock-shifting studies and in Chapter 4 we use this approach to show that meaningful measures of internal clock state can be extracted from shearwater activity patterns. Between the opportunity for both natural and artificial experiments, shearwaters might serve as a useful model for the study of the endogenous clock in the wild and its relation to animal navigation. As well as sun compass orientation, the clock appears to mediate the timing of foraging commutes and, by extension, perhaps also the allocation of time to homing. Beyond navigation, an accurate internal clock might be used to time foraging activity, in order to match the diel vertical migration of prey and thus maximise foraging success (Elliott & Gaston, 2015; Regular et al., 2010; Shoji et al., 2016; Siddiqi-Davies et al., 2025). The timing of behaviours such as rafting and return to the colony, important for successful chick-feeding and partner coordination, might also rely on the endogenous clock. The role of the endogenous clock in each of these cases could be revealed by the natural experiment of self-induced clock-shifts, whist the mechanistic basis of the clock in a wild animal might be studied through clock-shifting or free-running clock experiments in incubating shearwaters. As is the case in navigation, reliance on captive models has precluded investigation of the

adaptive value of the endogenous clock or how variation in chronobiological traits such as chronotype and clock plasticity influences breeding success and survival (Helm et al., 2017). Shearwaters and their remarkable movements might provide the key to answering these questions, all because they look up to a distant star and consult an invisible clock in order to find the way home.

## 7.4 Concluding remarks

Even in the full context of the wider literature, shearwaters have emerged as a powerful model for the study of navigation. It is perhaps only in Hymenopteran insects, especially ants, where we have a relatively comprehensive understanding of the sensory and cognitive basis of navigation in a wild animal, including the ontogeny of navigational mechanisms, how various cues interact and how they are used to achieve efficient navigation in the animal's daily life (Collett et al., 1992; Wehner, 1984; Wehner & Srinivasan, 2003). However, shearwaters might have the potential to become a second such example, in this case as truly global navigators. Shearwaters are mid-sized birds, return faithfully to enclosed spaces and are remarkably robust to disturbance, making them superbly suited to tracking, sensory manipulation and displacement. We know the sensory basis of shearwaters' maps (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015) and compasses (Padget et al., 2018; Takahashi et al., 2022), we know that these cues are probably used as part of an extrapolated grid representation (Padget et al., 2019) and we know that they likely use this map to estimate distances as well as directions (Padget et al., 2017; Padget et al., 2019; Shiomi et al., 2012). We are beginning to understand how these cues are used during natural movements, often in combination with one another (Chapters 2, 3 and 5), the mechanisms by which shearwaters achieve efficient navigation around their foraging grounds (Chapters 3 and 4), how information from these movements might contribute to homewards orientation (Lancaster-Reeves et al., unpublished-b) and the importance of these abilities for the taxon's wider ecology (Chapter 6). Rapidly

developing neurological approaches may yield deep insights into the precise mechanisms by which shearwaters represent space and direction (Takahashi et al., 2022), and how they control their movements. The wealth of existing tracking data makes new discoveries possible all the time – I am currently working on estimating the spatial resolution of shearwaters' maps based on the geometric relationships between distance from the colony and angular error. Like any model system, shearwaters have their drawbacks. The remoteness of their Atlantic migration makes its navigational underpinnings difficult to study. This is never clearer than in first time migrants who may spend more than three years at sea before first returning to their natal colony, and for years after that may not return to a fixed burrow. The ontogeny of shearwaters' navigational abilities remains, therefore, a mystery. This is not say that these questions are utterly intractable – interesting insights have been possible using traditional methods (Wynn, Padget, et al., 2020) and modern technology is rapidly accelerating our ability to peer into this part of shearwaters' lives. I hope that future DPhil students will have as much fun as I have had developing fanciful hypotheses, some of which turn out not to be so fanciful after all. I hope too that they continue to appreciate shearwaters as masterful mariners and incompetent landlubbers. Geoffrey Matthews and Ronald Lockley, mad as they may have seemed at the time, were on to something when they packed up shearwaters and mailed them all over the world, wondering beyond any reasonable hope whether they might return home. Perhaps one day we will be able to marvel not just at the remarkable feats of shearwaters but at the intricacies of their navigational machinery – surely more beautiful even than Harrison's Marine Timekeeper H4.

## References

Alerstam, T., Bäckman, J., Strandberg, R., Gudmundsson, G. A., Hedenström, A., Henningsson, S. S., Karlsson, H., & Rosén, M. (2008). Great-circle migration of Arctic passerines. *The Auk*, *125*(4), 831-838. https://doi.org/10.1525/auk.2008.07142

Alerstam, T., Gudmundsson, G. A., Green, M., & Hedenstrom, A. (2001). Migration along orthodromic sun compass routes by arctic birds. *Science*, *291*(5502), 300-303. https://doi.org/10.1126/science.291.5502.300.

Alerstam, T., & Pettersson, S.-G. (1991). Orientation along great circles by migrating birds using a sun compass. *Journal of Theoretical Biology*, *152*(2), 191-202. https://doi.org/10.1016/S0022-5193(05)80452-7

Beetz, M. J., & el Jundi, B. (2023). The neurobiology of the Monarch butterfly compass. *Current Opinion in Insect Science*, *60*, 101109. https://doi.org/10.1016/j.cois.2023.101109

Beetz, M. J., Kraus, C., & el Jundi, B. (2023). Neural representation of goal direction in the monarch butterfly brain. *Nature Communications*, *14*(1), 5859. https://doi.org/10.1038/s41467-023-41526-w

Berthold, P. (1984). The endogenous control of bird migration: a survey of experimental evidence. *Bird Study*, *31*(1), 19-27. https://doi.org/10.1080/00063658409476810

Berthold, P. (1990). Spatiotemporal programs and genetics of orientation. *Experientia*, *46*(4), 363-371. https://doi.org/10.1007/BF01952169

Biro, D., Freeman, R., Meade, J., Roberts, S., & Guilford, T. (2007). Pigeons combine compass and landmark guidance in familiar route navigation. *Proceedings of the National Academy of Sciences*, *104*(18), 7471-7476. https://doi.org/10.1073/pnas.0701575104

Bonadonna, F., Bajzak, C., Benhamou, S., Igloi, K., Jouventin, P., Lipp, H.-P., & Dell'Omo, G. (2005). Orientation in the wandering albatross: Interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *272*, 489-495. https://doi.org/10.1098/rspb.2004.2984

Bonadonna, F., Chamaillé-Jammes, S., Pinaud, D., & Weimerskirch, H. (2003). Magnetic cues: are they important in Black-browed Albatross *Diomedea melanophris* orientation? *Ibis*, *145*(1), 152-155. https://doi.org/10.1046/j.1474-919X.2003.00117.x

Bonadonna, F., & Gagliardo, A. (2021). Not only pigeons: avian olfactory navigation studied by satellite telemetry. *Ethology Ecology & Evolution*, *33*(3), 273-289. https://doi.org/10.1080/03949370.2021.1871967

Boström, J. E., Åkesson, S., & Alerstam, T. (2012). Where on earth can animals use a geomagnetic bi-coordinate map for navigation? *Ecography*, *35*(11), 1039-1047. https://doi.org/10.1111/j.1600-0587.2012.07507.x

Brooke, M. (1990). *The Manx Shearwater*. T. & A. D. Poyser, London, United Kingdom. ISBN: 9780856610578

Burda, H., Marhold, S., Westenberger, T., Wiltschko, R., & Wiltschko, W. (1990). Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae). *Experientia*, *46*(5), 528-530. https://doi.org/10.1007/BF01954256

Chappell, J., & Guilford, T. (1995). Homing pigeons primarily use the sun compass rather than fixed directional visual cues in an open-field arena food-searching task. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *260*(1357), 59-63. https://doi.org/10.1098/rspb.1995.0059

Chen, C., Buhl, E., Xu, M., Croset, V., Rees, J. S., Lilley, K. S., Benton, R., Hodge, J. J. L., & Stanewsky, R. (2015). *Drosophila* Ionotropic Receptor 25a mediates circadian clock resetting by temperature. *Nature*, *527*(7579), 516-520. https://doi.org/10.1038/nature16148

Chernetsov, N., Pakhomov, A., Kobylkov, D., Kishkinev, D., Holland, R. A., & Mouritsen, H. (2017). Migratory Eurasian Reed Warblers Can Use Magnetic Declination to Solve the Longitude Problem. *Current Biology*, *27*(17), 2647-2651.e2642. https://doi.org/10.1016/j.cub.2017.07.024

Cheung, A., & Vickerstaff, R. (2010). Finding the Way with a Noisy Brain. *PLoS computational biology*, *6*(11), e1000992. https://doi.org/10.1371/journal.pcbi.1000992

Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proceedings of the National Academy of Sciences*, *107*(25), 11638-11643. https://doi.org/10.1073/pnas.1001401107

Collett, T., Graham, P., & Heinze, S. (2025). The neuroethology of ant navigation. *Current Biology*, *35*(3), R110-R124. https://doi.org/10.1016/j.cub.2024.12.034

Collett, T. S., Dillmann, E., Giger, A., & Wehner, R. (1992). Visual landmarks and route following in desert ants. *Journal of Comparative Physiology A*, *170*(4), 435-442. https://doi.org/10.1007/BF00191460

Dayananda, S. K., Mammides, C., Liang, D., Kotagama, S. W., & Goodale, E. (2021). A review of avian experimental translocations that measure movement through human-modified landscapes. *Global Ecology and Conservation*, *31*, e01876. https://doi.org/10.1016/j.gecco.2021.e01876

DeCoursey, P. J. (2004). The behavioral ecology and evolution of biological timing systems. In *Chronobiology: Biological timekeeping.* (pp. 27-65). Sinauer Associates, Sunderland, MA, United States. https://doi.org/10.1016/j.physbeh.2004.07.001, ISBN: 0-87893-149-X

Dobben, W. H. V. (1953). Bird migration in the Netherlands. *Ibis*, *95*(2), 212-234. https://doi.org/10.1111/j.1474-919X.1953.tb00686.x

Dreyer, D., Adden, A., Chen, H., Frost, B., Mouritsen, H., Xu, J., Green, K., Whitehouse, M., Chahl, J., Wallace, J., Hu, G., Foster, J., Heinze, S., & Warrant, E. (2025).

Bogong moths use a stellar compass for long-distance navigation at night. *Nature*, *643*(8073), 994-1000. https://doi.org/10.1038/s41586-025-09135-3

Dreyer, D., Frost, B., Mouritsen, H., Günther, A., Green, K., Whitehouse, M., Johnsen, S., Heinze, S., & Warrant, E. (2018). The Earth's Magnetic Field and Visual Landmarks Steer Migratory Flight Behavior in the Nocturnal Australian Bogong Moth. *Current Biology*, *28*(13), 2160-2166.e2165. https://doi.org/10.1016/j.cub.2018.05.030

Duff, S. J., Brownlie, L. A., Sherry, D. F., & Sangster, M. (1998). Sun compass and landmark orientation by black-capped chickadees (*Parus atricapillus*). *Journal of Experimental Psychology: Animal Behavior Processes*, *24*(3), 243-253. https://doi.org/10.1037/0097-7403.24.3.243

Dufour, P., Lees, A. C., Gilroy, J., & Crochet, P.-A. (2024). The overlooked importance of vagrancy in ecology and evolution. *Trends in Ecology & Evolution*, *39*(1), 19-22. https://doi.org/10.1016/j.tree.2023.10.001

Elliott, K. H., & Gaston, A. J. (2015). Diel vertical migration of prey and light availability constrain foraging in an Arctic seabird. *Marine Biology*, *162*(9), 1739-1748. https://doi.org/10.1007/s00227-015-2701-1

Emlen, S. T., & Emlen, J. T. (1966). A Technique for Recording Migratory Orientation of Captive Birds. *The Auk*, *83*(3), 361-367. https://doi.org/10.2307/4083048

Fleischmann, P. N., Grob, R., Müller, V. L., Wehner, R., & Rössler, W. (2018). The Geomagnetic Field Is a Compass Cue in *Cataglyphis* Ant Navigation. *Current Biology*, *28*(9), 1440-1444.e1442. https://doi.org/10.1016/j.cub.2018.03.043

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *The Journal of Experimental Biology*, *216*(12), 2165-2171. https://doi.org/10.1242/jeb.070250

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *The Journal of Experimental Biology*, *216*(15), 2798-2805. https://doi.org/10.1242/jeb.085738

Gagliardo, A., Ioalè, P., Odetti, F., & Bingman, V. P. (2001). The ontogeny of the homing pigeon navigational map: evidence for a sensitive learning period. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1463), 197-202. https://doi.org/10.1098/rspb.2000.1350

Goforth, K. M., Lohmann, C. M. F., Gavin, A., Henning, R., Harvey, A., Hinton, T. L., Lim, D. S., & Lohmann, K. J. (2025). Learned magnetic map cues and two mechanisms of magnetoreception in turtles. *Nature*, *638*(8052), 1015-1022. https://doi.org/10.1038/s41586-024-08554-y

Gordon, D. A. (1948). Sensitivity of the Homing Pigeon to the Magnetic Field of the Earth. *Science*, *108*(2817), 710-711. https://doi.org/10.1126/science.108.2817.710

Goto, Y., Yoda, K., & Sato, K. (2017). Asymmetry hidden in birds' tracks reveals wind, heading, and orientation ability over the ocean. *Science Advances*, *3*(9), e1700097. https://doi.org/10.1126/sciadv.1700097

Guerra, P. A., Gegear, R. J., & Reppert, S. M. (2014). A magnetic compass aids monarch butterfly migration. *Nature Communications*, *5*(1), 4164. https://doi.org/10.1038/ncomms5164

Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S., & Perrins, C. M. (2008). GPS tracking of the foraging movements of Manx Shearwaters Puffinus puffinus breeding on Skomer Island, Wales. *Ibis*, *150*(3), 462-473. https://doi.org/10.1111/j.1474-919X.2008.00805.x

Harris, S. M., Bishop, C. M., Bond, S., Fernandes, P. G., Guilford, T., Lewin, P. J., Padget, O., Robins, P., Schneider, W. T., Waggitt, J. J., Wilmes, S. B., & Cordes, L. S. (2025). Adjustable wind selectivity in shearwaters implies knowledge of the foraging landscape. *Current Biology*, *35*(4), 889-897.e883. https://doi.org/10.1016/j.cub.2024.12.017

Harten, L., Katz, A., Goldshtein, A., Handel, M., & Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science*, *369*(6500), 194-197. https://doi.org/10.1126/science.aay3354

Heinze, S., Narendra, A., & Cheung, A. (2018). Principles of Insect Path Integration. *Current Biology*, *28*(17), R1043-R1058. https://doi.org/10.1016/j.cub.2018.04.058

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T., & Bloch, G. (2017). Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *372*(1734), 20160246. https://doi.org/10.1098/rstb.2016.0246

Hirschie Johnson, C., Elliott, J. A., & Foster, R. (2003). Entrainment of Circadian Programs. *Chronobiology international*, *20*(5), 741-774. https://doi.org/10.1081/CBI-120024211

Holland, R., Filannino, C., & Gagliardo, A. (2013). A magnetic pulse does not affect homing pigeon navigation: a GPS tracking experiment. *Journal of Experimental Biology*, *216*(12), 2192-2200. https://doi.org/10.1242/jeb.083543

Holland, R. A., Thorup, K., Gagliardo, A., Bisson, I. A., Knecht, E., Mizrahi, D., & Wikelski, M. (2009). Testing the role of sensory systems in the migratory heading of a songbird. *The Journal of Experimental Biology*, *212*(24), 4065-4071. https://doi.org/10.1242/jeb.034504

Jaggers, P. E. (2023). *Causes and consequences of individual behavioural variability in a pelagic seabird.* [MPhil Thesis, University of Oxford]. Oxford, United Kingdom.

Jandačka, P., Burda, H., & Ščučka, J. (2022). Investigating the impact of weak geomagnetic fluctuations on pigeon races. *Journal of Comparative Physiology A*, *208*(1), 177-184. https://doi.org/10.1007/s00359-021-01534-x

Jorge, P. E., Marques, A. E., & Phillips, J. B. (2009). Activational Rather Than Navigational Effects of Odors on Homing of Young Pigeons. *Current Biology*, *19*(8), 650-654. https://doi.org/10.1016/j.cub.2009.02.066

Jorge, P. E., Marques, P. A. M., & Phillips, J. B. (2010). Activational effects of odours on avian navigation. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1678), 45-49. https://doi.org/10.1098/rspb.2009.1521

Keeton, W. T., Larkin, T. S., & Windsor, D. M. (1974). Normal fluctuations in the earth's magnetic field influence pigeon orientation. *Journal of comparative physiology*, *95*(2), 95-103. https://doi.org/10.1007/BF00610108

Kelly, D. M., Cheng, K., Balda, R., & Kamil, A. C. (2019). Effects of sun compass error on spatial search by Clark's nutcrackers. *Integrative Zoology*, *14*(2), 172-181. https://doi.org/10.1111/1749-4877.12302

Kempton, J. A., Wynn, J., Bond, S., Evry, J., Fayet, A. L., Gillies, N., Guilford, T., Kavelaars, M., Juarez-Martinez, I., & Padget, O. (2022). Optimization of dynamic soaring in a flap-gliding seabird affects its large-scale distribution at sea. *Science Advances*, *8*(22), eabo0200. https://doi.org/10.1126/sciadv.abo0200

Kishkinev, D., Anashina, A., Ishchenko, I., & Holland, R. A. (2020). Anosmic migrating songbirds demonstrate a compensatory response following long-distance translocation: a radio-tracking study. *Journal of Ornithology*, *161*(1), 47-57. https://doi.org/10.1007/s10336-019-01698-z

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., & Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Current Biology*, *25*(19), R822-R824. https://doi.org/10.1016/j.cub.2015.08.012

Kishkinev, D., Packmor, F., Zechmeister, T., Winkler, H.-C., Chernetsov, N., Mouritsen, H., & Holland, R. A. (2021). Navigation by extrapolation of geomagnetic cues in a migratory songbird. *Current Biology*, *31*(7), 1563-1569.e1564. https://doi.org/10.1016/j.cub.2021.01.051

Kluijver, H. N. (1935). Ergebnisse eines Versuches über das Heimfindevermögen von Staren. *Ardea*, *24*(3-4), 227-239.

Kramer, G. T. (1949). Über Richtungstendenzen bei der nächtlichen Zugunruhe gekäfigter Vögel. *Ornithologie als biologische Wissenschaft*, 269-283.

Lancaster-Reeves, L., Wynn, J., Lewin, P., Morford, J., Guilford, T., & Padget, O. (unpublished-a). *Evidence for learning in the circumnavigation decisions of at-sea obstacles in free-ranging shearwaters*.

Lancaster-Reeves, L., Wynn, J., Lewin, P., Morford, J., Guilford, T., & Padget, O. (unpublished-b). *The role of outward journey information in the homing performance of the Manx shearwater*.

Lednor, A. J., & Walcott, C. (1983). Homing pigeon navigation: The effects of in-flight exposure to a varying magnetic field. *Comparative Biochemistry and Physiology Part A: Physiology*, *76*(4), 665-671. https://doi.org/10.1016/0300-9629(83)90127-5

Lindecke, O., Elksne, A., Holland, R. A., Pētersons, G., & Voigt, C. C. (2019). Experienced Migratory Bats Integrate the Sun's Position at Dusk for

Navigation at Night. *Current Biology*, *29*(8), 1369-1373.e1363. https://doi.org/10.1016/j.cub.2019.03.002

Lohmann, K. J., & Catherine, M. F. L. (1993). A Light-Independent Magnetic Compass in the Leatherback Sea Turtle. *Biological Bulletin*, *185*(1), 149-151. https://doi.org/10.2307/1542138

Lohmann, K. J., Goforth, K. M., Mackiewicz, A. G., Lim, D. S., & Lohmann, C. M. F. (2022). Magnetic maps in animal navigation. *Journal of Comparative Physiology A*, *208*(1), 41-67. https://doi.org/10.1007/s00359-021-01529-8

Lohmann, K. J., Putman, N. F., Johnsen, S., & Lohmann, C. M. F. (2024). Animal magnetic sensitivity and magnetic displacement experiments. *Communications Biology*, *7*(1), 650. https://doi.org/10.1038/s42003-024-06269-4

Massa, B., Ioalè, S. B. P., Lo Valvo, M., & Papi, F. (1991). Homing of Cory's shearwaters (*Calonectris diomedea*) carrying magnets. *Bollettino di zoologia*, *58*(3), 245-247. https://doi.org/10.1080/11250009109355760

Matthews, G. V. T. (1951a). The Experimental Investigation of Navigation in Homing Pigeons. *Journal of Experimental Biology*, *28*(4), 508-536. https://doi.org/10.1242/jeb.28.4.508

Matthews, G. V. T. (1951b). The Sensory Basis of Bird Navigation. *Journal of Navigation*, *4*(3), 260-275. https://doi.org/10.1017/S0373463300046051

Miller, M. G. R., Petrovic, S., & Clarke, R. H. (2025). A global review of Procellariiform flight height, flight speed and nocturnal activity: Implications for offshore wind farm collision risk. *Journal of Applied Ecology*, *62*(8), 1795-1819. https://doi.org/10.1111/1365-2664.70088

Mistlberger, R. E., & Rusak, B. (2021). Biological Rhythms and Behavior. In J. J. Bolhuis, L.-A. Giraldeau, & J. A. Hogan (Eds.), *The Behavior of Animals: Mechanisms, Function, and Evolution* (2nd ed., pp. 78-110). John Wiley & Sons, Hoboken, NJ, United States. https://doi.org/10.1002/9781119109556.ch4, ISBN: 9781119109518

Mittelstaedt, M. L., & Mittelstaedt, H. (1980). Homing by path integration in a mammal. *Naturwissenschaften*, *67*(11), 566-567. https://doi.org/10.1007/BF00450672

Morford, J., Wynn, J., Lewin, P., Jaggers, P., Lancaster-Reeves, L., Sibeaux, A., Padget, O., & Guilford, T. (2025). Map and compass navigation: the mechanism and ontogeny of animal maps. *Animal Behaviour*, *227*, 123272. https://doi.org/10.1016/j.anbehav.2025.123272

Mouritsen, H. (1998). Modelling migration: the clock-and-compass model can explain the distribution of ringing recoveries. *Animal Behaviour*, *56*(4), 899-907. https://doi.org/10.1006/anbe.1998.0826

Mouritsen, H., Huyvaert, K. P., Frost, B. J., & Anderson, D. J. (2003). Waved albatrosses can navigate with strong magnets attached to their head. *Journal*

*of Experimental Biology*, *206*(22), 4155-4166. https://doi.org/10.1242/jeb.00650

Mrosovsky, N. (1999). Masking: history, definitions, and measurement. *Chronobiology international*, *16*(4), 415-429. https://doi.org/10.3109/07420529908998717

Muheim, R. (2011). Behavioural and physiological mechanisms of polarized light sensitivity in birds. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *366*(1565), 763-771. https://doi.org/10.1098/rstb.2010.0196

Muheim, R., Moore, F. R., & Phillips, J. B. (2006). Calibration of magnetic and celestial compass cues in migratory birds - a review of cue-conflict experiments. *Journal of Experimental Biology*, *209*(1), 2-17. https://doi.org/10.1242/jeb.01960

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Clarendon Press, Oxford, United Kingdom. ISBN: 0198572069

Padget, O., Bond, S. L., Kavelaars, M. M., van Loon, E., Bolton, M., Fayet, A. L., Syposz, M., Roberts, S., & Guilford, T. (2018). *In situ* clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology*, *28*(2), 275-279.e272. https://doi.org/10.1016/j.cub.2017.11.062

Padget, O., Dell'Ariccia, G., Gagliardo, A., González-Solís, J., & Guilford, T. (2017). Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. *Scientific Reports*, *7*(1), 9668. https://doi.org/10.1038/s41598-017-09738-5

Padget, O., Gillies, N., Syposz, M., Lockley, E., & Guilford, T. (2022). Shearwaters sometimes take long homing detours when denied natural outward journey information. *Biology Letters*, *18*(2), 20210503. https://doi.org/10.1098/rsbl.2021.0503

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M., & Guilford, T. (2019). Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the National Academy of Sciences*, *116*(43), 21629-21633. https://doi.org/10.1073/pnas.1903829116

Pakhomov, A., & Chernetsov, N. (2020). A hierarchy of compass systems in migratory birds. *Biological Communications*, *65*(3), 262–276. https://doi.org/10.21638/spbu03.2020.306

Phillips, J. B. (1986). Two magnetoreception pathways in a migratory salamander. *Science*, *233*(4765), 765-767. https://doi.org/10.1126/science.3738508

Phillips, J. B., & Borland, S. C. (1992). Behavioural evidence for use of a light-dependent magnetoreception mechanism by a vertebrate. *Nature*, *359*(6391), 142-144. https://doi.org/10.1038/359142a0

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., & Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific Reports*, *5*(1), 1-10. https://doi.org/10.1038/srep16486

Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *Journal of comparative physiology*, *137*(3), 243-248. https://doi.org/10.1007/BF00657119

Regular, P. M., Davoren, G. K., Hedd, A., & Montevecchi, W. A. (2010). Crepuscular foraging by a pursuit-diving seabird: tactics of common murres in response to the diel vertical migration of capelin. *Marine Ecology Progress Series*, *415*, 295-304. https://doi.org/10.3354/meps08752

Rubin, A., Yartsev, M. M., & Ulanovsky, N. (2014). Encoding of Head Direction by Hippocampal Place Cells in Bats. *Journal of Neuroscience*, *34*(3), 1067-1080. https://doi.org/10.1523/JNEUROSCI.5393-12.2014

Schiffner, I., & Wiltschko, R. (2011). Temporal fluctuations of the geomagnetic field affect pigeons' entire homing flight. *Journal of Comparative Physiology A*, *197*(7), 765-772. https://doi.org/10.1007/s00359-011-0640-y

Schmidt-Koenig, K. (1990). The sun compass. *Experientia*, *46*, 336-342. https://doi.org/10.1007/BF01952166

Schneider, W. T., Holland, R. A., Keišs, O., & Lindecke, O. (2023). Migratory bats are sensitive to magnetic inclination changes during the compass calibration period. *Biology Letters*, *19*(11), 20230181. https://doi.org/10.1098/rsbl.2023.0181

Schneider, W. T., Packmor, F., Lindecke, O., & Holland, R. A. (2023). Sense of doubt: inaccurate and alternate locations of virtual magnetic displacements may give a distorted view of animal magnetoreception ability. *Communications Biology*, *6*(1), 187. https://doi.org/10.1038/s42003-023-04530-w

Schneider, W. T., Wynn, J., Packmor, F., Lindecke, O., & Holland, R. A. (2024). Reply to: Animal magnetic sensitivity and magnetic displacement experiments. *Communications Biology*, *7*(1), 651. https://doi.org/10.1038/s42003-024-06270-x

Sergio, F., Barbosa, J. M., Tanferna, A., Silva, R., Blas, J., & Hiraldo, F. (2022). Compensation for wind drift during raptor migration improves with age through mortality selection. *Nature ecology & evolution*, *6*, 989-997. https://doi.org/10.1038/s41559-022-01776-1

Seyfarth, E. A., & Barth, F. G. (1972). Compound slit sense organs on the spider leg: Mechanoreceptors involved in kinesthetic orientation. *Journal of comparative physiology*, *78*(2), 176-191. https://doi.org/10.1007/BF00693611

Shiomi, K., Yoda, K., Katsumata, N., & Sato, K. (2012). Temporal tuning of homeward flights in seabirds. *Animal Behaviour*, *83*(2), 355-359. https://doi.org/10.1016/j.anbehav.2011.11.010

Shoji, A., Dean, B., Kirk, H., Freeman, R., Perrins, C. M., & Guilford, T. (2016). The diving behaviour of the Manx Shearwater *Puffinus puffinus*. *Ibis*, *158*(3), 598-606. https://doi.org/10.1111/ibi.12381

Sibeaux, A., Newport, C., Green, J. P., Karlsson, C., Engelmann, J., & Burt de Perera, T. (2024). Taking a shortcut: what mechanisms do fish use? *Communications Biology*, *7*(1), 578. https://doi.org/10.1038/s42003-024-06179-5

Siddiqi-Davies, K., Lancaster-Reeves, L., Morford, J., Padget, O., Wynn, J., Bond, S., Lewin, P., Jaggers, P., & Guilford, T. (2025). Pre-laying sex differences in reproductive roles can constrain foraging behaviour in a monomorphic seabird. *Marine Biology*, *172*(7), 103. https://doi.org/10.1007/s00227-025-04666-9

Sjöberg, S., & Muheim, R. (2016). A New View on an Old Debate: Type of Cue-Conflict Manipulation and Availability of Stars Can Explain the Discrepancies between Cue-Calibration Experiments with Migratory Songbirds. *Frontiers in Behavioral Neuroscience*, *10*. https://doi.org/10.3389/fnbeh.2016.00029

Srinivasan, M. V. (2014). Going with the flow: a brief history of the study of the honeybee's navigational 'odometer'. *Journal of Comparative Physiology A*, *200*(6), 563-573. https://doi.org/10.1007/s00359-014-0902-6

Takahashi, S., Hombe, T., Matsumoto, S., Ide, K., & Yoda, K. (2022). Head direction cells in a migratory bird prefer north. *Science Advances*, *8*(5), eabl6848. https://doi.org/10.1126/sciadv.abl6848

Tello-Ramos, M. C., Hurly, T. A., & Healy, S. D. (2015). Traplining in hummingbirds: flying short-distance sequences among several locations. *Behavioral Ecology*, *26*(3), 812-819. https://doi.org/10.1093/beheco/arv014

Tinbergen, L. (1941). Over de rol van de Hollandse duinrij bij de orientatie van trekkende vinken en spreeuwen. *Limosa*, *14*(2), 1-20.

Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., & Nathan, R. (2020). Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. *Science*, *369*(6500), 188-193. https://doi.org/10.1126/science.aax6904

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*(4), 189-208. https://doi.org/10.1037/h0061626

Ugolini, A. (2001). Relationship between compass systems of orientation in equatorial sandhoppers. *Animal Behaviour*, *62*(2), 193-199. https://doi.org/10.1006/anbe.2001.1766

Van Doren, B. M., DeSimone, J. G., Firth, J. A., Hillemann, F., Gayk, Z., Cohen, E., & Farnsworth, A. (2025). Social associations across species during nocturnal bird migration. *Current Biology*, *35*(4), 898-904.e894. https://doi.org/10.1016/j.cub.2024.12.033

Ventura, F., Granadeiro, J. P., Padget, O., & Catry, P. (2020). Gadfly petrels use knowledge of the windscape, not memorized foraging patches, to optimize foraging trips on ocean-wide scales. *Proceedings of the Royal Society B:*

*Biological Sciences*, *287*(1918), 20191775. https://doi.org/10.1098/rspb.2019.1775

von Saint Paul, U. (1982). Do Geese Use Path Integration for Walking Home? In F. Papi & H. G. Wallraff (Eds.), *Avian Navigation* (pp. 298-307). International Symposium on Avian Navigation 1981, Pisa, Italy. Springer Berlin Heidelberg, Berlin, Germany. https://doi.org/10.1007/978-3-642-68616-0_30

Walcott, C. (1978). Anomalies in the Earth's Magnetic Field Increase the Scatter of Pigeons' Vanishing Bearings. In K. Schmidt-Koenig & W. T. Keeton (Eds.), *Animal Migration, Navigation, and Homing* (pp. 143-151). 1977, Tübingen, Germany. Springer, Berlin, Germany. https://doi.org/10.1007/978-3-662-11147-5_13

Walcott, C., Gould, J. L., & Kirschvink, J. L. (1979). Pigeons Have Magnets. *Science*, *205*(4410), 1027-1029. https://doi.org/10.1126/science.472725

Walcott, C., & Schmidt-Koenig, K. (1973). The Effect on Pigeon Homing of Anesthesia during Displacement. *The Auk*, *90*(2), 281-286. https://doi.org/10.1093/auk/90.2.281

Wallraff, H. G. (1965). Über das Heimfindevermögen von Brieftauben mit durchtrennten Bogengängen. *Zeitschrift für vergleichende Physiologie*, *50*(3), 313-330. https://doi.org/10.1007/BF00339483

Wallraff, H. G. (2005). *Avian navigation: pigeon homing as a paradigm*. Springer Science & Business Media, Berlin, Germany and New York, United States. https://doi.org/10.1007/b137573, ISBN: 3540223851

Wallraff, H. G., Papi, F., Ioalè, P., & Benvenuti, S. (1986). Magnetic fields affect pigeon navigation only while the birds can smell atmospheric odors. *Naturwissenschaften*, *73*(4), 215-217. https://doi.org/10.1007/BF00417729

Wehner, R. (1984). Astronavigation in insects. *Annual review of entomology*, *29*(1), 277-298. https://doi.org/10.1146/annurev.en.29.010184.001425

Wehner, R., Boyer, M., Loertscher, F., Sommer, S., & Menzi, U. (2006). Ant navigation: one-way routes rather than maps. *Current Biology*, *16*(1), 75-79. https://doi.org/10.1016/j.cub.2005.11.035

Wehner, R., & Srinivasan, M. V. (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour*. Oxford University Press, Oxford, United Kingdom. https://doi.org/10.1093/acprof:oso/9780198515241.003.0001, ISBN: 0198515243

Wikelski, M., Arriero, E., Gagliardo, A., Holland, R. A., Huttunen, M. J., Juvaste, R., Mueller, I., Tertitski, G., Thorup, K., Wild, M., Alanko, M., Bairlein, F., Cherenkov, A., Cameron, A., Flatz, R., Hannila, J., Hüppop, O., Kangasniemi, M., Kranstauber, B.,...Wistbacka, R. (2015). True navigation in migrating gulls requires intact olfactory nerves. *Scientific Reports*, *5*(1), 17061. https://doi.org/10.1038/srep17061

Wiltschko, R., Schiffner, I., & Wiltschko, W. (2009). A strong magnetic anomaly affects pigeon navigation. *Journal of Experimental Biology*, *212*(18), 2983-2990. https://doi.org/10.1242/jeb.032722

Wiltschko, R., Stapput, K., Bischof, H.-J., & Wiltschko, W. (2007). Light-dependent magnetoreception in birds: increasing intensity of monochromatic light changes the nature of the response. *Frontiers in Zoology*, *4*(1), 5. https://doi.org/10.1186/1742-9994-4-5

Wiltschko, R., & Wiltschko, W. (1981). The development of sun compass orientation in young homing pigeons. *Behavioral Ecology and Sociobiology*, *9*(2), 135-141. https://doi.org/10.1007/BF00293584

Wiltschko, R., & Wiltschko, W. (2003). Mechanisms of orientation and navigation in migratory birds. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian migration* (pp. 433-456). Springer, Berlin, Germany and New York, United States. ISBN: 3540434089

Wiltschko, W., & Balda, R. P. (1989). Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). *Journal of Comparative Physiology A*, *164*(6), 717-721. https://doi.org/10.1007/BF00616744

Wiltschko, W., & Wiltschko, R. (1972). Magnetic compass of European robins. *Science*, *176*(4030), 62-64. https://doi.org/10.1126/science.176.4030.62

Wiltschko, W., & Wiltschko, R. (2001). Light-dependent magnetoreception in birds: the behaviour of European robins, *Erithacus rubecula*, under monochromatic light of various wavelengths and intensities. *Journal of Experimental Biology*, *204*(19), 3295-3302. https://doi.org/10.1242/jeb.204.19.3295

Wiltschko, W., Wiltschko, R., & Keeton, W. T. (1976). Effects of a “permanent” clock-shift on the orientation of young homing pigeons. *Behavioral Ecology and Sociobiology*, *1*(3), 229-243. https://doi.org/10.1007/BF00300066

Wiltschko, W., Wiltschko, R., & Munro, U. (2000a). Light-Dependent Magnetoreception in Birds: Does Directional Information Change with Light Intensity? *Naturwissenschaften*, *87*(1), 36-40. https://doi.org/10.1007/s001140050006

Wiltschko, W., Wiltschko, R., & Munro, U. (2000b). Light-dependent magnetoreception in birds: the effect of intensity of 565-nm green light. *Naturwissenschaften*, *87*(8), 366-369. https://doi.org/10.1007/s001140050742

Wittlinger, M., Wehner, R., & Wolf, H. (2006). The Ant Odometer: Stepping on Stilts and Stumps. *Science*, *312*(5782), 1965-1967. https://doi.org/10.1126/science.1126912

Wynn, J., Collet, J., Prudor, A., Corbeau, A., Padget, O., Guilford, T., & Weimerskirch, H. (2020). Young frigatebirds learn how to compensate for wind drift. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *287*(1937), 20201970. https://doi.org/10.1098/rspb.2020.1970

Wynn, J., Kürten, N., Moiron, M., & Bouwhuis, S. (2025). Selective disappearance based on navigational efficiency in a long-lived seabird. *Journal of Animal Ecology*, *94*(4), 535-544. https://doi.org/10.1111/1365-2656.14231

Wynn, J., Padget, O., Mouritsen, H., Fayet, A. L., Kobylkov, D., Siddiqi-Davies, K., Syposz, M., Trapp, S., Gillies, N., & Guilford, T. (2021). *Twilight cue manipulation suggests a pelagic seabird uses a magnetic compass to calibrate its sun compass.* [Doctoral Thesis Chapter, University of Oxford]. Oxford, United Kingdom.

Wynn, J., Padget, O., Mouritsen, H., Morford, J., Jaggers, P., & Guilford, T. (2022). Magnetic stop signs signal a European songbird's arrival at the breeding site following migration. *Science*, *375*(6579), 446-449. https://doi.org/10.1126/science.abj4210

Wynn, J., Padget, O., Mouritsen, H., Perrins, C., & Guilford, T. (2020). Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology*, *30*(14), 2869-2873.e2862. https://doi.org/10.1016/j.cub.2020.05.039

Yoda, K., Okumura, M., Suzuki, H., Matsumoto, S., Koyama, S., & Yamamoto, M. (2021). Annual variations in the migration routes and survival of pelagic seabirds over mountain ranges. *Ecology*, *102*(6), 1-4. https://doi.org/10.1002/ecy.3297

Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M., & Yamamoto, M. (2017). Compass orientation drives naïve pelagic seabirds to cross mountain ranges. *Current Biology*, *27*(21), R1152-R1153. https://doi.org/10.1016/j.cub.2017.09.009

Zeil, J. (1998). Homing in fiddler crabs (*Uca lactea annulipes* and *Uca vomeris*: Ocypodidae). *Journal of Comparative Physiology A*, *183*(3), 367-377. https://doi.org/10.1007/s003590050263

Zimmerman, P. H., Pope, S. J., Guilford, T., & Nicol, C. J. (2009). Involvement of the sun and the magnetic compass of domestic fowl in its spatial orientation. *Applied Animal Behaviour Science*, *116*(2-4), 204-210. https://doi.org/10.1016/j.applanim.2008.09.006